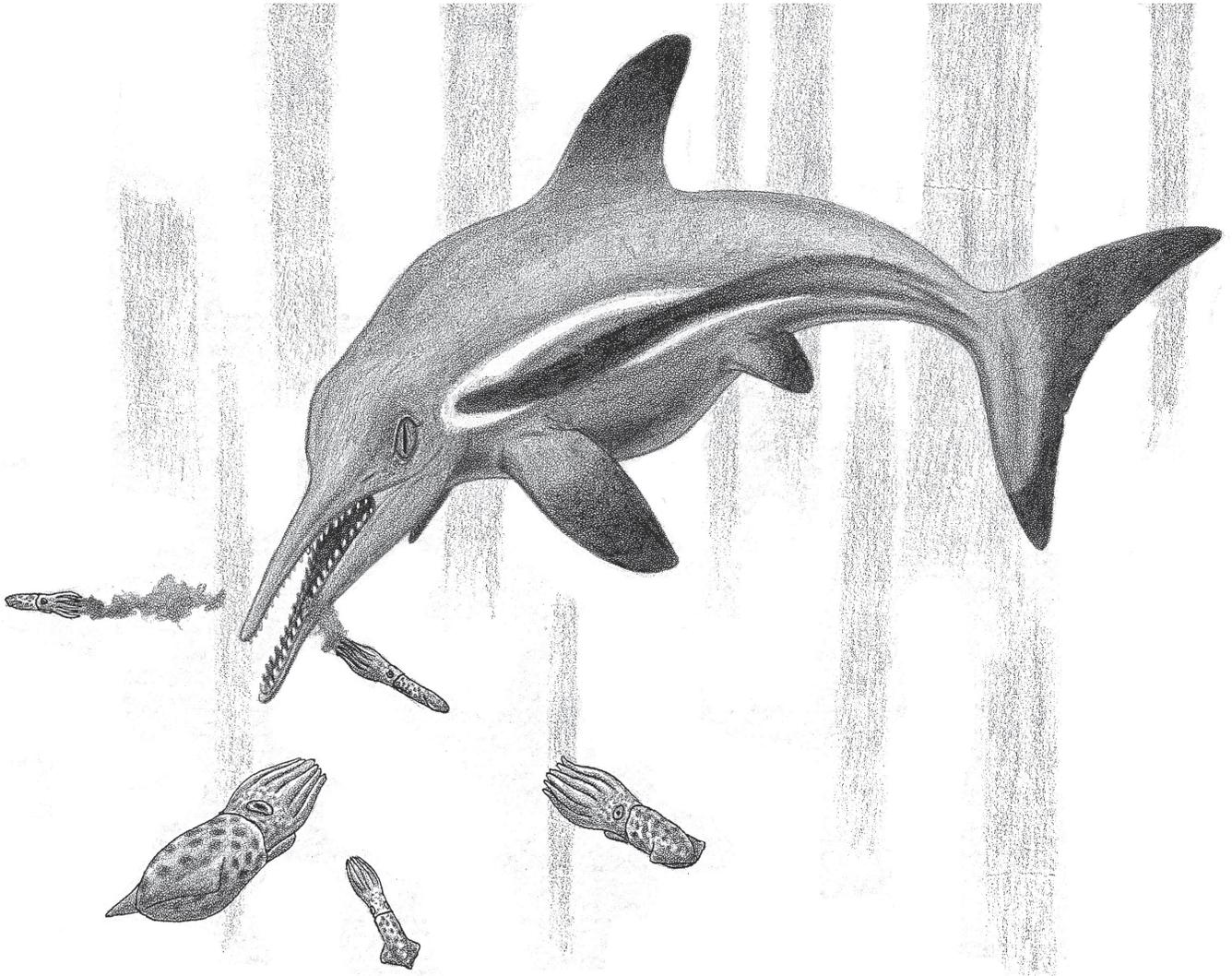


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INTRODUCTION





Peloneustes philarchus

HISTORY OF DISCOVERY AND RESEARCH

The remains of ancient sea reptiles have been found by humans for millennia and may have helped form the basis for belief in mythical beasts, including dragons and sea serpents. In the prescientific West the claim in the Genesis creation story that the planet and all life were formed just two or three thousand years before the great Egyptian pyramids were built hindered the scientific study of fossils. The peculiar, incomplete remains of plesiosaurs become public knowledge, albeit without any understanding of what they were, well back in the 1600s and continuing into the 1700s, when the also incomplete and fishlike fossils of ichthyosaurs, thought to be those of fish, also came to public attention. In the late 1700s mosasaurs began to show up, and in the early 1800s a budding scientific community, increasingly aware that many fossils represented creatures no longer alive on the planet, began to realize that plesiosaurs, ichthyosaurs, and mosasaurs represented exotic extinct groups of aquatic reptiles, often quite large. Mosasaurs in particular were recognized—by the great anatomist Georges Cuvier, who helped establish paleozoology—as true lizards specialized for a marine lifestyle, while the systematic position of the other groups remained obscure other than that they were some form of reptile, not the fish, amphibians, crocodylians, marine mammals, or prelood humans some had been mistaken for.

Western Europe, with its increasingly scientific orientation, and with plenty of ancient marine Jurassic and Cretaceous sediments to produce aquatic fossils, remained the center of the first generation of sea reptile discoveries and research. Along with flying pterosaur fossils, which became available in the late 1700s, the new marine reptiles including *Mosasaurus*, *Plesiosaurus*, and *Ichthyosaurus* played an important role in overturning the faith-based belief in a very young earth in which life had not undergone major transformations or extinctions over deep time, and they did so before the existence of dinosaurs was realized in the 1820s. Of particular importance to the first generation of modern maritime reptile finds was the renowned Mary Anning, who collected major Jurassic plesiosaur and ichthyosaur skulls and skeletons on the southwest coast of England from the 1810s to the 1840s. Anning prospected, often under dangerous winter conditions at the base of unstable coastal cliffs, even though the severe societal limitations on the working class as well as her gender hindered the analytical side of her work. But in part because she was a very atypically female fossil collector, she became widely known (and remains so today) for her major contributions by both the populace and the otherwise patriarchal scientific establishment of the time. Also entering the scene were major early official paleozoologists, most notably Richard Owen, who named hundreds of species, albeit invalidly based mostly on fragmentary remains. Also revealed were other sea reptiles—placodonts, nothosaurs, and crocodile relatives such as *Teleosaurus*. Marine reptiles became highly popular with a public fascinated by these sometimes big, usually bizarre

Mesozoic forms during an age of new and exciting scientific and technological progress.

After the American Civil War, the United States entered the ancient maritime reptile scene with the discovery of a host of often well-preserved mosasaurs and plesiosaurs from Cretaceous marine beds in the Great Plains. The first such fossil apparently sparked the fossil war between Othniel Marsh and an oversensitive Edward Cope, when the former pointed out to the latter that he had made the embarrassingly obvious anatomical error of mistaking the extraordinarily long neck of the famed plesiosaur *Elasmosaurus* for the tail, and the short tail for the neck. The ensuing rivalry contributed to Cope and Marsh naming a long list of species, again mostly invalid, although *Tylosaurus* and *Platecarpus* are real. Also uncovered were late Mesozoic sea turtles, including the gigantic *Archelon*.

From the late 1800s into the early 1900s, Mesozoic sea reptile discoveries continued at a good clip, with Samuel Williston being the lead researcher in the United States. And in Australia, the Cretaceous plesiosaur then known as *Kronosaurus* (currently *Eiectus*) set a new size standard. Popular interest in marine reptiles remained substantial, although they had been somewhat displaced by the dinosaurs of the land and the pterosaurs of the sky. The world wars and Great Depression put a damper on the science of sea reptiles, so that they came to be seen, along with dinosaurs and pterosaurs, as evolutionary dead ends of limited importance—good for getting crowds into museum halls, but not worthy of deep intellectual attention. Even so, skeletons of the whale-sized Triassic ichthyosaur *Shonisaurus*, first recognized in the 1920s, were excavated in Nevada from the 1950s to 1970s. In the 1960s Dale Russell produced a major study on the mosasaurs.

The great revival and revolution of scientific and popular interest in dinosaurs and pterosaurs—which began in the late 1960s, picked up in the 1970s, and went into the 1980s and beyond—at first passed marine reptiles by, as they continued to be seen as conservative reptilians. This began to change in the 1990s and continued into the current century. In British Columbia the remains of an exceptionally big early ichthyosaur were excavated. In this century it was realized that the last of the mosasaurs had evolved compact bodies and more vertical, symmetrical tails that indicate they were high-speed swimmers of the open ocean. It is also being discovered that—much as dinosaurs have proven to have had high, rather than reptilian, metabolic rates—ichthyosaurs, plesiosaurs, and mosasaurs had elevated metabolisms and warm bodies. And turning up in recent years are marine reptiles with heads like hammers, and others with heads like that of the duck-billed platypus.

After centuries of research, much of it using the sophisticated technologies of the last few decades, what is known about the basic paleobiology of Mesozoic marine reptiles is unlikely to undergo a dramatic change in the future. Even so, the research and

WHAT IS A MESOZOIC SEA REPTILE?

discovery is nowhere near its end. To date, over 400 valid marine reptile species in over 300 genera or so have been discovered and named. This probably represents at most a quarter, and perhaps a much smaller fraction, of the species that have been preserved in sediments that can be accessed. And, as astonishingly strange

as many of the reptiles of Mesozoic seas uncovered so far are, there are equally odd species waiting to be unearthed. Reams of work based on as-yet undeveloped technologies and techniques will be required to further detail both their biology and the world they lived in.

WHAT IS A MESOZOIC SEA REPTILE?

The first criterion is that the aquatic reptile lived in the Mesozoic, which began 252 million years ago, after the end of the Paleozoic, and ended 66 million years ago, before the beginning of the Cenozoic, which continues today. Next is that the reptile dwelled mainly or entirely in salt waters or was descended from such. Reptiles that lived in the ancient seas and oceans were a widely diverse lot of distantly related groups, the origins of which are often obscure.

To understand what sea reptiles actually were and are, we must first start higher in the scheme of animal classification. The Vertebrata are animals with backbones—they include fish, most of which are entirely dependent on getting oxygen from water, but not entirely because a few can also breathe air. Tetrapoda are the vertebrates that became adapted to a great or full extent for life on land, or their descendants—amphibians, reptiles, mammals, birds, and the like. Most are entirely air breathers, but not all; some amphibians, for example, have gills during at least part of their life cycle, and some adults can even absorb oxygen through their thin skin; notably, there is no evidence that any amphibian was ever marine. Amniota comprises those tetrapod groups that reproduce by laying shelled eggs, with the important proviso that some have switched to live birth. Although most amniotes get all their oxygen via their lungs, sea snakes also absorb some through their skin. Amniotes include three great groups. One is the anapsids, which are basal forms whose skulls lack openings aside from those for the nostrils and orbits; some sea reptiles may stem from this group, although this is doubtful. Another major amniote group is the synapsids, which include the archaic pelycosaurs, the more advanced therapsids, and mammals—they play no role in this story. The third group is the diapsids, typified by two skull openings behind the orbits, surviving examples of which include the lizard-like tuataras, actual lizards and snakes, crocodilians, and birds. The latter are the direct descendants of the dinosaurs, which, along with crocodilians and other groups including pterosaurs, form the archosaurs that dominated the land and sky during the Mesozoic and still rule the daytime skies as birds. It is likely that all sea reptiles are diapsids.

Although tetrapods appeared as the result of the vertebrate conquest of land, and amniotes secured it, the latter have been repeatedly prone to returning to water-immersed lifestyles. The sea reptiles we will be examining are the thalattosaurs; helveticosaur; sauropterygians, which in turn include atopodontians, placodontiformes, saurophargians, pachypleurosaurs,

nothosaurs, pistosaurs, and plesiosaurs; ichthyosauromorphs, which include hupehsuchians and ichthyosaurs; aigialosauromosasaurs as well as dolichosaurs and ophidian sea snakes; dermochelyoid sea turtles; tanystropheids; and thalattosuchian sea crocs. Most of these groups appear in the fossil record already well developed in their core configuration, leaving little in the way of transitional forms that interlink them with other clades, and often rendering it difficult to discern their exact relationships. Fortunately, this situation is gradually changing as phylogenetically informative transitional fossils are showing up in some cases.

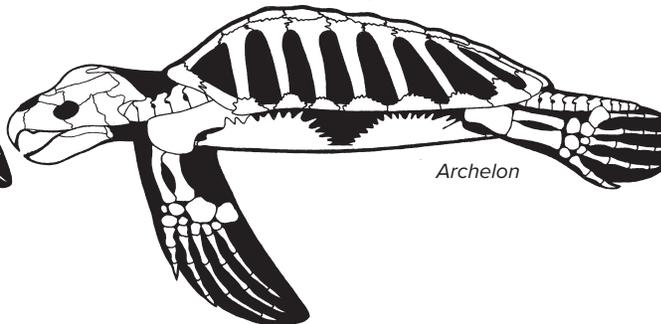
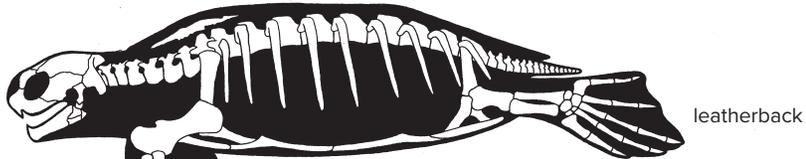
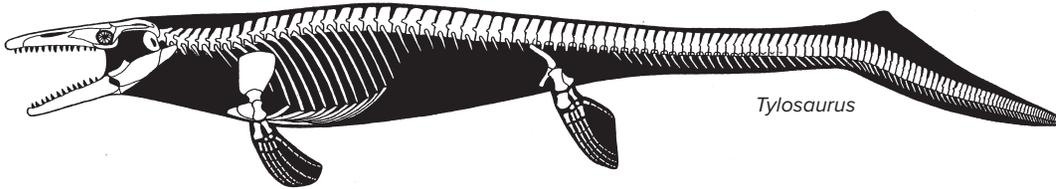
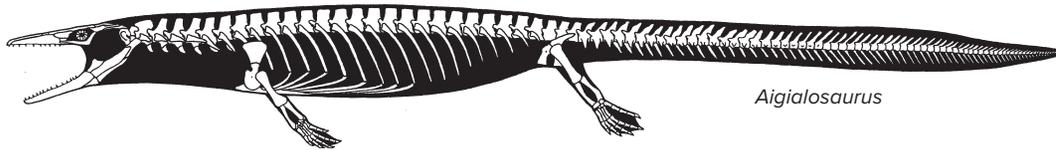
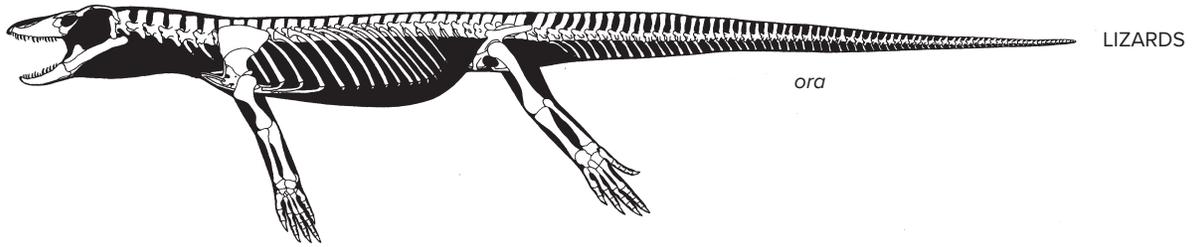
Because they lack extra skull openings, it was long thought that turtles, the chelonids, were the only surviving anapsids. But various lines of evidence, including a recently found apparent early turtle relative with additional skull openings, favor their being diapsids. If that is correct, the next question is, what kind of diapsids? Research suggests that they are either close to archosaurs or even are archosaurs, although other work suggests that they are not particularly close to that group. The first archaic turtle fossils appear in the late Triassic, although there is reason to think that the group dates back to the early Triassic. The fully marine chelonioideans appear in the Early Cretaceous and are still with us. The possible intrarelationships of the chelonioideans are all over the chelonid phylogenetic map, to the point that it is not possible to reliably sort them into distinct families at this time.

The biggest group of Mesozoic marine reptiles, the sauropterygians, appear in the fossil record almost immediately after the beginning of that era, in the early Triassic. They quickly became very diverse, but at the end of the Triassic all went extinct except for the plesiosaurs, which were then common all the way to the end of the Mesozoic. Sauropterygians were diapsids and may or may not be close relatives to turtles, and may or may not be near the archosaurs. No sauropterygians made it into the Cenozoic.

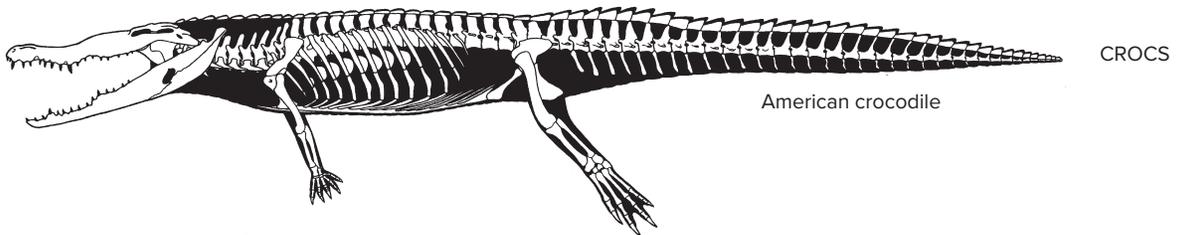
The ichthyosaurs, or more inclusively the ichthyosauriformes, which often resembled high-speed fish, sharks, and dolphins, appeared in less streamlined forms in the Early Triassic and were a major component of the global marine fauna until the middle Cretaceous. These were diapsids and may have been close relations to sauropterygians, and as such they may form a supergroup of aquatic sea reptiles.

The thalattosaurs and helveticosaur were two small groups of early sea swimmers whose relationships to other diapsids remain obstinately unclear.

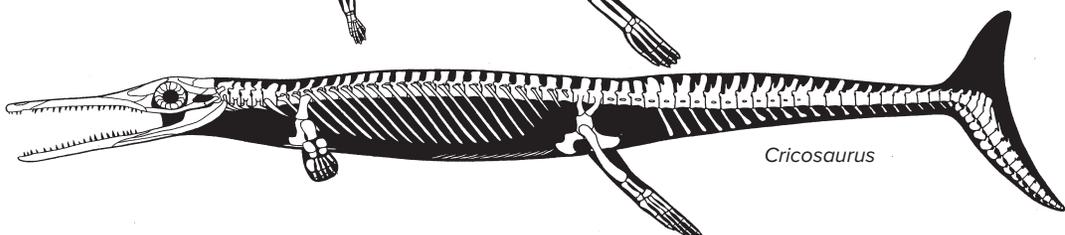
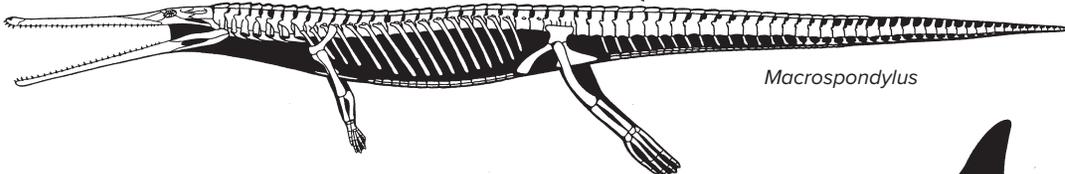
WHAT IS A MESOZOIC SEA REPTILE?



