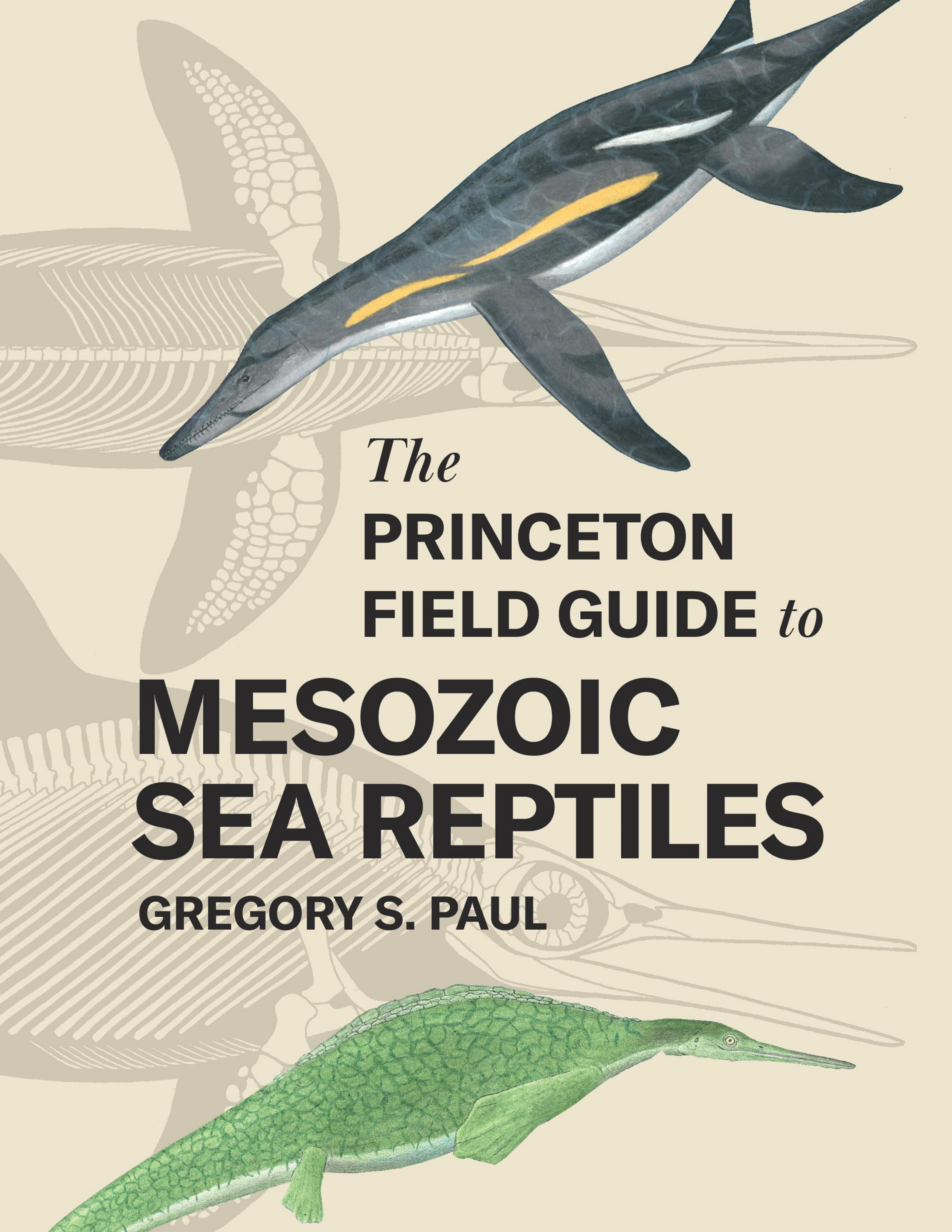


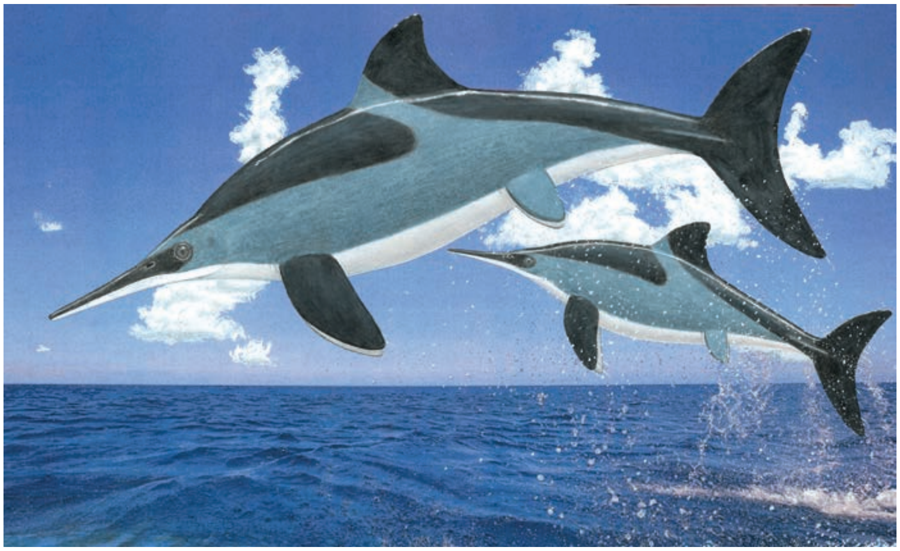
# *The* PRINCETON FIELD GUIDE *to* MESOZOIC SEA REPTILES