TURTLES



CROCS



Mesozoic sea reptiles with living relatives

DATING SEA REPTILES

Not so obscure are the basic relationships of the thalattosuchian sea crocs, which were close relatives to the crocodilians that still exist. This group of marine crocs lasted from the Middle Jurassic to well into the Early Cretaceous.

Also understood is the basic phylogenetic position of the mosasaurs; they were clearly lizards, which lack the bony bar below the skull opening behind the orbit. Still unsettled is their exact relationship to other lizards, which is not surprising because the phylogenetics of lizards as a whole are very unsettled. Some propose that mosasaurs were close relatives of monitor lizards. Others see them as closer to snakes, which some think evolved from lizards as aquatic forms, represented in the fossil record as dolichosaurs—but others conclude that early snakes were underground diggers. Mosasaurs were limited to the Late Cretaceous, up to the final Mesozoic extinction. Sea snakes are still in force.

Representing a collection of unrelated groups, other than being assorted diapsids, sea reptiles have not shared a common body form, aside from all exhibiting a degree of hydrodynamic streamlining, and some degree of modification of the appendages into joint-stiffened paddles or flippers that are of limited or no use for moving about onshore. Some were fairly small, but

most were fairly large, going up to gigantic. Most Mesozoic sea reptiles were predators of one kind of another, downing invertebrates and vertebrates, from small to gigantic. A much lesser number appear to have been herbivores, none of which were particularly large.

Some sea reptiles were not especially peculiar—the mosasaurs were logical evolutionary versions of lizards adapted for swimming; the metriorhynchids were the same for crocodilians; and the fast ichthyosaurs were the predictable dolphin-like form for high-speed marine amniotes. Other sea reptiles seem strange, especially the superlong-necked plesiosaurs, which have no living equivalents, but that is just because we are mammals biased toward assuming that the modern fauna is familiar and normal, and past forms are exotic and alien. Consider that elephants are bizarre creatures, with their combination of big brains, massive limbs, oversized ears, a pair of teeth turned into tusks, and noses elongated into hose-like trunks. And if animals could think about it, they might find humans bizarre. Nor were ancient marine reptiles part of an evolutionary progression that was necessary to set the stage for mammals, culminating in humans. What the swimming reptiles of Mesozoic times do show is a parallel world, one in which the familiar marine mammals were absent.

DATING SEA REPTILES

How can we know that Mesozoic marine reptiles lived in the Mesozoic, first appearing in the fossil record in the Early Triassic about 250 million years ago and then disappearing at the end of the Cretaceous 66 million years ago? As gravels, sands, and silts are deposited by water and sometimes wind, they build up in sequence atop the previous layer, so the higher in a column of deposits a sea reptile is, the younger it is relative to reptilian swimmers lower in the sediments. Over time sediments form distinctive stratigraphic beds called formations. For example, the mosasaur *Tylosaurus* and sea turtle *Toxochelys* are respectively found in the progressively more recent Niobrara Formation and Pierre Shale Formation.

Geological time is divided into a hierarchical set of names. The Mesozoic is an era—preceded by the Paleozoic and followed by the Cenozoic—that contained three progressively younger periods, Triassic, Jurassic, and Cretaceous. These are then divided into Early, Middle, and Late, except the Cretaceous is split into only Early and Late despite being considerably longer than the other two periods (this was not known when the division was made in the 1800s; likewise, the Early Triassic proved to cover just 5 million years, while the Early Cretaceous was nine times longer at 45 million). The periods are further subdivided into stages. The Niobrara Formation, for example, began to be deposited during the last part of the Coniacian stage and continued to form through the Santonian and into the very beginning of the Campanian, when the Pierre Shale began to be laid down.

The absolute age of recent fossils can be determined directly by radiocarbon dating. Dependent on the ratios of carbon

isotopes, this method works only on bones and other specimens going back 50,000 years, far short of the Mesozoic era. Because it is not possible to directly date ancient marine reptile remains, we must instead date the formations in which the specific species are found. This is viable because a given sea reptile species found as a fossil lasted only a few hundred thousand to a few million years.

The primary means of absolutely determining the age of Mesozoic formations is radiometric dating. Developed by nuclear scientists, this method exploits the fact that radioactive elements slowly decay in a very precise, constant manner over time. The main nuclear transformations used are uranium to lead, potassium to argon, and one argon isotope to another argon isotope. This system requires the presence of volcanic deposits that initially set the nuclear clock. These deposits are usually in the form of ashfalls, similar to the one deposited by Mount Saint Helens over neighboring states, that leave a distinct layer in the sediments. Assume that one ashfall was deposited 144 million years ago, and another one higher in the sediments 141 million years ago. If a marine reptile is found in the deposits in between, then the sea reptile lived between 144 and 141 million years ago. If the fossil is just above the 144-million-year-old layer, then it is probably closer to that age than to 141 million years, and so on. As technology advances and the geological record is increasingly better known, radiometric dating is becoming increasingly precise. The further back in time one goes, the greater the margin of error, and the less exactly the sediments can be dated.

THE EVOLUTION OF SEA REPTILES AND THEIR MESOZOIC WORLD

Volcanic deposits are often not available, and other methods of dating must be used. Doing so requires biostratigraphic correlation, which can in turn depend in part on the presence of “index fossils.” Index fossils are organisms, usually marine invertebrates, that are known to have existed for only geologically brief periods, just a few million years at most. Assume an oceanic reptile species is from a formation that lacks datable volcanic deposits. The sediments contain distinctive invertebrate species that lasted for only a few million years or less. Somewhere else in the world, the same species of marine life was deposited in a marine formation that includes volcanic ash-falls that can be radiometrically dated to 84 to 81 million years.

It can then be concluded that the reptile in the first formation is also 84 to 81 million years old. Because marine reptiles were inherently living in coastal and marine habitats, this correlation method is almost always effective. It is not, however, when the exact location at which a fossil is found is not properly documented. This often happened in the earlier years of paleozoology when fossil hunters did not fully understand the importance of precise stratigraphy. It can also happen when fossils fall off tall cliffs before being found, although sometimes a detailed examination of the sediments encasing or contained in the fossil can allow researchers to recover the layer of ancient sediment it fell away from.

THE EVOLUTION OF SEA REPTILES AND THEIR MESOZOIC WORLD

It is not yet certain where the oceans came from. Contenders for the source of water are the solar nebula and asteroids; both may have contributed. Three billion years ago, when all life was microbial, the already 1.5-billion-year-old planet was largely a water world, with only one continent, Ur, which was about the size of Australia. The atmosphere was free of oxygen—it is not even certain whether the skies were blue in those days. As the Precambrian eon progressed to the Phanerozoic eon we live in, plate tectonics slowly built up the continents, in both number and size, while oxygen levels increased. Both developments were necessary for the evolution of large sea creatures. Streams and rivers flowing off land carry enormous amounts of nutrients into the upper levels of oceans, where they can be utilized by sea life. At the same time, the oceans surrounding land provide moisture for rains, which promote the growth of terrestrial life and mostly end up going down rain-fed rivers and sometimes glaciers into the seas. The abundant life on the sea surface, fertilized by continental runoff, includes photosynthetic plankton that produces most of the oxygen that complex multicellular animals need to exist and function. Also, long, often intricate coastlines provide shoreline floras and faunas that supply resources and nurseries for many marine vertebrates. This land-water-land-water feedback loop allows the oceans to be filled with large, sophisticated creatures—a water world with little or no land would be a comparatively barren liquid desert with ironically rather little in the way of marine life.

As the sun fuses hydrogen into denser helium, the extreme pressures and heat at its core rise even further, speeding up the nuclear reaction. As a result, the sun is getting hotter all the time, by about 10 percent every billion years. Back in the remote past, dense greenhouse gases generally kept our planet reasonably warm despite the cooler sun, but on occasion the balance between solar radiation and greenhouse gases went off the rails, resulting in bouts of a snowball earth in which the entire planet was glaciated and the sea surface iced. The last of the deep freezes occurred about 650 million years ago—the sun has since become too hot for its little satellite earth to completely ice up.

At the beginning of the great Paleozoic era over half a billion years ago, the Cambrian Revolution saw the advent of complex, often hard-shelled organisms, of which the trilobites are the best known. Also appearing were the first, very simple vertebrates, which became increasingly sophisticated fish and sharks during the Paleozoic. In terms of size, fish slowly got bigger for 200 million years, until the appearance of jawed fish was swiftly followed by the appearance of the 9 m (30 ft), 4 tonne (1 tonne = 1.1 US tons) armored *Dunkleosteus*. Seaweeds evolved in various green, red, and brown forms, the latter including kelp-type giants—vascular plants never did become marine. But there was all that space on land to exploit, and first plants and then animals began to invade the land, opening a whole new world to exploitation by multicellular organisms. Among creatures, invertebrates were the first on the ground, although exactly when is not certain. They were followed by Devonian amphibians that evolved from lung-bearing fish less than 400 million years ago. Generally semiaquatic, amphibians are tied to water at least for reproduction by their unshelled eggs—interestingly, considering their water connection, no amphibians have ever dwelled in salt water; their thin skins and shell-less eggs cannot cope with the high sodium content of seawater. The Age of Amphibians evolved into the Age of Reptiles as the first amniotes evolved from amphibians around 350 million years ago in the Carboniferous. Their eggs were shelled, or they could give live birth, so reptiles have had the potential to dwell in any terrestrial habitat that the adults could make a living in, including deserts.

Then a funny thing happened. Having established true land living to varying degrees, some reptile clades began to head back to the water. Actually, this is not truly surprising. Evolution is not an intelligently directed system with set paths and goals. It is a highly randomized affair in which the mindless DNA coding of a given species exists because of its survival via sufficiently successful reproduction. Whatever it takes to continue to successfully reproduce in competition with other species—natural selection—is operative at any moment, and if that happens to

THE EVOLUTION OF SEA REPTILES AND THEIR MESOZOIC WORLD

mean a major reversal in course, that is what happens. Tetrapods came into existence because these DNA-driven species could access new, land-based lifestyles not available to fish and amphibians, and again and again and again natural selection has favored assorted amniotes returning to a highly aquatic lifestyle, which is possible because their nonporous skins do not allow the inflow of salt. Aside from the reptiles described in this guide, highly or fully aquatic tetrapods include a variety of birds and a number of mammals, of which the most extreme examples are whales, which some still consider fish. Interestingly and oddly, no dinosaurs besides birds became full-blown sea swimmers over their 170 million years of existence. That may be because of the way dinosaur bodies and tails flex compared to those of reptiles and mammals. In both of the latter, the trunk and tail flex the same consistent way within each group—side to side in reptiles, up and down in mammals—facilitating the undulations of swimming. Dinosaur trunks and tails were not consistent with one another; the laterally undulating tails of reptiles were retained, but because dinosaurs were erect legged, like mammals, their trunks were most prone to vertical flexion, an awkward combination not optimal for underwater propulsion. Also holding dinosaurs back from going maritime may have been that many or all of them laid well-calcified, hard-shelled eggs, which may have precluded giving live birth, and this would have been a problem for animals so fully adapted to ocean life that they could not get onto land to lay their eggs. On the other hand, some dinosaurs may have produced soft-shelled eggs, in which case the issue does not apply to the entire group.

Also aiding early moves back to the life aquatic is that some early reptiles never became highly terrestrial in the first place. The evolutionary selective temptation to go aquatic was particularly high in those amniotes that were already adapted at least somewhat to live on shorelines, whether the water was fresh or salty. The ancestors of such forms may have been more terrestrial or frequented shorelines, perhaps always if the group descended from basal reptiles that remained persistently semi-aquatic. Even fully terrestrial animals usually have the general ability to wade and swim—an interesting exception to the latter is hippos, in that they are so dense bodied they are hard pressed to swim at the surface; they are bottom walkers that stick to shallow waters—and shoreline examples may feed in part on aquatic organisms near or at the waterline. Increasing the consumption of aquatic organisms, whether plants, animals, or both, requires being better anatomically adapted for aquatic life. Among such adaptations are shorter, stiffer-jointed paddle limbs with splayed fingers and toes, and webbing between the digits to better deal with soft watery muds and sands and to provide hydrodynamic propulsion. In addition or instead, the tail can become a long, flattened, well-muscled sculling organ; because reptiles tend to flex their bodies sideways, the tail flattening and sculling is lateral, unlike in mammals, whose vertically flexible trunks favor dorsoventral flattening and undulation. Nostrils can migrate backward to aid breathing when the snout is submerged.

Because evolution is not automatically progressive, anatomical aquatic adaptations may progress no more than the above. Or selective pressures can result in further aquatic specializations until species are entirely waterborne, with the limbs becoming flippers so hydrodynamically specialized that the animals can no longer go ashore. The irregularity of noncognitive evolution is why modern mammals that dwell in salt water range from those with minimal adaptations, such as sea otters with fairly conventional webbed feet, to others that are more specialized with hydrodynamic flippers yet spend considerable time on beaches, such as seals, all the way to the supermarine whales that die when stranded.

Going marine can occur when amniotes first become freshwater creatures that move into brackish waters and then out into oceans, or when amniotes living along brackish or saltwater coastlines become increasingly aquatic. Becoming a persistent inhabitant of seas is not evolutionarily easy because it requires the development of some means of dealing with high salt loads. Another basic feature of land animals becoming marine is that no matter how specialized they are, they cannot reevolve a means of extracting large amounts of oxygen directly from water, so they cannot avoid returning to the surface periodically to breathe, a few hours being the longest that reptiles can hold their breath. Ergo, aquatic amniotes cannot match fish or gilled amphibians in their ability to stay underwater for their entire lives, which excludes residing in deep seas for extended periods. On the other hand, being able to take in oxygen directly from oxygen-rich air can have advantages over pulling it out of less oxygen-rich water.

The first known reptiles that show signs of specialization for nonfreshwater habitats and are found in saltwater deposits are the small mesosaurs of the Early Permian, whose appearance marked the beginning of 290 million years of some form of sea reptiles living in salt waters up to the marine turtles and snakes of modern oceans. It is possible that their early amniote ancestors had never been highly terrestrial and, retaining fairly well-developed hands and feet, these coastal forms may have been amphibious. Apparently highly specialized with slender teeth for feeding on specific tiny crustaceans, mesosaurs did not last long. Nor did the cludiosaurs of the Late Permian, which also were only moderately adapted to saltwater habits. In the Permian, synapsids were dominant on land, first the reptilian-appearing pelycosaurs, followed by the increasingly mammalian therapsids. Tending to be low-slung, broad-footed forms, they appear to have been prime candidates for spawning aquatic types, and some appear to have been freshwater dwellers. Yet for reasons unknown none became highly specialized swimmers, much less marine. There was an array of bony fish and sharks to compete with any reptiles that went aquatic, but this issue would not limit their ability to do so in the next era.

The end of the Paleozoic era was marked by a tremendous extinction, one that in many regards exceeded that at the end of the Mesozoic. The event appears to have been driven by extended

THE EVOLUTION OF SEA REPTILES AND THEIR MESOZOIC WORLD

supervolcanism, which formed the enormous Siberian Traps and severely contaminated the air, and via that the oceans, over a considerable period. Yet while marine invertebrates took big hits, including the liquidation of the last trilobites and reef-forming creatures, bony fish and sharks were relatively little affected. On land, extinctions were very serious, but the major tetrapod groups did make it through, albeit with depleted diversity.

As the Mesozoic got started, the world was both ancient and surprisingly recent—it is a matter of perspective. The human view that the time of the Mesozoic marine reptiles, which largely corresponded with the Age of Dinosaurs, was remote is an illusion that results from our short life spans, as well as the recent appearance of our genus and species in the last few million and couple of hundred thousand years, respectively. A galactic year, the time it takes our solar system to orbit the center of the galaxy, is 200 million years, so the earth is a mere two dozen galactic years old. And just one and a half galactic years ago marine reptiles had begun to appear on planet Earth. When sea reptiles appeared, our solar system was already over four billion years old, and 95 percent of the history of our planet had already passed. A time traveler arriving on the earth when great reptiles were swimming the oceans would have found it both comfortably familiar and marvelously different from our times.

As the moon slowly spirals out from the earth because of tidal drag, the length of each day grows. When reptiles became marine, a day was about 22 hours and 45 minutes long and the year had 385 days; when they went largely extinct, a day was up to 23 hours and over 30 minutes, and the year was down to 371 days. The moon that glowed down upon Mesozoic waves would have looked a little larger and would have more strongly masked the sun during eclipses—there would have been none of the rare annular eclipses in which the moon is far enough away in its elliptical orbit that the sun rings the moon at maximum. The “man in the moon” leered down on the marine reptile planet, but the prominent Tycho crater was not blasted into existence until toward the end of the Early Cretaceous. The ever-warming sun was about 2 percent cooler than it is now when maritime reptiles showed up, and around 0.5 percent cooler than it is now when most disappeared.

Near the beginning of the Mesozoic era, in the Early Triassic, a number of reptile clades began to move into the oceans. Why that happened on such a large scale at that time, rather than sooner or later, or never, is obscure. It was probably associated in some manner with the disruption of the biosphere and global fauna by the great extinction. Perhaps reduced competition from amphibians in freshwater habitats was involved, but that is not clear. The radiation of assorted diapsids after the Permian/Triassic extinction is another viable factor; certainly for one or more reasons, a number of members of the clade became semiaquatic and then increasingly more water loving.

By the end of the Paleozoic the continents had joined into the great C-shaped supercontinent Pangaea, which straddled the equator and stretched nearly to both poles. As a result, there was

no Atlantic. So at the beginning of the Triassic, 70 percent of the world consisted of the colossal Panthalassic superocean, which was almost 5,000 km (3,000 mi) farther across than is today's Pacific, nearly 25,000 km (15,000 mi) from east to west. Virtually none of the ancient floor of the Panthalassic exists—it has since been subducted by the plate tectonics that created the basin in the first place—so the islands that must have dotted the superocean are lost. The other great ocean of the time was the Tethys, which formed a large, subtriangular wedge of sea that projected into the supercontinent like an arrowhead from the east, its western apex separating Europe from Africa and touching the northeastern edge of North America. At its greatest expanse it was about two-thirds the size of the supercontinent, but these days the Mediterranean is all that is left of the Tethys. The deposits of that relatively shallow ocean, with its extensive coastlines and embayments, are a major source of Mesozoic sea reptile fossils. During all of that time, much of Europe, especially the western portion, constituted an archipelago of islands—sometimes large, often small, and rather reminiscent of Indonesia—which began immediately northeast of North America. The shallow seas surrounding the Euro-islands often connected the western Tethys to the northeastern Panthalassic/Pacific. Other shallow seaways were not extensive in the Triassic. India was then attached to Africa, as were Antarctica and Australia.

Driven by carbon dioxide levels well above even modern industrial levels, the global climate was—despite the slightly cooler sun of those times—overall tropical and subtropical, with the only cool climes at sea level being at the then temperate poles during winter, and there were no low-altitude glaciers. Near the equator, ocean temperatures were so extreme during parts of the early Triassic, up to 40°C (104°F), that sea life was severely restricted, and low-latitude reefs were microbial. Swimming invertebrates centered on ammonoids and nautiloids, which were not especially closely related despite often sharing classic spiral shells, and octopi were also present. Although barnacles were around as early as the Paleozoic, they are oddly uncommon in the fossil record until fairly recent times, and there is no evidence that they anchored on the skin of ancient sea reptiles the way some do on whales. Bony fish were abundant, and many were fairly modern in form, although they were not particularly large. It is often said that sharks are living fossils that have changed little since ancient times, but the classic sleek sharks like great whites, tigers, whitetips, and the like were not yet extant; those of the early Mesozoic were more archaic in form, as some still are.

Sediments from the latter portion of the Early Triassic, just three or so million years after the great extinction, record the appearance of a number of semimarine and fully marine reptiles—the shoreline evolutionary events that led to all these more water-adapted forms must have been under way since the Paleozoic-Mesozoic boundary, if not before. The first sauropterygians appear in the form of the vaguely lizard-like, ambush-fishing pachypleurosaurs, and corosauers. Also coming onto the scene for the first time were ichthyosauromorphs. Some

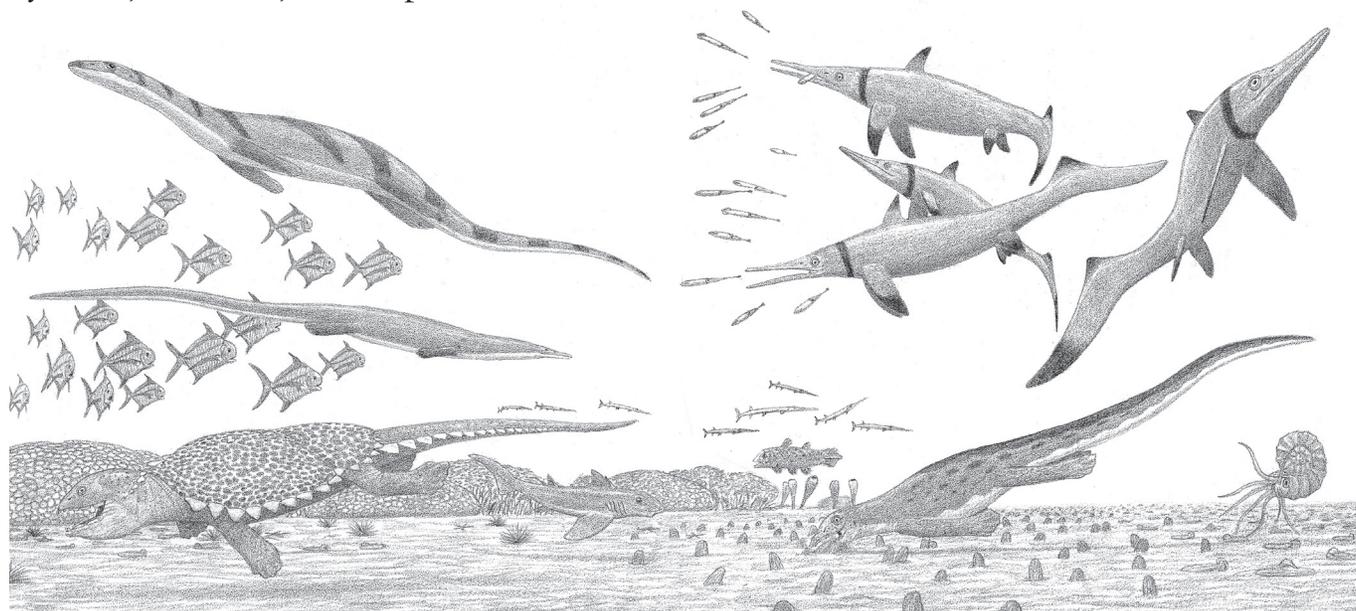
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were hupehsuchians, often sporting armor—one version with a strikingly platypus-like head looks like it was using electrical fields to seek and dabble up prey items in murky waters and at night—while nasorostrans appear to have sucked up their victims. All the above were shallow-water creatures with mediocre hydrodynamic forms, and clawed toes and fingers that could probably clamber onto coastal beaches, including to reproduce. But also coming onto the evolutionary line were streamlined, fusiform, true-flipped, hydrotailed ichthyosaurs that were the first amniotes with incipient fish-style forms, and they had little if any ability to get onshore—which indicates that they bore live young. It is all the more startling that some of the very early ichthyosaurs got quite large—approaching 15 m (50 ft) and 10 tonnes, they were the first big air-breathing game hunters of the oceans. While recent assertions that some of these reptiles reached nearly 50 tonnes at this time are far too extreme in terms of both sheer size overestimation and the rate of evolution required for such a uniquely and extremely massive and fast size expansion, gigantism did evolve swiftly after the initial appearance of early Mesozoic sea reptiles, a quick evolutionary pace that would later be seen among early whales in the early Cenozoic. So it took just five million years for salt water-loving reptiles to evolve a startling degree of maritime diversity, experimentation, size, sophistication, and hydrodynamic refinement. Thus began the Mesozoic Age of Sea Reptiles, which would last 185 million years.

In the Middle Triassic, the superhot climate eased up a bit as the first small protodinosauroids, dinosaurs, and pterosaurs appeared among a terrestrial fauna dominated by the other

archosaur wing of the diapsids, as well as therapsids, which also persisted in not going maritime. Appearing on the marine scene were weakly developed reefs made largely of sponges and corals, and an increasing diversity of bony fish and sharks. As for the reptiles of the sea, it seems that the electrical field dabblers did not persist and would not be seen again in reptilian version, as all the hupehsuchians for some reason apparently bought the paleofarm. Same for the corosaurs, although the also lizard-like pachypleurosaurs did ease into the Middle Triassic, when some of them appear to have become the smallest known saltwater reptiles. Coming onto the marine scene was yet another clade of lizard-like, diapsid, nearshore ambush predators with paddle limbs—thalattosaurs. Some of these became less lizard-like by developing the upper jaw into a stout, forward-projecting spike. Others took a curiously different rostral direction by curving their snouts strongly downward. Making a very brief appearance on the marine reptile stage were early members of the archosaurian complex, the tanystropheids, which often sported amazingly long necks. In their case the group had already developed freshwater habits before dipping their evolutionary toes in saltwater nearshore habitats, as far as we know only during the early Middle Triassic. Also not around very long were the poorly known helveticosaurs. Similarly short-lived, albeit better documented by fossils, were the sauropterygian atopodontatians, which developed hammer-shaped heads with which to scrape off algae, rendering them perhaps the first aquatic herbivorous tetrapods. Other sauropterygians to appear in the fossil record at this time were the beefy placodontiformes, with flattened teeth forming pavements to crush shelled creatures, or perhaps to pulp algae

The Middle Triassic *Serpianosaurus*, *Askeptosaurus*, *Cyamodus*, *Mixosaurus*, and *Paraplocodus*



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like reptilian manatees as some researchers contend. Usually armored to a lesser or greater degree, some retained fairly conventional barrel-shaped trunks, but the cyamodontoids greatly expanded their bodies sideways into broad carapaces flattened top to bottom like those of the turtles that these placodonts predated. Also on the evolutionary stage were the saurosphargians, which developed turtle-like forms. Pachypleurosaurs did better in the Middle Triassic than they did in the Early Triassic. None of the above were sleek swimmers. Doing better in terms of streamlining were the protoplesiosaurs and nothosaurs, which became abundant at least in Eurasia, and the pistosaurs. Some of the ichthyosaurs developed knob-shaped teeth in the back of their jaws suitable for crushing shelled organisms.

The marine reptile size rise took off in the early and middle Late Triassic, as shonisaur and megamarinasaur ichthyosaurs approached 17 m (55 ft) and ~20 tonnes. This early peak in sea reptile size was similar to sei whales but—contrary to claims by some researchers—fell well short of sperms, fins, blues, and the future biggest fish of the Mesozoic and Cenozoic. Never again would water-loving reptiles be as big as those of these times, at least in length. Another clan of big ichthyosaurs evolved short but broad, toothless bills that some think were used for sucking in prey, but others disagree. Some Late Triassic ichthyosaurs, in the form of the first parvipelvians, also went highly hydrodynamic with the advent of the first full-blown pursuit hunters with symmetrical, lunate tail flukes that produced powerful thrusts and high speeds, although the group did not yet evolve compact thunniform bodies. The swift ichthyosaurs show that sea reptiles now included pelagic forms with no particular connection to coastlines. The turtle-style placodonts and saurosphargians made it into the Late Triassic, perhaps to the end of the period, and some of the former appear to have had baleen-like structures suitable for filter feeding. None of the lizard-style swimmers persisted—pachypleurosaurs have been found in a Late Triassic deposit, so the time of tiny sea reptiles came to a quick end—nor were nothosaurs present. Pistosaurs were there but were not very abundant. Among fish, the teleosts, which would become the dominant bony fish, first appear in the fossil record.

The Triassic was, as is obvious from the fossil record, an Age of Radical Marine Reptile Evolutionary Experimentation. Aside from the development of giants and swift swimmers, all sorts of widely divergent body forms and especially feeding types evolved, some of them quite astonishing—placodonts featuring pavement teeth for grinding or pulping food, and/or turtle-type carapaces; tanystropheids with never-ending necks; atopodontians sporting a cartoonish hammerhead-shaped shovel mouth for grubbing or grazing along sea bottoms; and perhaps even more extraordinary eretmorhipians whose heads were astonishingly close in form to those of the mammalian duck-billed platypus. One kind of sea creature not yet seen were massive-headed hunter-killers. Evolutionarily perplexing is why the archosaur plesiosaurs—thecodonts that evolved a very croc-like form as well as high-placed nostrils for breathing while otherwise entirely

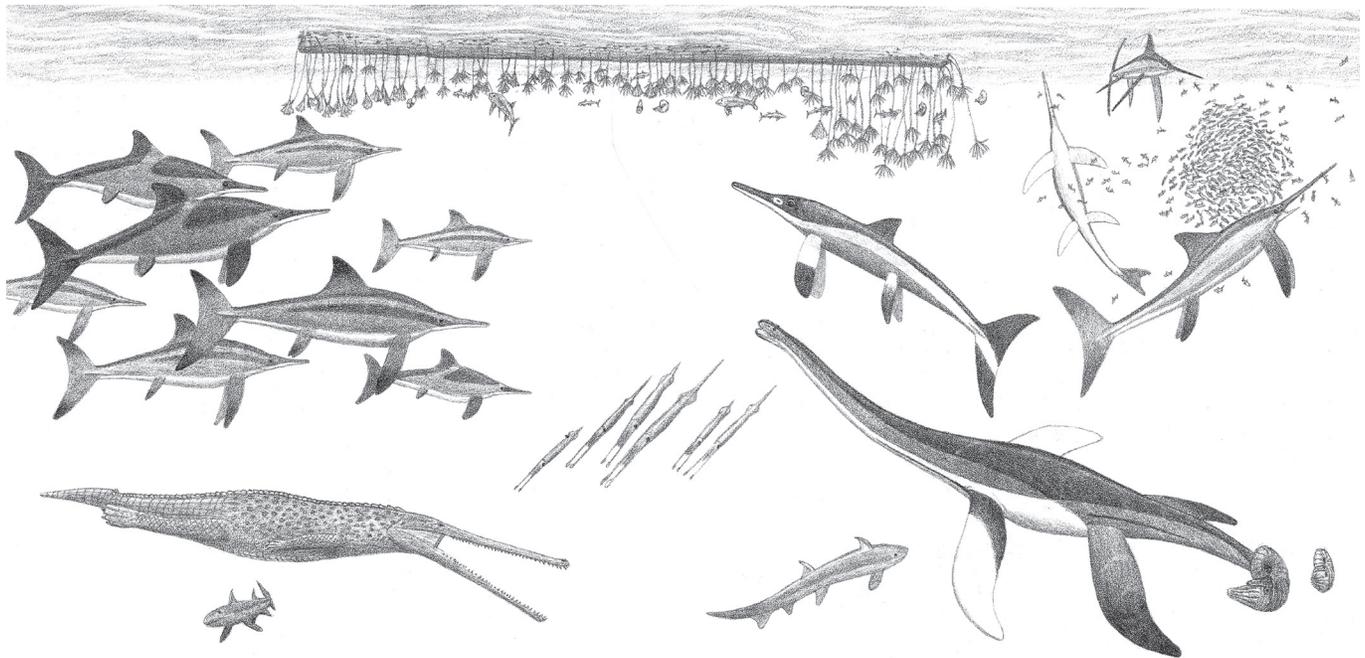
submerged—despite being about as well adapted for aquatic life as crocodilians, did not develop a major marine wing of the group. Bioevolution is not logical.

Up on the supercontinent, dinosaurs were becoming diverse and sometimes large, as other archosaurs and the therapsids declined. The first at least partly shelled prototurtle fossils are present and show indications of being semiaquatic, but not yet marine. Land lizards are likely to have gotten their start at this time. Some small pterosaurs were probably flapping and soaring over and feeding on and just off shorelines, but they were not truly marine, leaving the open oceans still free of aerial animals.

The end of the Triassic about 200 million years ago saw another extinction event, whose cause is murky. A giant impact occurred in southeastern Canada, but it was millions of years before the extinction; again, supervolcanoes—associated this time with the initial rifting along the proto-Atlantic region—may have been responsible. Among oceanic invertebrates, the ammonoids took it on the diversity chin but were not entirely knocked out. Reefs, which had become extensive in the Late Triassic, dropped off sharply. Above sea level the thecodonts and therapsids suffered the most: the former were wiped out, plesiosaurs included, except for crocodilians, and only scarce remnants of the therapsids survived along with their newly evolved mammalian relatives. In contrast, dinosaurs sailed through the crisis into the Early Jurassic with little apparent disruption, as the sauropods became gigantic. Note that marine reptiles toward the end of the Triassic were already not as diverse as they had been. The placodonts, saurosphargians, and pistosaurs, not especially abundant in any case, were liquidated by the crisis for unknown reasons, ending the rather brief era of radical marine reptile experimentation. Also unable to survive events were ichthyosaurs with old-fashioned asymmetrical tails, which included those with crushing teeth. The biggest ichthyosaurs did make it into the Jurassic. Meanwhile, for similarly not entirely understood causes, a depleted reptile ocean fauna of plesiosaurs and lunate-tailed ichthyosaurs made it into the Jurassic—the superior hydrodynamic power of the latter presumably helped them survive into the new period. And it may be pertinent that only marine reptiles that appear not to have had to beach themselves to lay their eggs made it into the dinosaur-dominated Jurassic.

In Early Jurassic oceans the external-shelled ammonoids were joined by the squid-like belemnites, which possessed a conical internal hard structure. Some belemnites became large, but none are known to have become gigantic, like some squid. Until the early Jurassic, it was common for often large, floating tree logs to become heavily adorned over time with bivalves and the somewhat flowerlike sea lilies, becoming long-drifting biorafts that provided surface habitats for small fish and cephalopods until the logs sank or cast up onshore. This came to an end in the later Jurassic as wood-boring shipworms, the teredos, appeared and began to make short work of driftwood. Teleosts became increasingly numerous and diverse. Early Jurassic plesiosaurs diverged into long-necked, small-headed ambush fishers

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The Early Jurassic *Stenopterygius quadriscissus*, *S. uniter*, *Macrospondylus*, *Suevoleiathan*, *Eurhinosaurus*, and *Seelyosaurus*

that preferred shallower waters; short-necked, big-headed pursuit forms more prone to favor deeper waters; and others in between—these two types were once thought to represent just two distinct phylogenetic groups, but more sophisticated analysis shows that necks evolved different lengths in a complex variety of groups, and some were edging toward gigantic. A few of these early plesiosaurs are found in freshwater deposits, suggesting some level of exploitation of such waters; it is hard to tell from the fossils whether the animals were permanent residents in low-sodium water, as are some cetaceans, or temporary visitors. No evidence of nonmarine ichthyosaurs has yet turned up, which is interesting considering that there are riverine and lake dolphins, and some sharks will enter freshwaters. Although abundant, Jurassic ichthyosaurs actually became less diverse than the Triassic expressions, as all evolved into streamlined, swordfish-, tuna-, and dolphin-shaped fusiforms suitable for high-speed cruising and dashing about in pursuit of slippery prey. No members of the group were well adapted for nearshore shallows as most Triassic species had been, for reasons unknown. Some Jurassic ichthyosaurs were quite big, although none came close to matching the Late Triassic shonisaur for reasons that are mysterious. In the early Jurassic, large, sleek leptonektid ichthyosaurs developed extralong, slender sword beaks similar to those of billfish for slashing and dicing their prey. What is peculiar is that this particular experiment, which seems to be an eminently sound evolutionary adaptation, was for unclear reasons very brief; sword-billed reptiles were never to be seen again. Also not successful in the long term were the always big, even fairly gigantic,

big-headed and large-toothed temnodontosaurid ichthyosaurs, the most powerful marine killers yet seen; they were also inexplicably limited to the Early Jurassic. More successful were the high-speed ichthyosaurs with compact thunniform bodies like those of the fastest sharks, tunas, porpoises, and dolphins, a highly hydrodynamic body design that would last through the rest of the Jurassic. Coming into the marine fauna were the crocodile-related thalattosuchians (not to be confused with the earlier thalattosaurs), this being another case of a group initially going freshwater aquatic and then moving to salt water. Aside from already having oddly small arms, the first of these seagoing crocs—teleosaurs and pelagosaur—were not radically different from their continental relations and were armored, albeit less so than freshwater crocs. Medium to large in size, they were ambush predators that probably laid hard-shelled eggs on land. Toward the end of the Early Jurassic, the Toarcian oceanic anoxic event apparently drove a bout of marine extinction limited largely to invertebrates, including ammonoids. Sea reptiles appear to have been relatively little bothered.

During the Early and Middle Jurassic, major tectonic forces were initiating big changes on a geographic geological scale, as the collection of the continents into one began to reverse. First was the splitting of North America from Africa, which created a narrow North Atlantic that gradually extended to an incipient Gulf of Mexico, which in turn divided the Americas while connecting the western Tethys to what was now a Pacific Ocean that became at first only a tad smaller than the preceding Panthalassic. For the rest of the Mesozoic the increased tectonic activity

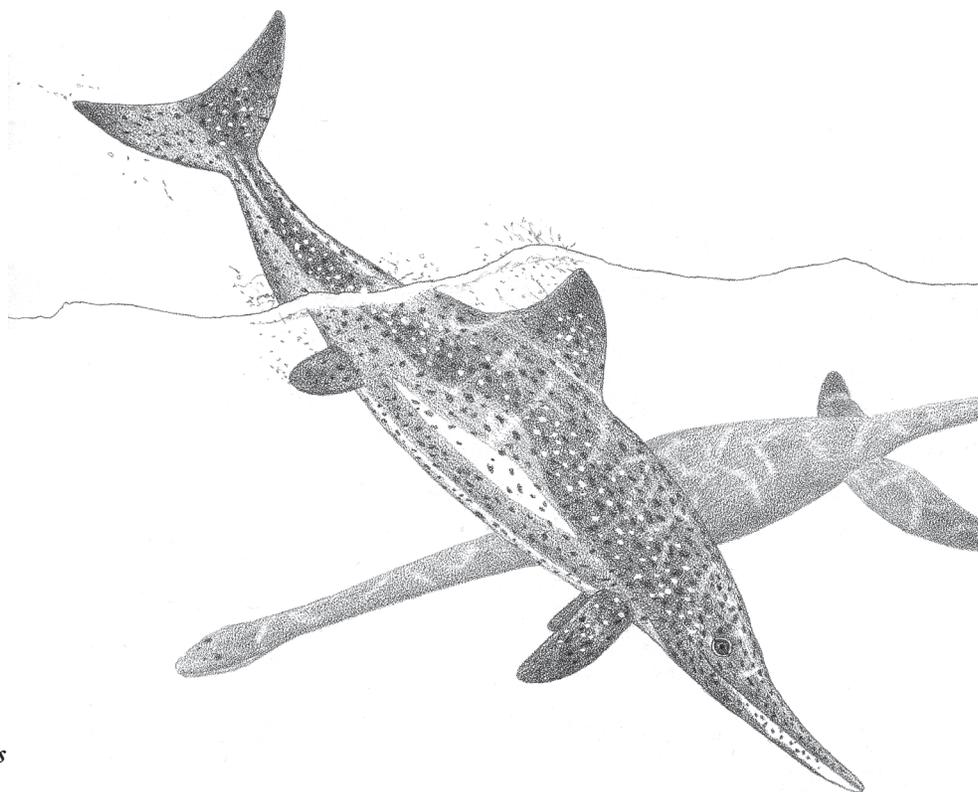
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of the continent-bearing conveyor belts formed by the mantle caused the oceans' floors to lift up, slowly but persistently spilling the oceans onto the continents in the form of shallow seaways that began to increase the connections between the big oceans, favoring a more global marine fauna. The extension of the temperature-moderating seas into the supercontinent cooled the land a little. But the greenhouse effect was running high, with ocean temperatures at a peak.

A relatively poor fossil record hinders full assessment of the state of the marine fauna in the Middle Jurassic. It is known that a group of filter-feeding fish that appeared in the Early Jurassic, the pachycormids, swiftly ballooned to produce *Leedsichthys*, the biggest known bony fish of all times, in the middle of the period. At some 15 m (50 ft) and 30 tonnes (perhaps even bigger when size variation is considered), about the size of a humpback whale, *Leedsichthys* approached and could have matched the largest living plankton-eating fish, the whale shark of up to 17 m (55 ft) and 40 or more tonnes, and may have been competitive with the biggest shark of all time, megalodon. How and why *Leedsichthys* got so big is not mysterious; filter feeding on enormous masses of small sea creatures is the best means of doing so. Also getting big were the large-headed and large-toothed pliosaurs—in the Late Jurassic the largest known example achieved 9 m (30 ft) and 8 tonnes. Destined to be an enduring evolutionary success, these powerful big game-hunting superplesiosaurs may explain the failure of the temnodontosaurid ichthyosaurs, which

they rather resembled. Another interesting size phenomenon of the Middle and Late Jurassic is that the sauropod dinosaurs, which were coping with living under a force of 1G, became land colossi, approaching and perhaps exceeding 100 tonnes, much larger than any known sea reptiles. At the opposite size extreme, mammals were persistently small, from house-cat size on down, and were diverse enough to include some highly aquatic forms rather similar to the platypus, beavers, and otters, but none made an evolutionary move into the marine realm for reasons unknown. Starting to do so marginally were some small coastal turtles. The air over the open oceans remained barren of flying creatures as the Jurassic approached its end. This was another pinnacle of ichthyosaur evolution, with the pelagic thunniform stenopterygiids and ophthalmosaurines spinning off an array of species, and the first of the platypterygiines showing up. Among the sea crocs the metriorhynchoids had lost their armor, evolved true flippers, and developed sharklike tails with a boneless upper lobe better suited for pursuit tactics in open seas.

Shallow seaways regressed somewhat toward the end of the Jurassic. At the same time, widening a few centimeters each year, the North Atlantic-Gulf-Caribbean complex was becoming a substantial ocean by the Late Jurassic—broadly similar in size to today's Mediterranean, and connected to the Tethys and Pacific—when rays with flattened crushing teeth first appear as fossils. Teleost fish continued to radiate, but for mysterious reasons the pachycormids do not seem to have been as colossal as they had



The Late Jurassic *Cryopterygius* and *Ophthalmothule*

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once been, and as filter feeding should have allowed them to be. Ocean temperatures were dropping about 6°C (10°F) from the earlier Jurassic high. That does not seem to have done the high-energy ichthyosaurs and plesiosaurs, some of which inhabited high-latitude seas, any harm. But the armored crocodilians with their low reptilian energetics went into sharp decline, while the metriorhynchids, sporting higher metabolic power, did not decline as sharply. Polar seas were a little chilly and had a distinctive fauna. Coral reefs became more extensive during the Jurassic and reached a major peak in the last stages of the period.

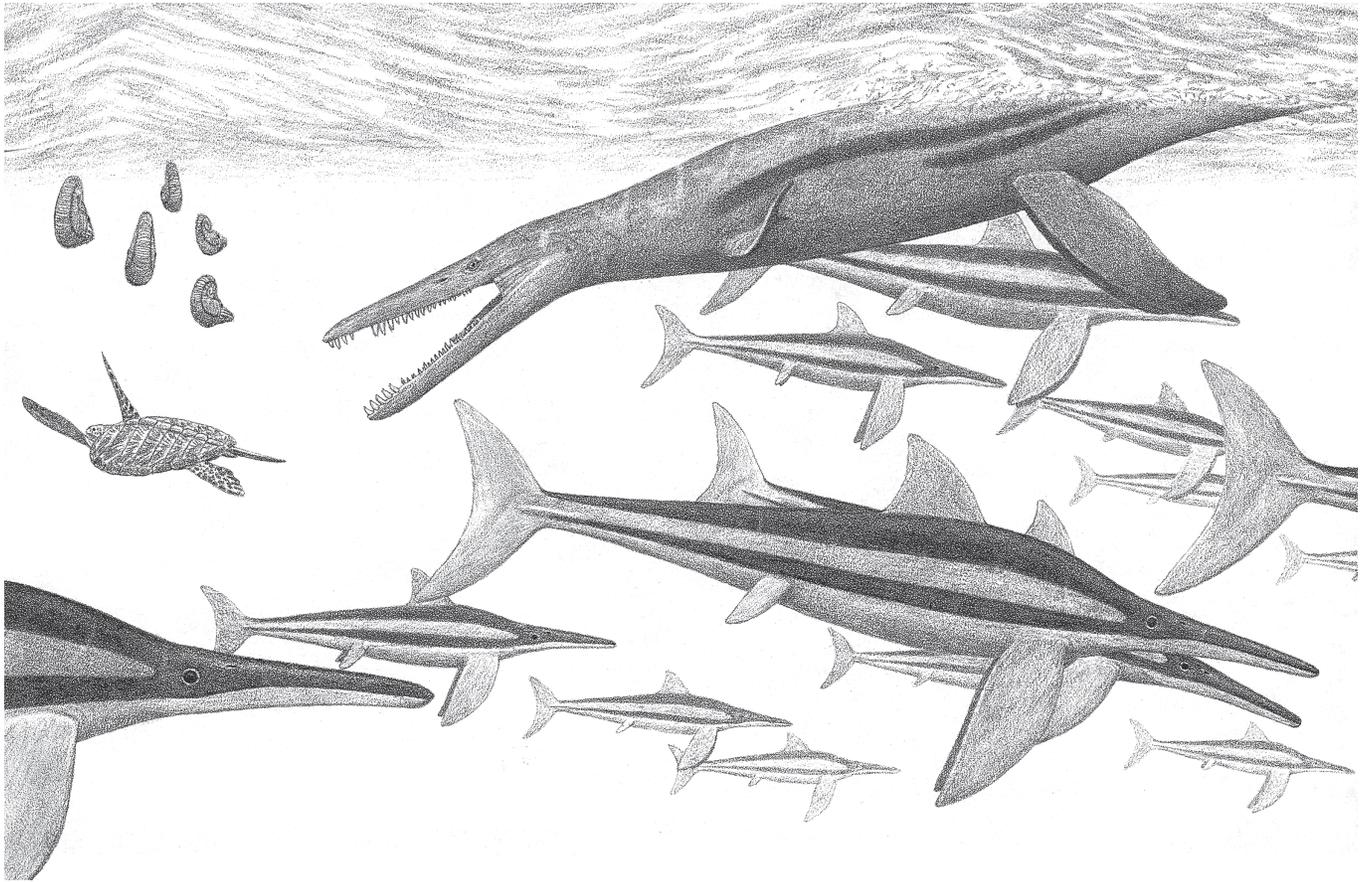
A notable and peculiar feature of the Jurassic and the following Cretaceous is that the broad array of coastal, shallow-water reptiles of the Triassic was not replicated by a similarly extensive array of similarly adapted forms. There would never be sea reptiles with grinding pavement teeth in the Jurassic-Cretaceous. Nor any with shovel-shaped mouths. Or with platypus heads. Why this was so is not entirely obvious—the appearance of rays with pavement teeth can explain the lack of reptiles with the same, but fish with shovel mouths did not appear, nor did fish or for that matter marine mammals with platypus heads. In the Jurassic and Early Cretaceous there were no swimming reptiles with knob-shaped teeth for crushing purposes. Ichthyosaurs did not take another stab at evolving short, broad-snouted, toothless bills. Or giants of Triassic shonisaur dimensions. Similarly peculiar is that there were no turtle-shaped sea reptiles in the Jurassic. Or anything particular in the way of small reptiles in the salty seas.

Also not well understood is what happened to the global fauna at the end of the Jurassic, the information gap resulting from a scarcity of sufficient deposits. The Cretaceous began 145 million years ago. This long period would see an explosion of oceanic reptile evolution as the continents continued to split, the South Atlantic began to open, and shallow (i.e., not miles deep) seaways crisscrossed the continents—the splitting of land by tectonics and transgressions maximized the coastlines that could boost marine diversity. Greenhouse conditions became less extreme as carbon dioxide levels gradually edged downward, although never down to the modern preindustrial level. Early in the Cretaceous, the warm Arctic oceans kept conditions up there balmy even in the winter. At the other pole, the combination of Antarctica and Australia made for a chillier regional climate frigid enough to sometimes form permafrost and some glaciers, but the surrounding seas were not extremely cold, and sea temperatures in general were similar to those in the Late Jurassic, albeit rising. Corals took a blow as the Cretaceous began, with reefs becoming dominated by the rudist bivalves, apparently because they were better able to handle the warm waters of the time than corals—the last point being of growing concern in our warming world, all the more so because rudists are not on hand to take over. Ammonoids, nautiloids, and belemnites continued to be the primary swimming invertebrates. As teleosts continued to further modernize and included more fusiform forms, so did the evolving sharks, which would not look out

of place in today's seas, although the fully thunniform lamnids apparently did not appear in the era. None of the fish of the period, bony or otherwise, appear to have been enormous. In the Early Cretaceous a series of anoxic events began that would repeatedly afflict the oceans during the period—most but not all had little obvious impact on the marine reptile fauna.

Plesiosaurs both short and long necked, ichthyosaurs, and sea crocs made it into the Cretaceous in good order. As with the invertebrates and fish, extreme gigantism was not the maritime order of the day in the early Early Cretaceous—unlike on land, where the towering sauropods continued to be colossal. One dinosaur clade dabbled with the life aquatic in the Early Cretaceous, the predaceous spinosaurs with rather croc-like heads starting before the end of the Jurassic and lasting through the Cretaceous. Some became very large, but they remained shoreline bipeds well adapted for walking. Spanning 45 million years as the Atlantic continued to open along its entire length, considerable evolution occurred among marine reptiles as the Early Cretaceous rolled on. The never very numerous thalattosuchians appear to have gone extinct not long into the Early Cretaceous. That the nostrils of sea crocs remained for unclear reasons near the tip of the snout, rather than migrating well aft on the rostrum, may have hindered the evolution of the group, which never included gigantic examples. Some ophthalmosaurs inhabited the Early Cretaceous, but most of the ichthyosaurs of the period were platypterygiines with marvelously intricate pavement-boned foreflippers—biohydrofoils of such sophistication would never be seen again. Interestingly, ichthyosaurs with highly compact thunniform bodies like those of their Late Jurassic predecessors have not yet been documented, although such cannot be ruled out with the data on hand. Reptiles with very broad, flat-shelled bodies finally returned to the marine realm as the first true sea turtles at last appeared. It is possible that some of these rapidly got about as big as sea turtles have been known to get. The small aquatic pelomedusids may have had a nearshore element in the Early Cretaceous, or they may well have been limited to fresh and brackish waters as they are today. Definitely oceanic were the generally hefty chelonioideans with their big foreflippers. Also in the salt waters were the paddle-sporting aigialosaurids that, being true lizards, returned lizard-form ambush-fishing reptiles to nearshore habitats for the first time since the Triassic. Still having webbed limbs rather than true flippers, they, like the turtles, probably beached to breed. Also coming onto the scene were the short-necked polycotyloid plesiosaurs, which resembled but were not closely related to the similarly proportioned pliosaurus. Some of the latter become as hefty as sea reptiles got, at 12 m (40 ft) and 20 tonnes matching the bulk of the earlier shonisaurus, with oversized heads approaching 3 m (10 ft) long; these were the most powerful heads to appear among ocean-going reptiles, with a biting force that easily exceeded that of the largest predaceous dinosaur heads. Some plesiosaurs of this time have been found in freshwater sediments, where they may or may not have been permanent residents.

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The Early Cretaceous *Notochelone*, ?*Kronosaurus*, and *Longirostra*.

Also in the middle of the Early Cretaceous competition for marine fishers, reptilian and otherwise, large to gigantic, ornithocheirid pterodactyls appeared in the skies above the waves, with wings spanning up to 9 m (30 ft). No doubt these dynamic soaring and flapping pterosaurs patrolled the oceans in search of water surface disturbances as sea reptiles, sharks, and other big fish drove schools of small fish and belemnites up near the surface, where the tops of the resulting bait balls were easy picking for the water-dipping aerialists. And ornithocheirids certainly ended up going down the gullets of marine reptiles, either snatched under when they dared float on the surface, or scavenged.

Starting in the late Jurassic as protobird dinosaurs and accelerating in the Early Cretaceous as birds with rapidly improving aerial abilities, some early, toothed avians became shorebirds on fresh and salt waters, then semiaquatic fliers, and then fully marine flightless birds, the loon-like diving hesperornithiforms that could barely clamber onto beaches to nest.

In the Late Cretaceous, which began 100 million years ago, sea temperatures rose until they reached a new peak early in the Late Cretaceous, maybe even toastier than in the Jurassic. But carbon dioxide levels and sea temperatures then dropped. As a result, the dark Arctic winters sometimes became cold

enough to match the conditions seen in today's high-latitude northern forests, and polar waters became chilly, especially in winter, as glaciers crept down high-latitude mountains. The continents were separating fast by geological standards, to the degree that by the end of the Mesozoic they were assuming a fairly modern configuration. India had detached and become an isolated subcontinent, sailing remarkably swiftly for such a huge mass of crustal rock north toward its Cenozoic collision with Asia—in the process the Tethys would evolve and split into the Indian Ocean and Mediterranean Sea. The tectonic separation and the continuation of numerous interior seaways resulted in increasing division of continents. Europe remained a complex of islands large and small, although it was drifting away from North America. A great seaway divided western and eastern North America during the bulk of the period, producing many of the best sea reptile fossils. On land, mammals were increasingly modern yet remained small and inexplicably nonmarine. Dinosaurs saw their ultimate radiation, including titanic titanosaurs sauropods, horned giants, duckbills, and the great tyrannosaurs; spinosaurs hung on for a while as shoreline hunters and fishers. The crested pteranodont ornithocheirids, some gigantic, picked up fish from the waves they cruised over

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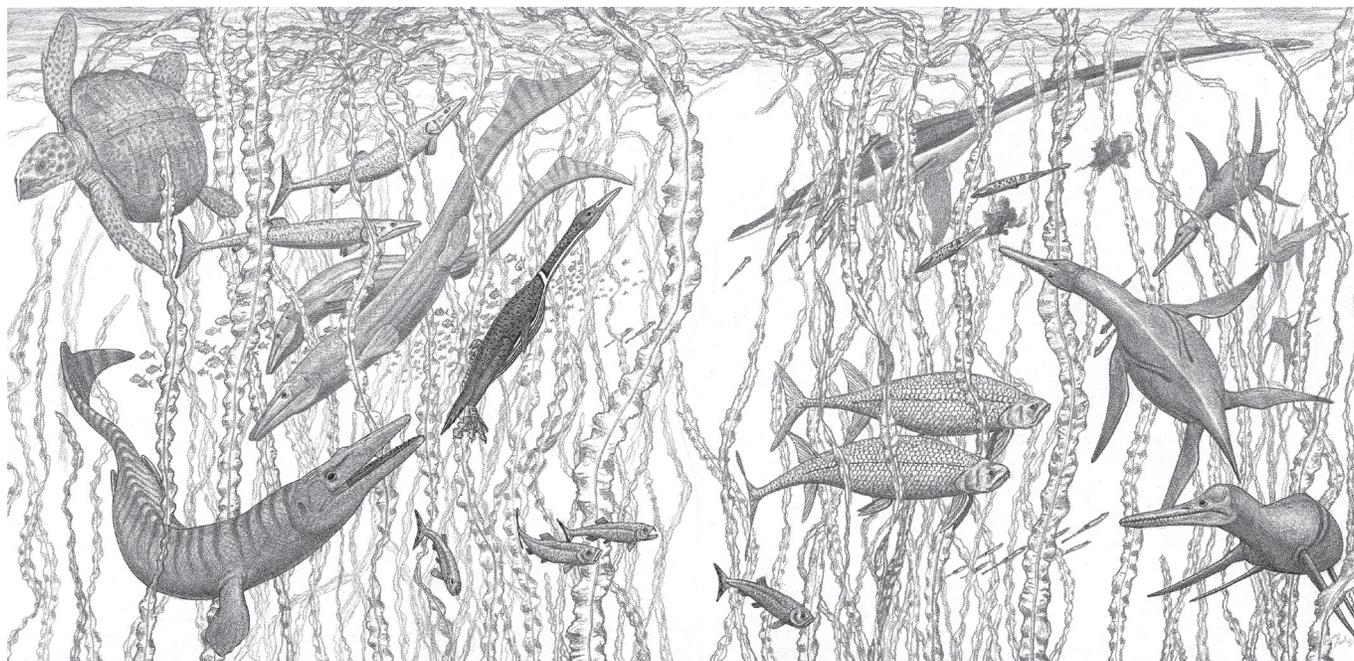
like pterodactyloid albatross. Little ichthyornid birds resembled toothy gulls and petrels, but evidence that large flocks of flying birds were crash diving among the sea reptiles to snatch fish in the manner of gannets, boobies, and pelicans is absent.

In the oceans of the long Late Cretaceous, which spanned nearly 45 million years, hesperornithiforms did well, becoming fairly large in some cases, and some of the smooth-feathered birds appear to have been adapted for the cool waters of high latitudes. Most of the oceans were warm, and reefs remained composed largely of rudists. Some ammonoids went gigantic, their spiral shells reaching from 2 to over 2.5 m (6 to 8 ft) in diameter—notably, there were no supersized spiral-shelled ammonoids in North America's interior seaway—but nautiloids stayed more conventional in size. So did the first squids, some of which were very large, but the similar belemnites continued to be more abundant. Among bony fish the filter-feeding pachycormids remained in force and large, but peculiarly not titanic. Competing with the planktivorous fish were filter-feeding sharks early in the Late Cretaceous, but they too were not especially large and seem to have disappeared later in the subperiod. The first open-water swimming rays showed up. Some of the sleek sharks become quite large, exceeding the size of great whites. But lacking big filter-feeding prey to chomp down on, no predatory shark became titanic.

A big change happened shortly after the start of the Late Cretaceous as the ocean-going reptiles most extremely adapted for the life marine, the ichthyosaurs, quickly declined and then disappeared. The diversity of the group was not high to begin with by this time—all were fast swimmers with long, low snouts with small

or absent teeth—leaving the old and not uniform clade vulnerable to evolutionary liquidation. Competition from similarly sleek teleosts and sharks—which did not need to constantly pop to the surface for oxygen—is a possible cause for their basic decline. Perhaps the platypterygians would have squeaked through if not for the alleged final killing agent, the great Cenomanian-Turonian anoxic event, which occurred over 90 million years ago. Perhaps the worst such crisis of the Jurassic-Cretaceous, this sea disaster was apparently driven by intense ocean floor volcanism in the Caribbean that led to a series of effects involving a bout of excessive carbon dioxide and subsequent ocean heating and acidification that depleted water oxygen levels. That event disrupted marine fauna severely enough to liquidate the last ichthyosaurs, which had ironically all become too fishlike for their own long-term good. Had they been more diverse, including some of the shallow-water species last seen in the Triassic, some may have made it through.

The situation with the plesiosaurs was more complicated. After being in force for 75 million years, the short-necked, deep-water plesiosaurs also went extinct during the Cenomanian-Turonian anoxic event—why they did not make it when the similarly short-necked polycotyliids paddled through is not known; the latter did not become as huge as the plesiosaurs. Meanwhile, the long-necked plesiosaurs really took off via the ultimate in ambush-fishing tactics, elasmosaurs, which took neck elongation to new extremes. One plesiosaur group developed very slender teeth for filter feeding, but plesiosaur skulls were too small for them to evolve the enormous sieving complexes of baleen whales. The chelonioidean turtles thrived, with some being gigantic.



The Late Cretaceous *Protostega*, *Tylosaurus*, *Clidastes*, *Styxosaurus*, and *Dolichorhynchops*

The big evolutionary sea reptile event of the Late Cretaceous was the advent of the fully marine mosasaur lizards. First appearing early in the subperiod, they quickly diversified and became a major portion of oceanic reptiles. The earliest examples were tail-sculling ambush predators of shallow waters, with some latter mosasaurs evolving big, knob-shaped teeth suitable for crushing big ammonoids and other shelled creatures. But a number of them quickly became fast-cruising fusiforms best suited for deeper seas. There is evidence that some mosasaurs spent at least some time in freshwaters, where they would have had to contend with continental and nearshore standard crocodylians, some of which became enormous at 7–8 tonnes, for a rather short period before the last stage of the Cretaceous. The biggest known sea lizards were themselves up to 13 m (43 ft) long but, being fairly slender, maxed out at some 7 tonnes.

Toward the end of the Cretaceous, crocodylians made another partial stab at life in at least brackish if not salty waters via the dyrosaurids, which retained hands and feet and were therefore semimarine. Also appearing were the snakelike dolichosaurs and their close relations the marine snakes, which wiggled into nooks and crannies of reefs—the latter reaching a new climax in the last stages of the Cretaceous—and mangroves in search of their small prey. Heralding a return of small reptiles to high-sodium waters, Mesozoic snakes were nonvenomous.

Over some 180 million years a diverse array of reptiles had been the dominant air-breathing marine tetrapods in every Mesozoic ocean and sea. In the process they often successfully competed with an array of gilled invertebrates and fish. After developing into a remarkable assortment of varying, sometimes weird forms in the Triassic, most of those early evolutionary experiments quickly disappeared. At the other end of the

DNA-driven survival spectrum were the plesiosaurs, which lasted from nearly the beginning of the Age of Sea Reptiles to the end. Others came and usually went over shorter periods. Croc relatives, lizards, and turtles made major moves into the marine realm. Many ichthyosaurs became streamlined, swift sea cruisers as fast as the bony fish, lamnid sharks, and dolphins. A number of plesiosaurs evolved necks of a length never seen in aquatic creatures since, exceeded only by the terrestrial browsing sauropods. Plesiosaurs and ichthyosaurs sometimes evolved into substantial giants. Many sea reptiles, all of which evolved from low-metabolic ectotherms, developed high-metabolic endothermy and in some cases dwelt in chilly polar seas. It was a remarkable evolutionary accomplishment via the semirandom mechanism of bioevolution.

But for all they did, they did not do some things. No marine reptile—and for that matter no Mesozoic shark—happened to go down the selective path to become a pelagic plankton-swilling filter feeder like baleen whales; that was left to the fish of the time. To the best of our knowledge, no swimming reptile became nearly as colossal as the biggest bony fish, sharks, and whales of the Mesozoic or Cenozoic, so the size range from the smallest to largest sea creatures did not match that seen in the seas of the Neogene, including today. Nor did they have bites as powerful as megalodon. Marine reptiles never had brains that were particularly large or sophisticated, and none developed echolocation. No walrus equivalents appeared, and no seal types that were comfortable on beaches.

Near the terminus of the Cretaceous a burst of uplift and mountain building helped drain many of the seaways, including the one that had long split North America in two, although Europe remained a sea-swamped archipelago.

Then things went catastrophically wrong.

EXTINCTION

The mass extinction at the end of the Mesozoic is generally seen as the second most extensive in the earth's history, after the one that ended the Paleozoic. However, the earlier extinction did not entirely exterminate the major groups of large land animals the way this one did, while there were no significant marine tetrapods on hand to be killed off during that earlier crisis. At the end of the Cretaceous on the continents, all dinosaurs except for a small set of advanced birds were destroyed. Mammals squeezed through, as did most reptiles. All pterosaurs, marine and otherwise, were lost.

Matters were similarly grave under the waves. The rudist reefs were so wiped out that the bivalves went entirely extinct. So did the ammonoids and belemnites, while corals, nautiloids, squids, and octopi managed to survive, albeit severely depleted in diversity. A number of bony fish clades were liquidated, including the big filter feeders, which would never return. Sharks did fairly well in comparison, rays less so.

For marine reptiles the result was devastating, yet not an absolute knockout. Plesiosaurs long and short necked, all gone. Same for the mosasaurs. And some of the sea turtles look like they went belly-up. But although the Great Age of Sea Reptiles came to its end, not all marine reptiles bought the aquatic farm. Some of the chelonioidean turtles made it into the Cenozoic. So did the dyrosaurid crocs and palaeophid snakes.

A changing climate has often been offered as the cause of the demise of the sea reptiles and other life. But the climatic shifts near the end of the Cretaceous were neither strong nor greater than those already seen in the Mesozoic, and the world remained largely tropical and subtropical—specifically, sea temperatures were a dash higher than at the end of the Jurassic, when most marine reptiles did just fine and if anything were edging up. Also changing were the seaways, which were withdrawing at the time. That would have cut down on the coastlines and shallow salt waters most favorable to a wide diversity and

EXTINCTION

large populations of marine creatures. But while this might be expected to tamp down marine diversity, with reptiles specialized to live in shallow seaways taking a particular hit, the regression was not exceptional by Mesozoic standards, leaving many thousands of miles of coastline edging the Pacific, Atlantic, and Tethys Oceans and their embayments, sufficient to sustain a healthy aquatic fauna, reptilian and otherwise. Competition from evolving teleosts and sharks may well have played a role in killing off the ichthyosaurs earlier in the Cretaceous, but dramatic innovations that could have turned fish into marine reptile killers were not appearing toward the end of the period. The competition for fish by the marine pteranodonts and birds was too slight to be a problem, and those archosaurs went extinct at the same time in any case. The mammals that would soon dominate the Cenozoic seas made no move to do so in the Mesozoic.

The solar system is a shooting gallery full of large rogue asteroids and comets, to which can be added the occasional interstellar interloper that can create immense destruction. There is widespread but not universal agreement that the Cretaceous-Paleogene (K/Pg) extinction was caused largely or entirely by the impact of at least one meteorite, a mountain-sized object that formed a crater 180 km (over 100 mi) across on the Yucatán peninsula of Mexico. The evidence supports the object being an asteroid rather than a comet, so speculations that a perturbation of the Oort cloud as the solar system traveled through the galaxy and its dark matter are problematic. There is evidence that the big bang occurred in the late spring or early summer. The explosion of 100 teratons surpassed the power of the largest H-bomb detonation by a factor of 20 million and dwarfed the total firepower of the combined nuclear arsenals at the height of the Cold War. The blast and heat generated by the explosion wiped out the fauna in the vicinity, and enormous tsunamis cleared many coastlines—but such waves have negligible impact in deep water. On a wider scale, the cloud of high-velocity debris ejected into space glowed hot as it reentered the atmosphere in the hours after the impact, creating a global pyrosphere that may have been searing enough to bake land animals to death as it ignited planetary wildfires, but this would not have bothered undersea life. More dangerous to the latter was that the initial disaster would have been followed by a solid dust pall that plunged the entire world into a dark, cold winter lasting for years, combined with severe air pollution and acid rain. The severe reduction of sunlight, sharp chilling of the oceans from equator to poles, and ocean acidification that would have hindered the formation of invertebrate shells from calcium carbonate would have crashed the coastal reefs and deep ocean plankton, resulting in a cascade of food pyramid collapses, while many sea creatures would have been unable to function in the suddenly cold waters. The resulting population losses would have left the seas largely barren in short order, less than a year according to some estimates. As the aerial particulates settled, the climate then flipped as enormous amounts of carbon dioxide—released when the impact happened to hit a

tropical marine carbonate platform—created an extreme greenhouse effect that broiled the planet for many thousands of years, further disrupting the life that managed to survive the initial effects. Ironically, had the orbit of the extraterrestrial rock coincided with that of the earth a little earlier or later that day and hit the deep ocean, then the cushioning effect of miles of water would have greatly reduced the effects and probably prevented the global extinction event.

If the impact was the only exceptional big event that occurred in association with the extinction, then the latter could be readily and fully assigned to the former. But unfortunately for the simplicity of the earth's history, there was also another, longer-running matter as the Mesozoic transitioned into the Cenozoic that may have complicated the situation. Another geologically atypical bout of massive volcanism occurred at the end of the Cretaceous, and enormous lava flows covered 1.5 million square km (over 579,000 square mi), a third of the Indian subcontinent, which was sailing across the ocean. It has been proposed that the massive air pollution produced from the repeated supereruptions damaged the global ecosystem so severely in so many ways that marine life populations collapsed in a series of stages, perhaps spanning tens or hundreds of thousands of years. Others disagree. This hypothesis is intriguing because unusually extreme volcanic activity also occurred during the great Permian-Triassic (P/T) extinction, and similar volcanism may have been behind the extinction at the end of the Triassic—as the solar system orbits within the galaxy, it is possible that periodic encounters with a postulated thin plane of dark matter heat the earth's interior enough to initiate such supervolcanism. Although the K/Pg Deccan Traps were being extruded before the Yucatán impact, evidence indicates that the latter—which generated earthquakes of magnitude 9 over most of the globe (11 at the impact site)—may have greatly accelerated the frequency and scale of the eruptions. If this is correct, then the impact was responsible for the extinction not just via its immediate, short-term effects but also by sparking a level of extended supervolcanism that prevented the recovery of sea reptiles. It is also possible that the Yucatán impactor was part of an asteroid set that hit the planet repeatedly, further damaging the biosphere.

In contrast to the question of why most marine reptiles died out is the question of why sea turtles, crocs, and snakes made it through the deadly crisis to the Cenozoic. Perhaps the low energy budgets of the turtles and crocs compared to the higher metabolic rates of plesiosaurs and mosasaurs allowed them to hang on in oceans short of food. On the other hand, the endothermy of some sea reptiles would seem to have been an advantage during the great ocean cool-off immediately after the impact, and such may help explain the survival of the marine snakes. That the dyrosaurids were semiaquatic shoreline forms able to access food resources both on land and in the water looks like it was an advantage. Whatever the reason, maritime reptiles were not totally victimized by the terrible K/Pg catastrophe.

AFTER THE AGE OF SEA REPTILES

On land, the first Age of Reptiles occurred in the late Paleozoic. In the oceans it lasted for nearly the entire Mesozoic. Ironically, a second, brief Age of Reptiles occurred not long after the loss of the dinosaurs, when superboa snakes much larger than any serpents alive today, and big freshwater crocodylians were the only large continental tetrapods, and sea turtles, dyrosaurids, and snakes—some early Cenozoic palaeophids reached 9 m (30 ft)—were the only large marine tetrapods. The sea reptiles swam in seas dominated by sharks, such as the Cannonball Sea, which for a short period partly recapitulated the Cretaceous seaway in the same location from the Arctic to the Dakotas, but without reconnecting with the embayment to the south. Although the above sea reptiles initially did well in the new era, presumably because of the lack of competition from plesiosaurs and mosasaurs, the last of the sea crocs did not last all that long, for reasons that are obscure. Presumably the appearance of marine mammals had something to do with it. But the saltwater turtles did well, enough so that they still grace the oceans, the females hauling themselves onto low-latitude beaches to lay their eggs. A few iguanas are semimarine.

Cenozoic dinosaurs have done fairly well in the marine realm, albeit in the form of flightless birds. Of those, the penguins of the Southern Hemisphere are the most prominent; some extinct examples were over twice as heavy as the biggest alive today. In the Northern Hemisphere the flightless seabirds were auks, which were driven to extinction in the 1800s. Other water bird groups have spun off neoflightless examples, such as ducks and cormorants.

The total absence of classic dinosaurs aside from birds, and the sharp decline of marine reptiles freed up space for mammals to evolve into similarly large animals that dominated the Cenozoic continents, and from there the oceans, although it took about two dozen million years for therians to fully begin to do so. Pinnipeds are marine carnivora the same way that mosasaurs were oceanic lizards. The sluggish sirenians seem to be phylogenetically connected to proboscideans. Cetaceans are artiodactyls probably related to the semiaquatic hippos. Some of the early whales, the remarkably serpentine basilosaurs particularly, had a rather sea reptile look to them—which is why they were errantly tagged with a reptilian name. Once the whale clan went fully marine with true flippers, some of the Paleogene basilosaurs became gigantic very rapidly, about as fast as the ichthyosaurs had back in the Triassic. Some smaller cetaceans mimicked highly fusiform teleosts, sharks, and ichthyosaurs in evolving hydrodynamically optimized bodies, with orcas being the largest highly fusiform predators in modern seas. A few whales, such as the sperm whale, became gigantic deep-diving hunters of squid and fish. Livyatans, close relatives of sperm whales, sported large teeth that allowed them to attack other big whales and sharks; these powerful sonar-deploying marine mammals easily outclassed the biggest-headed oceanic reptiles in killing capacity. Other cetacean giants traded teeth for baleen to become filter feeders. These did not, however, become really gargantuan until the recent severe ocean cooling of

the ice age. That created the powerful ocean currents underlying the unusually high plankton-based food production that has allowed the evolution of the bowhead, fin, and blue megawhales. The blue whale approaches 30 m (100 ft) and 200 tonnes, making it the biggest beast in all of the earth's history, with a low likelihood that any animals have been as large—its mass easily exceeds that of even the heftiest known early ichthyosaurs and pliosauroids by up to tenfold. Oceans have never before seen the minimum-maximum size range seen in these times. If ice age conditions are responsible for the existence of supersized whales, then when the current ice age comes to a permanent end, the greatest of whales may disappear from under the waves. In that case the megawhales of the Pleistocene are not a grand evolutionary culmination, but a temporary product of natural selection.

It was not only marine mammals that benefited from the absence of most sea reptiles. So did sharks, in three flavors. In one expression, a number of shark clades evolved into open-ocean filter feeders, of which the living whale shark is the largest known example. Meanwhile another line developed, the titanic, blade-toothed megalodon of the late Cenozoic. At perhaps 15 m (50 ft) and 30 tonnes and probably much more when normal size variation is considered, it was among the three biggest fish, the others being the whale shark and the Jurassic *Leedsichthys*. Megalodon is often restored looking like a colossal lamnid with compact thunniform proportions and a symmetrical top-to-bottom lunate crescent tail, like an overgrown great white. But it apparently was not a member of that clade—the only thunniform sharks are lamnids—and probably had a more archaic, slender form with a longer upper tail lobe less adapted for speed. It is not possible to be entirely certain because the nonbony skeleton is not preserved well enough to provide direct evidence, but no other ocean giants sport an extremely streamlined body form, the largest thunniforms being 9 m (30 ft) orcas. This shark at least matched the livyatans in whale-killing power. It is likely that the bevy of slow, vulnerable, medium-sized baleen whales that dominated the oceans of most of the later Cenozoic made megalodon possible. Megalodon went extinct just before the ice age, perhaps because the oceans were becoming too cold, and/or the new supersized rorqual whales of the ice age were too big and fast for the not very speedy megalodon to readily hunt. Not nearly as big but much swifter were the thunniform lamnid sharks, which first show up in the early Cenozoic.

Chelonioidean sea turtles remain a significant, albeit not major, component of ocean faunas. Most are hard-shelled cheloniids limited to warm waters. But the big leatherback is an unshelled dermochelyid reminiscent of some of the lightly armored chelonioideans of the Cretaceous. It can dwell in chilly high-latitude salt waters, and at over two-thirds of a tonne it is the largest living marine reptile, although the biggest coastal crocodiles reach a tonne. As for sea snakes, the fairly big palaeophids went extinct in the early Cenozoic, and their small but venomous hydrophiine relations are common in tropical waters.

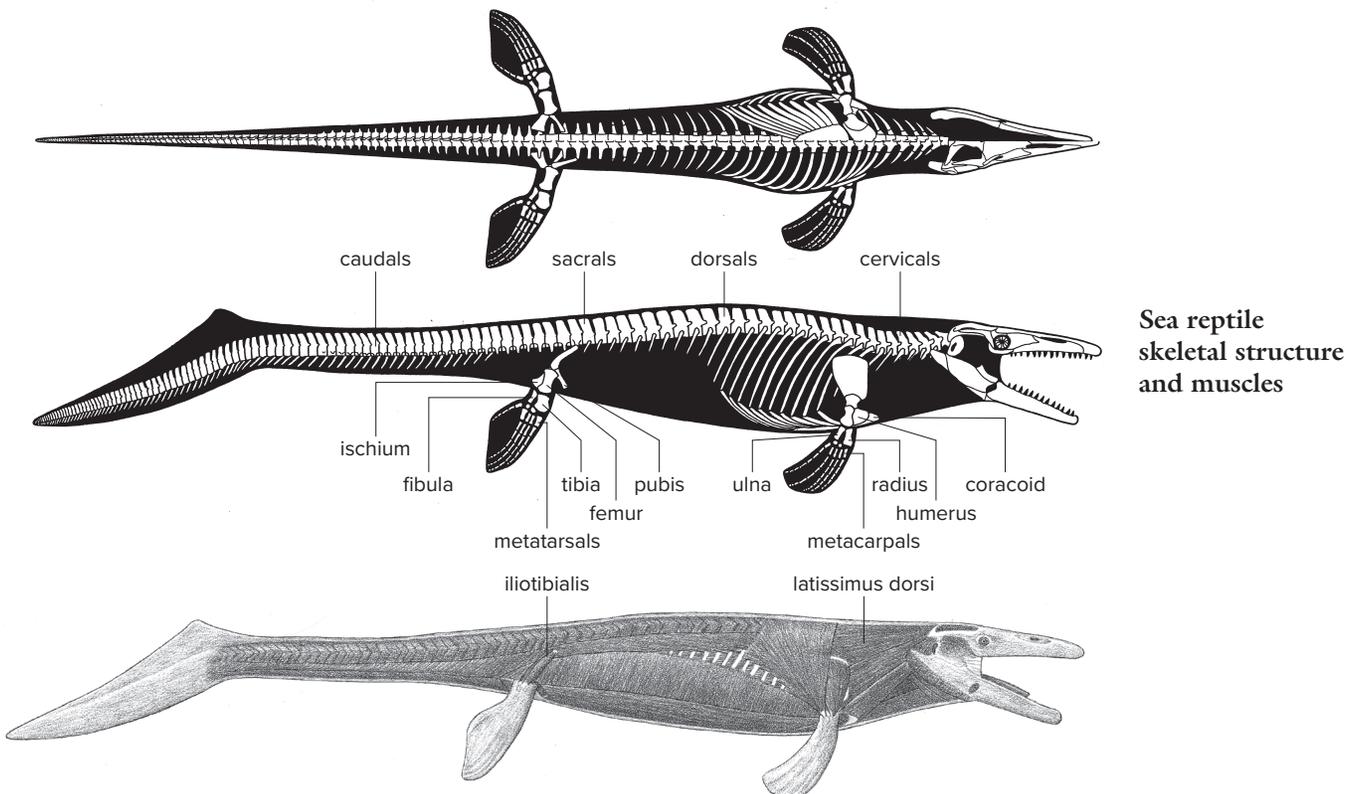
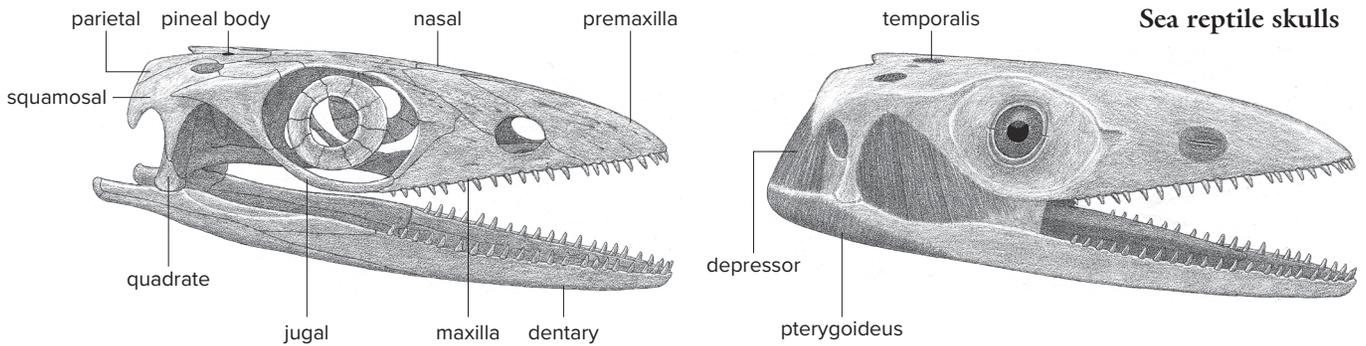
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General Anatomy

Most Mesozoic seagoing reptiles are known from their bones alone, but we know a surprising amount about their body soft tissues from a small but quickly growing collection of fossils.

Because Mesozoic marine reptiles consisted of a large variety of often distantly related groups, they did not share a substantial set of detailed anatomical features the way close relations do, such as dinosaurs or mammals. What they did share is the following. All were hydrodynamically streamlined, albeit to varying degrees. In nearly all cases the ribs were swept strongly down and back, whether articulated specimens are preserved on their sides or flattened top to bottom; the infrequent exceptions are probably

the result of bloating of the carcass. The often missed back-swept orientation had the effect of making the body less deep, which reduced frontal area—some restorations show the ribs directed vertically, resulting in implausibly deep, nonhydrodynamic chests. Exceptions include turtles and reptiles with similarly very broad-carapaced trunks whose ribs were directed strongly to the sides, except at the rear of the trunk in many cases. Body and tail flexion, if it existed, was lateral as in fish rather than vertical as it usually is in mammals, and tail fins if present were vertical, not horizontal as in cetaceans—plesiosaur tails may be an exception to this pattern. Because they did not bear weight in 1G, connections between the shoulder/pelvic girdles and the ribcage/vertebral column were reduced or eliminated to varying degrees.



Limbs were stiffened by different amounts along their length. The area of the hands and feet or flippers was significantly enlarged by soft tissues, at least by webbing between the digits, and by expansion of the trailing edge and length of fully developed flippers with rubbery soft tissues. In those cases in which the lower limbs became flippers, the outer bones became numerous and more uniform and tended to curve backward, giving the flippers an often back-swept, hydrodynamic wing configuration. Skeletons were heavily constructed and bones internally dense; this pachyostosis made the animals at least as dense as or a tad denser than water when the lungs were not fully inflated. Being reptiles, none bore any form of external insulation similar to fur or feathers. Teeth often had bulbous roots. Brains were small and not highly sophisticated. Sea reptile sensory systems were usually vision dominated; when eyeballs were internally supported by bony scleral rings, which helped prevent the large organs from being distorted by the flow of water, the rings were rather flattened, helping to produce the flat eyeball shape optimal for underwater vision. There is no evidence that any marine reptile was capable of echolocation, although low-power electrical sensors and pressure receptors appear to have been present in some cases. Notably—and perplexingly—none had nostrils placed high on top of the head like those of cetaceans.

Thalattosaurs, Helveticosaurs, Atopodontatians, Basal Placodontiformes and Hupehsuchians, Pachypleurosaurs, Aigialosaurs, and Dolichosaurs

A number of nearshore marine reptiles not closely related to one another possessed generally lizard-like forms, and some of the last examples were actually aquatic lizards. These low-grade, paddle-limbed swimmers represented groups in the early stages of adaptation for marine life. Armor if present was modest. Necks were not especially long and were sometimes very short. Trunks were laterally flexible, and rows of belly gastralata when present were simple, swept back, and very numerous and ranged from slender to massive. Tails were long, sometimes very much so, and the aft section straight. Limbs, although stiffened and webbed paddles, were not true flippers. Heads were never extremely large and were usually moderate in size, sometimes quite small. Most sported generalized lizard-like heads with pointed teeth probably covered by lips when the mouth was closed, but basal placodontiformes had stout heads with flattened crushing teeth, atopodontatians were hammerheads with delicate raking teeth, and hupehsuchians evolved a variety of head shapes including flat swords and duckbills; teeth were reduced or lost in some. Most skulls were akinetic in that they were solidly built and lacked mobile articulations aside from the jaw joint, the exception being the lizard aigialosaurs and dolichosaurs, which had the flexible skulls typical of the group, as further discussed concerning their mosasaur relations below.

Mosasaurus

The armor-free body form of mosasaurs was basically that of somewhat streamlined monitor lizards with flippers instead of legs, and hydrodynamically flattened rather than whip tails. Heads were of moderate size, elongated, subtriangular, and about as broad as deep, with a large snout. Fairly large nostrils were placed on top of the snout, well aft of its tip. The orbits, moderately large and with scleral rings, faced sideways. The quadrate, on which the lower jaw hinged, was modified into a semicircular bone with a rim supporting an eardrum that was ossified to resist changing water pressure. Space for jaw muscles was large, with similarly large upward-facing temporal openings to accommodate them. Mosasaurs possessed the paired vomeronasal structures in the front roofs of their mouths that are associated with forked tongues in some lizards and snakes. The tongue was probably robust, with short, broad forks, rather than the long, slender organ seen flicking out of the mouths of monitors. Lower jaws were moderately deep from midlength aft, and a big coronoid process increased the leverage of the jaw-closing muscles. Teeth were vertical, usually conical spikes atop bulbous roots, or sometimes blunt, forming regular rows along most of the length of the jaws. Teeth were also present on the midroof of the mouth, as in some other lizards, but not monitors. As in modern predaceous lizards, the lips may have covered the teeth even when the mouth was open. On the other hand, such an arrangement may have interfered with snagging slippery prey, so it is possible that the teeth were more exposed.

Like those of the lizards that they were, mosasaur skulls were kinetic. The snout could be elevated around a transverse line of flexion on top of the skull at the aft end of the orbit, an action facilitated by the loss of the bar below the lateral temporal fenestra. The latter lizard feature also allowed the lower end of the quadrate to rock back and forth and somewhat sideways, allowing the lower jaw to do the same thing relative to the main skull. The lower jaw was hinged at midlength to allow the dentary to drop and bow out. These features allowed mosasaurs to enlarge their mouths to better swallow food items, but some species lost kinesis to varying degrees.

Stout, short mosasaur necks had low mobility and blended smoothly into the body for maximal streamlining. Trunks were always streamlined and narrow, length varied from moderate to long, and depth was shallow. Trunks were laterally flexible, gastralata were absent, and a rib-free lumbar region was present. Tails were long, consisting of numerous vertebrae, so they were flexible, especially laterally. The aft portion of the tail was downcurved, sometimes fairly strongly via a kink, and a few fossil specimens show an upper fluke anchored atop the kink. The pelvis was barely attached to the vertebrae, and it and the shoulder girdles were usually small, indicating that only modest muscles operated the maneuvering flippers, which were short and rounded, with the aft flipper often more reduced than the fore—in a few examples, bigger girdles suggest that the flippers provided some propulsive thrust. Although clawless, the digits

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remained distinct rather than forming pavements, and the outer digits diverged from the others to broaden the flippers.

In at least some mosasaurs the skin consisted of small, well-ordered, diamond-shaped scales, which were keeled fore and aft on top of the body, and smoother on the underside. These overlaid a sheath of fat deposits that hydrodynamically streamlined the animals.

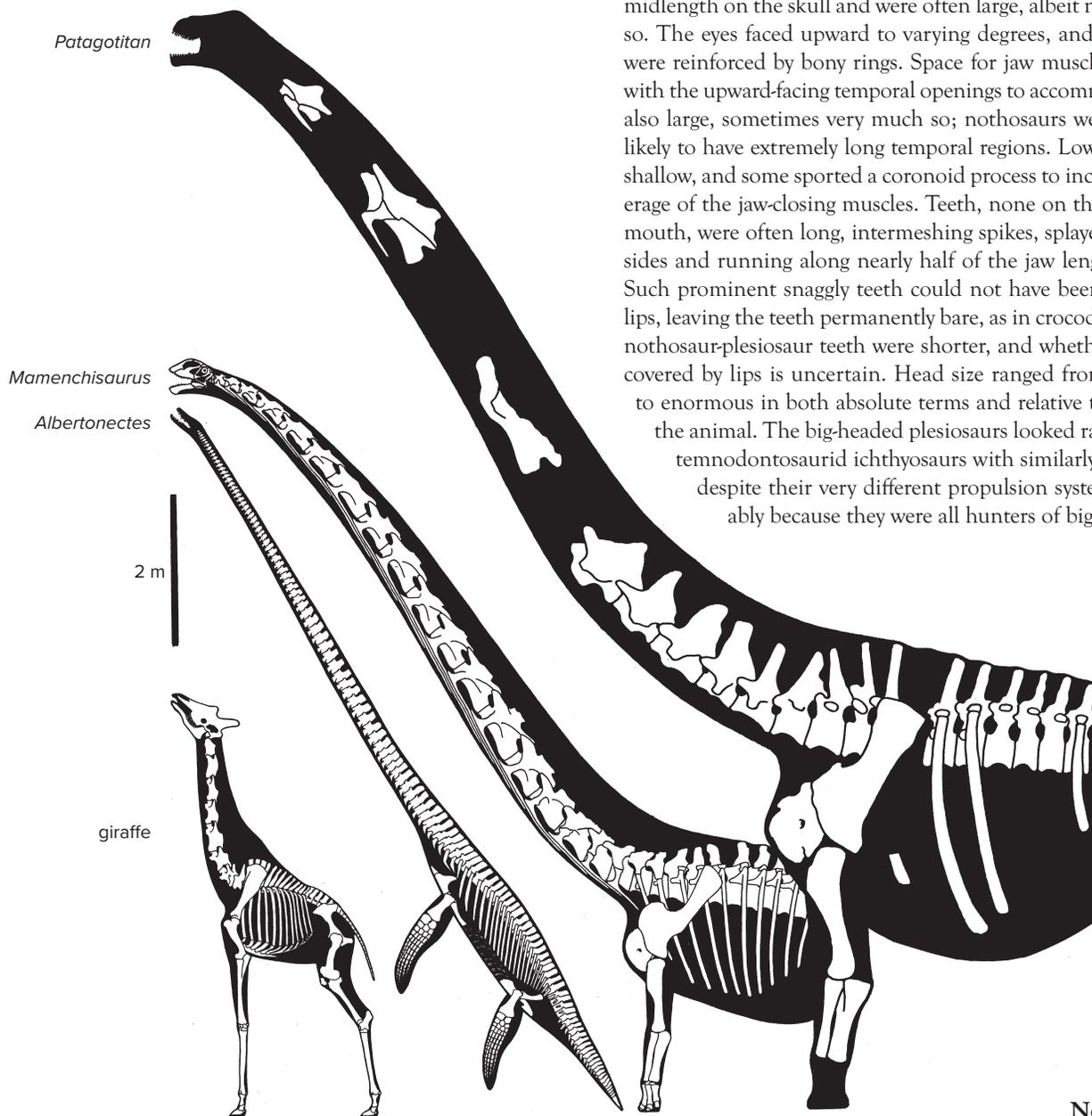
Marine Snakes

Trunks became hyperelongated, very slender, and superflexible via extremely high numbers of vertebrae sporting short ribs.

Tails have not been particularly long and are straight tipped. Girdles and limbs are severely reduced if not absent. Heads have been small, and skulls delicately boned and hyperkinetic. Teeth, some on the roof of the mouth, are strongly arched blades covered by lips. Tongues are forked and slender.

Plesiosaurs et al.

The heads of plesiosaurs and the earlier nothosaurs and pistosaurs were low, subtriangular, and solidly akinetic. Plesiosaur heads tended to be broader than those of nothosaurs. Plesiosaur nostrils were small and immediately in front of the orbits, more so in nothosaurs. The orbits in these groups were placed at about midlength on the skull and were often large, albeit not extremely so. The eyes faced upward to varying degrees, and the eyeballs were reinforced by bony rings. Space for jaw muscles was large, with the upward-facing temporal openings to accommodate them also large, sometimes very much so; nothosaurs were especially likely to have extremely long temporal regions. Lower jaws were shallow, and some sported a coronoid process to increase the leverage of the jaw-closing muscles. Teeth, none on the roof of the mouth, were often long, intermeshing spikes, splayed out to the sides and running along nearly half of the jaw length or more. Such prominent snaggly teeth could not have been covered by lips, leaving the teeth permanently bare, as in crocodylians. Some nothosaur-plesiosaur teeth were shorter, and whether they were covered by lips is uncertain. Head size ranged from very small to enormous in both absolute terms and relative to the rest of the animal. The big-headed plesiosaurs looked rather like the temnodontosaurid ichthyosaurs with similarly large crania despite their very different propulsion systems, presumably because they were all hunters of big prey.



Neck lengths

Trunks were rather short, low, broad, and stiffly constructed. In the shoulder girdle the scapula blade was short and overlapped the chest ribs little if at all. The chest sternals were large plates suitable for anchoring powerful propulsive arm muscles. The same was true for the lower pelvic elements in plesiosaurs, and for the gastralia that lined the belly between the girdles; in plesiosaurs, although the gastralia were not numerous, they were unusually complex and massively constructed. Most of their shafts ran straight across, but toward their lateral tips the gastralia curved strongly backward, a detail rarely shown in restorations. The pelvis was attached to the sacral vertebrae, albeit rather weakly. Nothosaurs lacked fully developed flippers. Plesiosaur flippers were long and narrow, with the humerus and femur fairly long. The fore and aft flippers were fairly similar in size, although sometimes one was somewhat larger than the other. Plesiosaur digits evolved into near pavements made up of rows of numerous, well-ossified elements. It was common for some of those elements to have odd, deep indentations on their leading or trailing edges.

Tails were rather short and stout. A single flattened specimen indicates that a small tail-tip fin was present in at least some plesiosaurs. This has usually been restored as a vertical rudder under the presumption that the tail was laterally flexible. But some propose that the articulation of the tail vertebrae show that the tail was—atypically for diapsids—most flexible vertically, and the tail was correspondingly tipped with horizontal flukes for auxiliary power production. Whether surfaces so much smaller than the flippers would be of significant propulsive use is questionable, but the situation is not resolvable with the limited data on hand.

Nothosaur and plesiosaur necks were moderate in length. Plesiosaur necks were slightly to extremely elongated. Yet none of the cervical vertebrae were long; the great length was entirely the result of the large number of cervicals, up to 75 in the longest-necked taxa. No other vertebrate has anywhere close to as many neck elements—birds have 25 at most, known sauropod dinosaurs had up to 19, giraffes just 7. Neck flexion is difficult to estimate, in part because the cartilage between the cervicals has been lost. Modern restorations indicate that long plesiosaur necks were moderately flexible, much less so than the vertebral series of snakes, but enough to allow the head to reach far from the center line in all directions. There appear to be differences between taxa, with some more able to reach laterally than vertically, others the reverse, and others about the same in all directions. It is possible that the necks of at least some plesiosaurs naturally articulated in a gentle S curve.

Fossils indicate that plesiosaur skin was smooth and overlay a modest layer of blubber that helped smooth out the body form for better streamlining.

Tanystropheids

While the very long necks of plesiosaurs were made up of many dozens of short vertebrae, the similarly extremely long necks of tanystropheids were elongated largely by lengthening of the

cervicals. The one known marine tanystropheid, for example, had just a little over two dozen neck bones. So tanystropheid necks were not as flexible as those of elasmosaurs, all the less so because the former had very long, overlapping cervical rib rods. The heads of salt water-loving tanystropheids were small and had sharp teeth, some of them on the roof of the mouth, and their rather elongated bodies, tails, and paddle limbs were conventional in form.

Ichthyosaurs

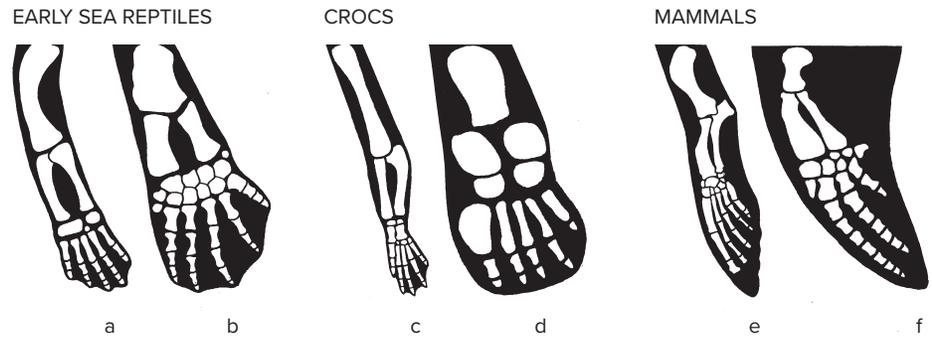
Ichthyosaurs were the most fish- and dolphin-like of the marine reptiles. Heads were usually large and elongated, especially the shallow and narrow snout, which flared out to the broader and deeper rear of the head. Skulls were akinetic. Nostrils, often surprisingly small, were set not far ahead of the orbits, which were placed well aft on the skull. Facing sideways and a little forward, the orbits were large to enormous and were nearly filled by big sclerotic rings that in some cases supported the largest known eyes, at least matching those of giant squid. Space for jaw muscles and the temporal openings to accommodate them were moderately large. Lower jaws were rather shallow, and coronoid processes were absent. There were no teeth on the roof of the mouth, and those lining the jaws tended to be vertical, short, and conical, forming long, regular rows along most of the length of the jaws in most cases—in a few early taxa, the aft teeth were blunt knobs for crunching shellfish. The teeth were probably covered by lizard-like lips to optimize streamlining, as in cetaceans. Sporting mammalian facial muscles, the latter can pull back their lips to bare their teeth when the mouth is open, but the reptilian ichthyosaurs, lacking such lip mobility, could not do so. Some long-jawed ichthyosaurs had very reduced teeth, to the degree that they were sometimes not functional. Ichthyosaur tooth roots were sometimes bulbous, sometimes not. A few early examples had smaller, shorter, more triangular heads with few or no teeth and appear adapted for suction feeding.

Stout and quite short, the back of the head being only a little forward of the shoulder girdle in the manner of fish, sharks, and cetaceans, inflexible ichthyosaur necks blended smoothly into the body for maximal drag minimization. Trunks were always well streamlined and never broader than deep, length varied from moderate to quite compact, and depth from somewhat shallow to fairly deep; many species sported highly hydrodynamic proportions. Because vertebral counts were very high, the trunk was laterally flexible. Always present, gastralia were simple, slender, swept back, and usually limited to the chest in highly evolved forms. The spindle-shaped tails were moderate in length. Consisting of numerous vertebrae, the tails were flexible, especially laterally as per the reptilian norm. The last portion of the tail was downcurved. In those with a shallow kink, the vertebrae at that location were tall and helped support a modest dorsal tail fluke. In those with a sharp kink, the vertebrae were slender and did not do much to support the large lower

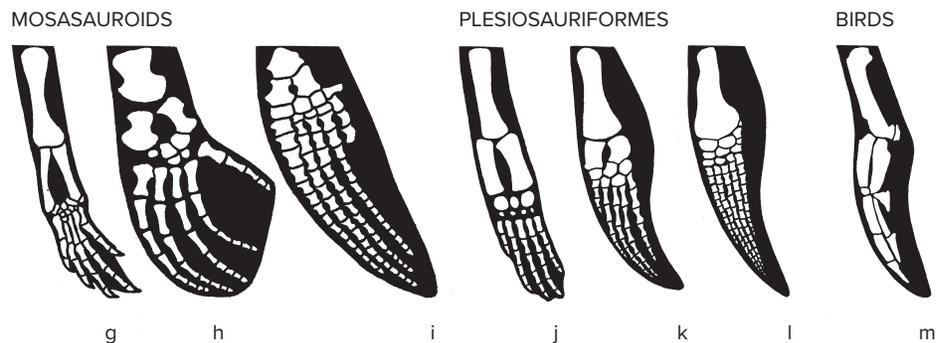
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Forepaddles and forefins of sea marine vertebrates

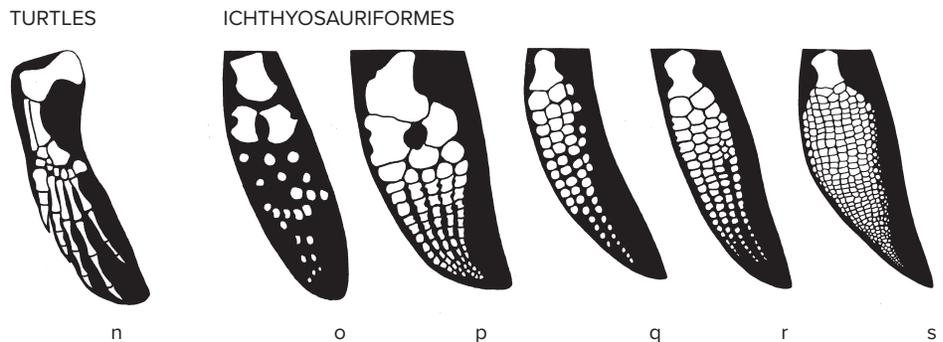
- a *Paraplacodus*
- b *Eretmorhipis*
- c *Macrospondylus*
- d *Cricosaurus*
- e sea lion
- f dolphin



- g *Aigialosaurus*
- h *Platecarpus*
- i *Plotosaurus*
- j *Pistosaurus*
- k *Archaeonectrus*
- l *Dolichorhynchops*
- m penguin



- n *Rhinochelys*
- o *Sclerocormus*
- p *Barracudasauroides*
- q *Eurhinosaurus*
- r *Stenopterygius*
- s *Platypterygius*



flake. Shoulder and pelvic girdles were small, and the latter were often not attached to the vertebral column, indicating that only modest muscles operated the flippers for stability and steering; flippers were usually rather short and rounded, with the aft flipper often especially reduced—it is interesting that these reptiles retained the aft set of fins like sharks, but unlike cetaceans, though it is not known why. The forefins of a variety of ichthyosaurs were quite large, presumably an adaptation for high maneuverability—the extralarge forefins of humpback whales give them exceptional turning performance, which they utilize while feeding and displaying. A few advanced ichthyosaurs had remarkably small flippers, but it is not obvious why. The bones from the elbow out tended to become increasingly numerous and uniform semihexagons, forming a tightly interlocking pavement into which even the radius and ulna were subsumed; the result was the most highly evolved flipper among all marine tetrapods. At the other extreme, the outer flipper bones of some ichthyosaurs, especially early examples, were poorly ossified for

obscure reasons, perhaps to increase the flexibility of the outer fins. Quite commonly, some of the elements below the elbow had the functionally mysterious strong indentations on their leading or trailing edges also seen in many plesiosaurs.

An example of preserved skin indicates that ichthyosaur integument consisted of very small, fine scales that produced a slick epidermal texture. Preserved soft tissue profiles indicate that the body was ensheathed in a smooth, contoured, hydrodynamic surface, created in part by a modest layer of blubber. Some specimens show that the upper, nonskeletal tail fin lobe was low in those examples with a shallow tail downturn, forming an asymmetrical tail. In those with a sharply downward-kinked lower tail, the upper lobe was equally prominent, forming a symmetrical, half-moon-shaped tail fin. At least one specimen of a lunate-tailed species demonstrates the presence of a prominent, triangular dorsal fin in the manner of sharks and dolphins. It has recently been claimed that the same is preserved in an early basal species, but the preservation is poorer, so that conclusion is not yet certain.

Marine Crocs

The head, trunk, and tail form of initial armored examples was not dramatically different from that of freshwater examples, except that the arms were greatly reduced to the point of being of little locomotory use in water or on land, and the hindlimbs were somewhat more paddle-like. More marine-adapted sea crocs lost the armor; the arms and hands were severely reduced, leaving them much smaller than the hindlimbs; the lower limbs were expanded and flattened into clawless steering paddles, although the digits remained separate; and the end of the tail was strongly kinked downward, indicating the presence of a prominent dorsal tail fluke. The solidly constructed, akinetic heads were large, with long snouts that ranged from fairly to very slender and sported typically crocodilian conical teeth anchored on bulbous roots, with stout to slender crowns; there are no teeth on the roof of the mouth in crocs. Eyes were of medium size, and bony supporting rings were present in some cases. The gasteralia were slender, swept backward, and restricted to the belly region; in the pelvis, which was attached to the sacrum, the pubis was mobile.

Turtle-like Placodonts and Saurosphargids

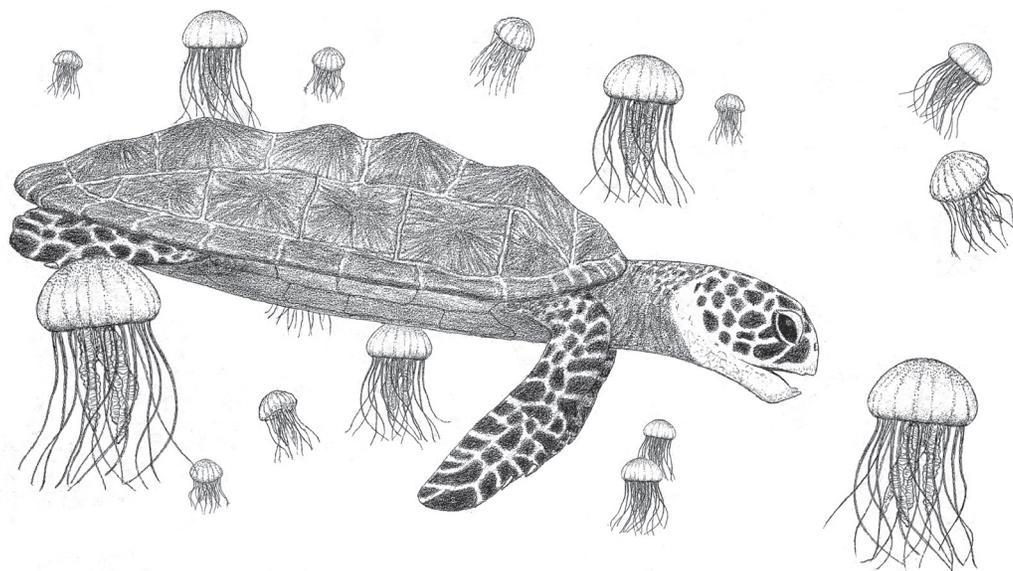
The cyamodontoid placodonts, and the similar but not closely related saurosphargids, sported shortened, dramatically broadened trunks that formed a shallow, turtle-style armored carapace, supported by extralong ribs that were not swept backward. In the cyamodonts the carapace was often split into a main trunk unit and a smaller one over the pelvis. Tails were moderate in proportion, armored, and straight tipped. Paddle limbs were never full flippers and in some cases were quite small. Most cyamodontoids had stout heads with pavement teeth for crushing

or pulping as in the more basal, barrel-trunked placodonts, but a few had smaller heads that apparently bore baleen-like filters.

Marine Turtles

The fully oceanic turtles of the Mesozoic were little different from those that grace our modern seas. Heads have been medium sized, fairly short, broad, deep, subtriangular, solidly built, and thoroughly akinetic. Teeth are absent, and beaks parrot-like. Fairly large nostrils are set fairly high on the front of the snout. Orbits are fairly large, set well forward, and face sideways and a little forward, and scleral rings are absent. Space for jaw muscles qualifies as large, but there are no skull openings for them. Large embayments at the rear of the skull have been separated by a prominent midline plate. Lower jaws range from shallow to moderately deep. One type of Cretaceous chelonioidean had a highly modified skull apparently adapted for sucking up food.

Marine turtles' necks have been quite short with very limited flexibility, as the head cannot not be pulled back into the carapace. The trunks are very broad and shallow, with a streamlined teardrop shape in lateral view. The top is more arced than the flatter underside, giving the carapace a winglike shape that may produce some hydrodynamic lift. Most Cretaceous chelonioideans did not have full hard-shelled carapaces; a bony structure of struts and partial plates was covered by leathery tissue. The shoulder girdle is encased within the ribcage, in which only the aft ribs have been swept backward. Tails are short. Flippers retain well-developed lower limb bones, except that the bones of the outer hindfins are poorly ossified in a few cases. The quite large, elegant foreflippers arc forward out from the carapace and then sweep out and backward. The smaller, broader aft flippers are directed somewhat backward. Foreflippers have always had a couple of exposed claws on the leading edge.



Santanachelys and jellyfish

BIOLOGY

Swimming

Water is close to 800 times denser than air at sea level. Increasing depth does not appreciably increase water density. Making water either warmer or cooler than about 4°C (40°F) reduces density, albeit negligibly. Salt is over three times denser than water—salt crystals sink when put in water—and seawater is about 3.5 percent salt, so salty seawater is 2 percent denser than fresh. Moving through water, whether fresh or salty, has numerous advantages over both ground locomotion and powered flying. One is that waterborne creatures, being similar in density to water, do not have to constantly work hard against the 1G pull of the entire planet, as do animals that walk, run, or fly by flapping. Another is that water is both slippery and, being dense, provides powerful propulsive force when accelerated aft from an object specialized to do so—as opposed to an unstreamlined swimming land tetrapod that lacks a specialized propulsive body or appendages. Depending on how streamlined a swimmer is, moving an animal of a given size a given distance through water costs three to a dozen times less than moving the same distance on land; the lower figure applies to, say, a crocodilian, the higher values to a swordfish, tuna, or dolphin. The advantage for swimmers applies at low to modest speeds. On land, the amount of energy expended per unit distance traveled is about the same regardless of speed—you do not burn far more calories running a mile than walking the same distance. Swimming is quite different because at greater speeds, hydrodynamic drag becomes more of a factor. Swimming slowly is very energy efficient per unit distance traveled. As speed increases, the cost rises substantially—the range of an *Iowa*-class battleship at 12 kts is 18,000 nautical miles, and at 30 kts just 5,300. Compared to flying, swimming is as much as four times more efficient over a given distance. The exception is soaring, which can be nearly energy-free under ideal circumstances, including the wave and dynamic soaring practiced by large oceanic aerialists. On the other hand, swimmers can use ocean currents to move across entire oceans without cost, if currents are going where they need to go, and they can afford the time. The energy efficiency of swimming and drifting allows marine creatures to readily migrate very long distances much more easily than land animals, for which migrations are arduous and dangerous work, and about as easily as fliers, which can also move great distances in a few weeks or months.

Swimming fully underwater is markedly more efficient than doing so constantly at the surface. An object moving at the surface generates a wake of large waves, of which the bow wave is the largest. Because the waves are little hills of water produced against gravity, they require expensive energy to generate. Also, the big bow wave causes the object to tilt up and forward, meaning the object is constantly trying to climb over its own bow wake against 1G. Remaining underwater eliminates all these problems, so well-streamlined submarines need about half as much power to move at a given speed underwater as they do on the surface, or compared to surface vessels of similar size.

Needing to come to the surface frequently to breathe therefore has a cost for swimming tetrapods compared to gill-breathing fish. This is particularly true for slow swimmers. Above around 10 kts efficiency can be improved by porpoising—periodically leaping at a shallow angle into the air. That works because air produces so little drag compared to moving through water over the same distance that it overcomes the cost of leaping against 1G. Porpoising can reduce swimming costs by a third and is especially efficacious for marine tetrapods that have to breathe air in any case; plus it may confuse predators, so tetrapods that can do so may as well porpoise when cruising from one place to another. Because their bodies undulate up and down anyway, dolphins and porpoises are ideally suited for porpoising, which is why the action is named after the latter. Only small and medium-sized fast swimmers can truly porpoise swim; marine turtles cannot do it, nor can large whales.

Below the surface, the deeper a fast-moving aquatic object is, the better it is for energy savings. When a propeller spins at high rpms, or a flipper or fluke flaps fast, there is a serious risk of cavitation. That occurs when an object moves through water at such high speed that the mass inertia of the dense water prevents it from closing immediately back together, creating a near-vacuum bubble. This is an advantage for flat-nosed, super-fast underwater missile-torpedoes, which streak at rocket speeds through their own, nearly friction-free bubbles. But the vacuum bubbles only degrade the hydrodynamics of thrust-producing blades, cutting back on top speed while costing considerable extra energy. Adding salt to the hydrodynamic wound is that cavitation bubbles, because they are empty items surrounded by dense water, quickly collapse with intense energy, enough to damage metal screws, as well as the fins and flippers of fast marine animals. The higher the water pressure, the harder it is for vacuum cavitation bubbles to form, and the deeper the water, the higher the pressure, so cavitation at speed can be minimized or eliminated when diving deep. Submarines can run deep to evade the problem, and so can fast swimmers.

When a body is entirely underwater, energy expenditure can be reduced by alternating bouts of propulsion with passive gliding. Yet another way to boost energy efficiency is to ride the bow wake of a much larger object, like a surfer on a wave. This is most famously practiced by dolphins that take advantage of the front wave of a ship, often by porpoising. It can also be done with a completely submerged big swimmer.

There are two primary ways for animals to power swim. One is axial undulation, using the body and/or tail to ripple through the water; this is practiced by most fish, swimming lizards and crocs, and cetaceans. The other is appendicular action, using fins as the primary propulsors. A number of fish do so, especially when moving slowly, and sea turtles and penguins are flipper flappers. Of the two types, undulations can have the advantage of being more energy efficient. The same body motions that generate drag also produce thrust, the latter more than canceling the former out—in effect the swimmer partly worms

its way through the water. Swimming by fins and flippers alone means that the entire inert body is just producing drag. True flippers are limbs in which all the bones and soft tissues are highly flattened and joined to form a single, fully streamlined fin in which the only joint that is actively and highly mobile is the shoulder or hip joint.

Because a major source of drag is friction along the surface of the skin, fluid flow should ideally be smoothly laminar. If the flow is turbulent, then drag increases. It might seem that the best way to minimize the frictional drag of skin is for it to simply be as smooth and slick as possible, in order to maximize laminar flow. This can work on leading sections of bodies and fins, but flow always goes turbulent over most of the aft of a body at high speeds. In that case the goal is to minimize drag by keeping the boundary layer of slow, calmly moving fluid that directly adheres to the skin from breaking away. Sharks accomplish this with very small skin denticles that are oriented with the pointed tips aft—the skin feels smooth if stroked front to back, but the opposite direction is so rough that shark skin is used as a form of fine-grained sandpaper. Dolphin skin takes the smooth and slippery way toward drag minimization.

If we assume that the shape of a hydrodynamic object remains identical, and so does its power-to-mass ratio, bigger is better for speed and for energy efficiency. Driven by 210,000-horsepower steam turbines, the 265 m (870 ft), 57,000 tonne *Iowa*-class battleships could do 32 kts. If one sails a 1 m long, 3 kg (3.3 ft, 6.6 lb) scale model of an *Iowa* with a scale-equivalent motor power of a tenth of a horsepower, then a walking person can easily keep pace with the model as it parallels the shoreline. The actual battleship had a cruising range of thousands of miles, the scale model only a few miles. Although destroyers can match the speed of much larger cruisers, battleships, and carriers, they have to be much more streamlined and higher powered relative to their size to do so, and they have shorter cruising range, to the point that destroyers often refuel from the bigger ships they escort. When vessels of varying size compete in a race, the larger ones have to be handicapped by a speed/length formula that gives the smaller boats a fair chance. Because of the size factor, the biggest sea creatures can move at a good clip—giant rorquals can do 45 km/h (30 kts), so fast that they could not be hunted and harpooned until the advent of powered vessels. But maximum muscle power cannot scale in direct correspondence to total body mass, so medium size is optimal for swimming animal speed, which is over half again as fast as that of rorquals. On the other hand, the biggest living swimmers do not possess the optimal shape for achieving the highest possible speeds, so it is possible that megaswimmers could have been faster than the biggest modern sharks and whales.

Fish are often up to 70 percent swimming muscles, which is one reason they are often good eaters; dolphins are up to 60 percent. Muscles come in two general types. White-fibered muscles are specialized to produce short bursts of very intense anaerobic power, so they are best suited for sprints but cannot sustain high

levels of activity over long periods. These are the muscles found in many fish, especially freshwater, that do not spend much time cruising about but need to be able to suddenly dash away from predators or toward prey. Colored by myoglobin, aerobic-dominant red-fibered muscles are able to produce high levels of power that, although not as extreme as what is possible with anaerobiosis, can be sustained over long periods. Persistent cruising at high speeds requires that up to 40 percent of body mass be red muscles. This is why some market fish, such as certain tuna, feature red meat. Muscles can and often do exhibit gradations between extremes. Some fish have only white-fibered muscles if they do not need to sustain speed, but no aquatic vertebrate has an entirely red musculature because the anaerobic burst of power from white muscles is occasionally useful to all swimmers.

The fastest swimmers can achieve very high speeds. Just how high is not certain because it is not possible to accurately measure and time the movement of large aquatic creatures moving very fast over substantial distances. Speeds around 80 km/h (50 kts) are apparently achievable by billfish and tuna among bony fish, as well as lamnid sharks and some dolphins. Claims of higher speeds are problematic—it is questionable whether the muscle power is available relative to total drag even when streamlining and muscle power burst are maximal—although some claims apply to porpoising fish. Not surprisingly, the fastest speeds are attributed to axial undulators, which can put so much of their body into it. The speed of the fastest swimmers is broadly comparable to that of animals on land, while the fastest level-flying birds such as pigeons and those with falcon- and swallow-type bodies are about twice as swift.

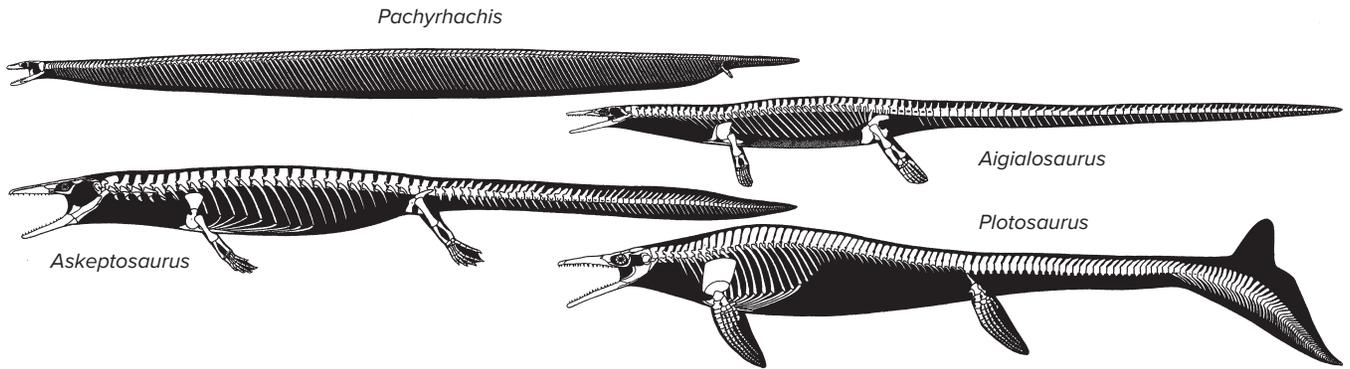
Hydrodynamic top speeds and energy efficiency depend strongly on body form—crocodilians are not nearly as fast and efficient as thresher sharks, which are less swift and efficient than tuna. In order to keep frontal drag as low as possible, a swimmer needs to be as slender as possible—a high length-to-beam ratio—as in eels and snakes. But that maximizes skin surface area. In order to keep skin drag as low as possible, a swimmer needs to have as little surface area as possible, which means being as spherical as possible, but plump spheres inherently have high frontal drag. The way to resolve these contradictory needs is via a teardrop, spindle, or fusiform shape with a moderate length-to-beam ratio, as observed in billfish, tuna, lamnid sharks, and dolphins.

Hydrodynamic body forms are as follows for swimmers that are axial undulators.

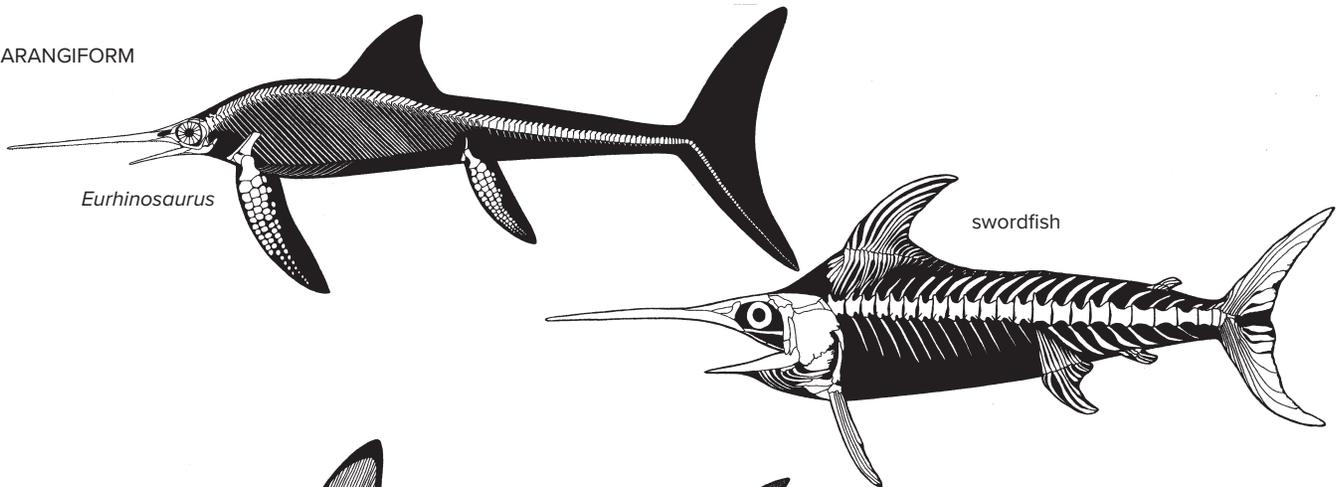
Anguilliforms have long, slender, highly flexible bodies and tails that generate thrust along the entire body and a gently tapering tail, and swimming muscles are mainly white fibered; these include many fish along with eels and sharks, sea snakes and crocodilians, and some early whales. Swimming energy efficiency is moderate, and cruising and top speeds are modest, although acceleration can be rapid because the entire body can suddenly generate thrust via the intense but short bursts from white-fibered muscles. Also high is maneuverability. If the limbs are not full flippers, they may be folded tightly against the body

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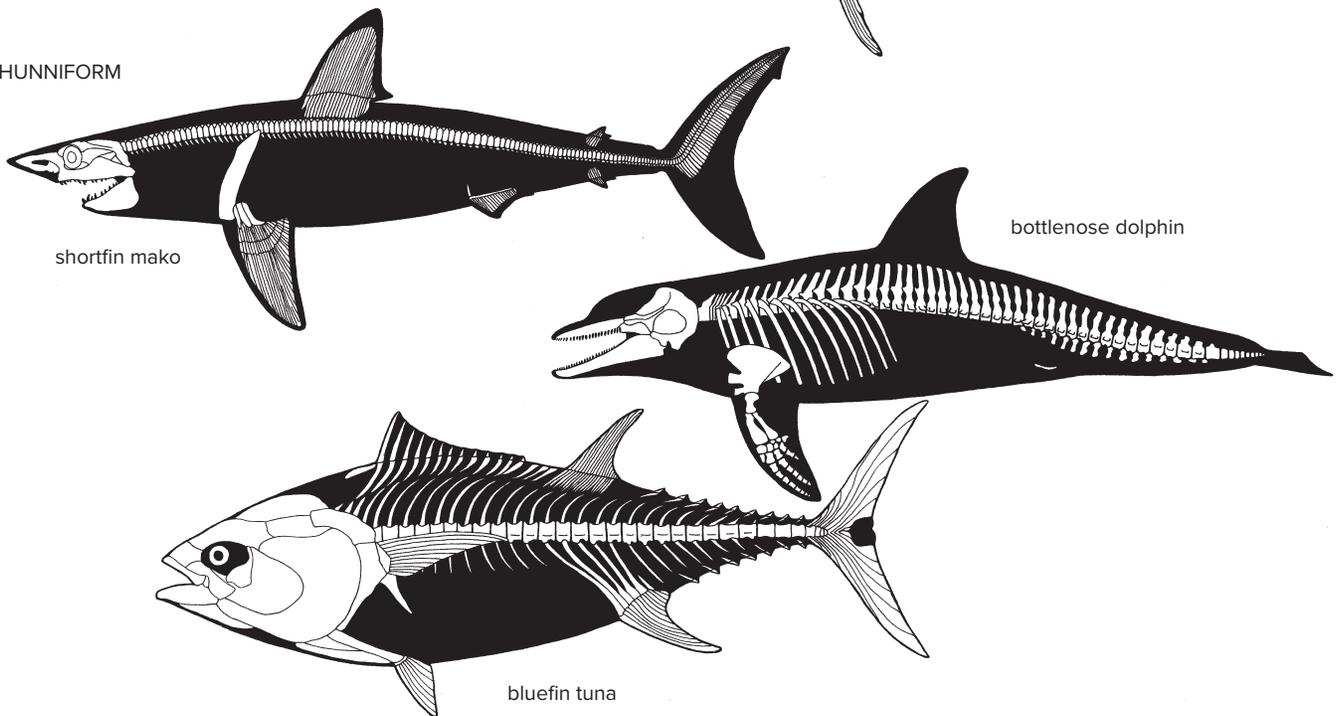
ANGUILLIFORM



CARANGIFORM



THUNNIFORM



Hydrodynamic body forms

to minimize the drag they create, as in cruising crocodylians. In snakes the limbs are nearly or entirely absent. Anguilliform is most often found in aquatic forms living in shallow waters, reefs, or dense kelp-style seaweed forests.

Carangiforms have more streamlined and somewhat more compact, fusiform, stiffer bodies and shorter, deeper tails that generate thrust along the back half of the body and tail—the tail flukes are generally asymmetrical in carangiform sharks, the upper lobe being longer; the flukes can be half-moon shaped in fast carangiforms such as billfish, and swimming muscles are more red fibered; these include most fish such as herring, salmon, barracuda, and billfish, many sharks such as dogfish and reef sharks, and freshwater dolphins and the whales. Energy efficiency can be very high, cruising and top speeds can be fairly to very fast, and maneuverability is modest. This generalized swimming form is highly flexible in terms of utility and is present in oceanic vertebrates from the coasts to the deep sea.

Thunniforms have extremely streamlined, very compact, fusiform, stiff bodies, and short tails that generate thrust at the very aft end of the body and tail, which ends with half-moon-shaped flukes; swimming muscles include extensive red fibers. These include tuna, lamnid sharks, and porpoises and dolphins. Energy efficiency is very high, cruising and especially top speeds are fast—very fast over short dashes—and maneuverability is modest. This specialized swimming form is found only in deep-ocean vertebrates.

Although all thunniform swimmers are fast, the configuration does not have a lower drag than the most streamlined version of the carangiform shape—the lower frontal drag of the latter balances the lesser surface drag of the former—which is why billfish are as fast as anything in the oceans. The fastest carangiforms and the thunniform fish can fold their body fins to maximize streamlining during bursts of high speed. Swift sharks and dolphins do not have this option, reducing their top speed potential by a few knots, as well as their energy efficiency.

Featuring elongated, narrow bodies and tails with high vertebral counts that allowed strong lateral flexion of the tail and/or trunk, and with modest-sized flippers operated by similarly modest muscles, thalattosaurs, helveticosaurs, atopodontians, basal placodontiformes and hupehsuchians, pachypleurosaurs, aigialosaurs, mosasaurs, dolichosaurs, sea snakes, marine crocs, and ichthyosaurs were body-undulating swimmers.

Of those undulators, the thalattosaurs, helveticosaurs, atopodontians, basal placodontiformes and hupehsuchians, pachypleurosaurs, aigialosaurs, basal mosasaurs, dolichosaurs, and sea snakes were highly maneuverable anguilliforms featuring largely white muscles, best suited for shallow and seaweed-forested waters, and the extraslender dolichosaurs and snakes bearing reduced limbs were especially suited for the nooks and crannies of reefs and mangrove roots.

It was long presumed that all mosasaurs were agile anguilliforms. But it is now known that some were less agile, swifter, more aerobically capable carangiforms better adapted for more

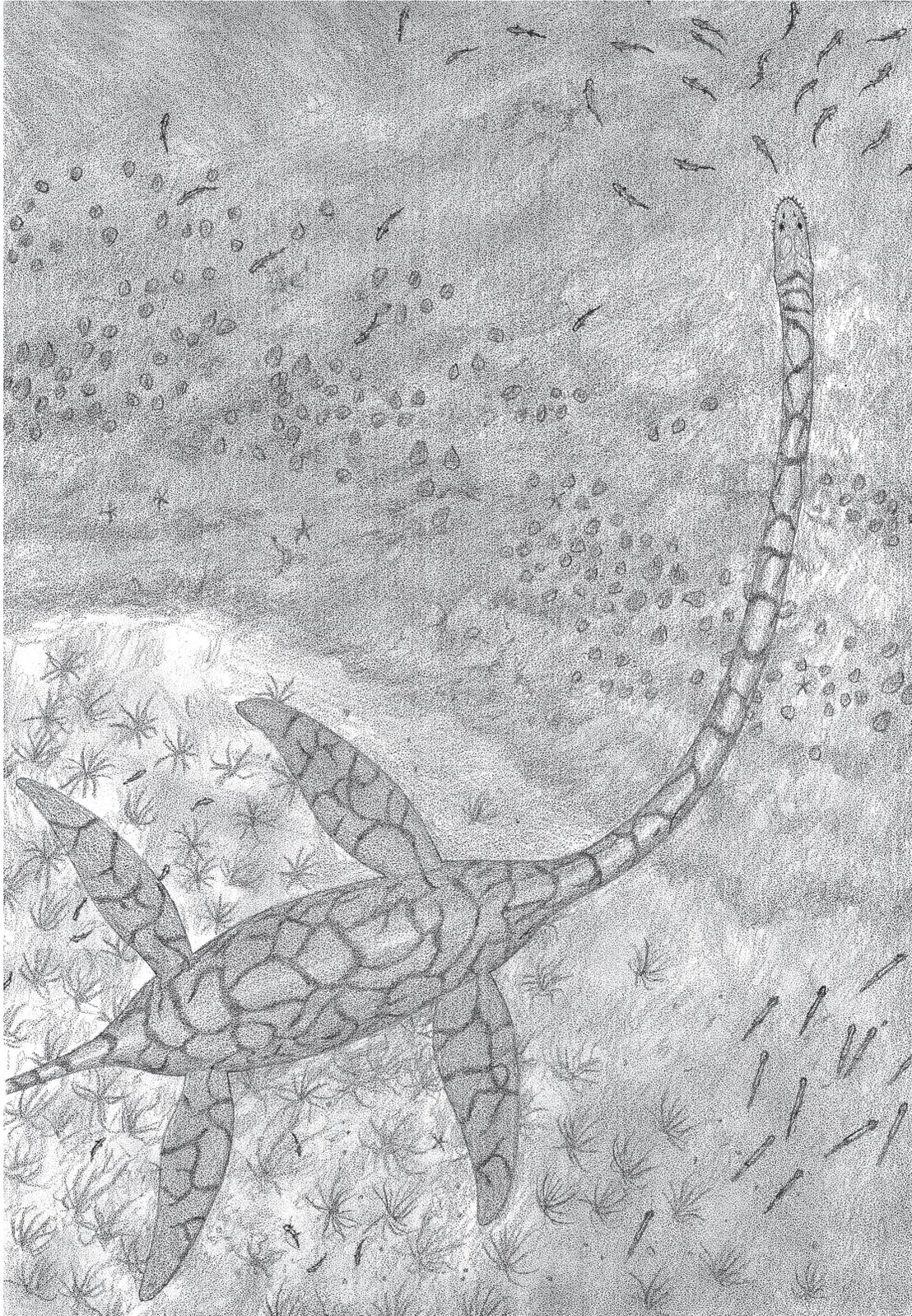
open, deeper waters. But because they lacked the highly refined hydrodynamic form of billfish, and their retractable fins, it is not likely they were as extremely fast. Nor were any full-blown thunniforms. It is possible but not at all certain that the most fusiform mosasaurs porpoised. While predominantly undulators, mosasaurs had fairly large shoulder girdles that may have anchored large arm muscles, allowing them to use their mobile-jointed flippers for active propulsion, either on their own under certain circumstances, or to supplement body-tail undulation. If so, the combined flipper-powered and body-and-tail-powered swimming of mosasaurs was atypical for sea reptiles, although it is common among bony fish. The ridged scales found on at least some portions of some mosasaurs were probably adapted to minimize the turbulent flow of skin drag.

Lacking twin lobed tails and burdened by heavy, irregular plates, armored anguilliform marine crocs were probably little better at swimming than their freshwater relations. The more hydrodynamically sophisticated carangiform metriorhynchids should have been broadly comparable to the similarly configured mosasaurs in aquatic performance.

The ichthyosaurs began as agile anguilliforms and quickly adapted carangiform proportions, and many were fast thunniforms optimized for aerobic cruising. Their inability to retract their body fins and flippers may have hindered top speeds by a few knots, making them most comparable to lamnid sharks and dolphins. The very small flippers of some advanced ichthyosaurs might seem to have been able to enhance speed by minimizing fin drag. But at least some of the species sporting such reduced appendages do not appear to have been especially fast forms, and having such small stabilizers and control surfaces could have resulted in control problems at high speeds. With their transitional anguilliform-carangiform bodies, the most gigantic ichthyosaurs were not such speedsters. Lacking air bladders, sharks are denser than water, and the upper lobes of their tails are almost always larger than the lower, so their tails generate a downward thrust that acts as lift to help keep the sharks from sinking. Because ichthyosaurs had lungs, they may have been less dense than water when the respiratory tract was fully inflated, and their tails were longer ventrally than dorsally. So ichthyosaur tail mass may have produced an upward thrust that helped keep the animal from rising when the forefins were given a negative angle of attack to keep the front of the body from rising. When the reptile needed to pop up to breathe, the front fins could be given a positive angle of attack to generate lift, while the tail continued to push downward, pitching the body strongly up toward the surface. Ichthyosaurs, especially the thunniforms, were better configured for porpoising than any other pelagic reptiles and may have been the only ones to do so. As far as we know from fossil examples, ichthyosaur skin looks as if it followed the smooth and slick route to drag minimization.

As for the appendicular flipper flappers, unlike in nonaquatic or semiaquatic animals with more conventional limbs, well-developed flippers are not used to row or paddle, with the

BIOLOGY



Flipper-flapping
Hydrotherosaurus

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