GREGORY S. PAUL

# *The* PRINCETON FIELD GUIDE *to* MESOZOIC SEA REPTILES

# *The* PRINCETON FIELD GUIDE *to* MESOZOIC SEA REPTILES

## GREGORY S. PAUL



Princeton University Press
Princeton and Oxford

Published by Princeton University Press
41 William Street, Princeton, New Jersey 08540
99 Banbury Road, Oxford OX2 6JX

press.princeton.edu

Library of Congress Cataloging-in-Publication Data

Names: Paul, Gregory S., author.
Title: The Princeton field guide to Mesozoic sea reptiles / Gregory S. Paul.
Description: Princeton : Princeton University Press, [2022] | Series: Princeton field guides | Includes bibliographical references and index.
Identifiers: LCCN 2022002212 (print) | LCCN 2022002213 (ebook) | ISBN 9780691193809 (hardback) | ISBN 9780691241456 (ebook)
Subjects: LCSH: Marine reptiles, Fossil—Mesozonic—Identification. | Paleontology—Mesozonic.
Classification: LCC QE861 .P39 2022 (print) | LCC QE861 (ebook) | DDC 567.9/37–dc23/eng20220420
LC record available at https://lccn.loc.gov/2022002212
LC ebook record available at https://lccn.loc.gov/2022002213

British Library Cataloging-in-Publication Data is available

Editorial: Robert Kirk and Megan Mendonça
Production Editorial: Kathleen Cioffi
Jacket Design: Wanda España
Production: Steven Sears
Publicity: Matthew Taylor and Caitlyn Robson
Copyeditor: Laurel Anderton

This book has been composed in Goudy Old Style (introduction), ITC Galliard Pro (species section and headings), and Proxima Nova (labels)

Printed on acid-free paper. ∞

Typeset and designed by D & N Publishing, Wiltshire, UK
Printed in Italy

10 9 8 7 6 5 4 3 2 1

# CONTENTS

**Introduction**

**Group and Species Accounts**

Index

# PREFACE

If I were, at about age twenty as a budding paleoresearcher and artist, handed a copy of this book by a mysterious time traveler, I would have been startled as well as delighted. The pages would reveal a world of new seagoing reptiles and ideas that I had only a hint of, if any such ideas existed at all. My head would spin at the revelation that some of the sea reptiles that had long been presumed to have low metabolic rates, like living turtles, lizards, and crocodilians, show signs of being highly energetic, more like seabirds and mammals. Also remarkable is the discovery that many of the mosasaurs, which literally are marine lizards, were not the tail-sculling crocodilian swimmers once thought but rather were configured for stiffer-bodied, higher-speed swimming. Or how about *Eretmorhipis* with its platypus-like head, and *Atopodentatus* with its hammerhead? Plus there are the novel formations, at least to my eyes and ears—Sticky Keep, Loon River, Ziliujing, Hiccles Cove, Xiashaxiamo, Paja, Guanling, Tamayama, Snow Hill Island, Katiki, Paso del Sapo, Lopez de Bertodano, Akrabou, Falang, Dukamaje, Arcadia Park, Muwaqqar Chalk, Hakel, Bet-Meir, Cerro del Pueblo, Romualdo, Phu Kradung, Snowshoe, Rosso Ammonitico. The sheer number of new sea reptiles with exotic names—*Endennasaurus*, *Miodentosaurus*, *Xinpusaurus*, *Helveticosaurus*, *Sinosaurosphargis*, *Majiashanosaurus*, *Borealonectes*, *Stenorhynchosaurus*, *Sachicasaurus*, *Wapuskanectes*, *Attenborosaurus*, *Kawanectes*, *Futabasaurus*, *Vegasaurus*, *Albertonectes*, *Kaiwhekea*, *Aristonectes*, *Morturneria*, *Thililua*, *Sclerocormus*, *Phantomosaurus*, *Barracudasauroides*, *Kyhytysuka*, *Qianichthyosaurus*, *Guanlingsaurus*, *Keilhauia*, *Undorosaurus*, *Simbirskiasaurus*, *Tethysaurus*, *Russellosaurus*, *Taniwhasaurus*, *Kaikaifilu*, *Tenerasaurus*, *Aphanizocnemus*, *Haasiophis*, *Mexichelys*, *Santanachelys*, *Indosinosuchus*, *Zoneait*, *Neptunidraco*—would indicate that an explosion in discoveries and research, well beyond anything that had previously occurred, and often based on new high technologies, marked the end of the twentieth century going well into the twenty-first.

A major and coincidental aid to the production of this book was that while it was being created, a new wave of research at long last cleared up much of what had been a perplexing and often misleading plethora of old names often based on poor material and errant assignments of fossil specimens. So the name *Steneosaurus*, which had been applied to a number of sea crocs, has now been obsolesced out, replaced by the likes of *Macrospondylus*, *Yvridiosuchus*, *Proexochokefalos*, *Plagiophthalmosuchus*, and *Bathysuchus*.

Remaining frustratingly unresolved is the evolutionary origin of some marine reptile groups. The specific origin of turtles as a whole remains unresolved. Also still mysterious are the derivations of *ichthyosaurs*, *thalattosaurs*, and *helveticosaurs*.

Producing this volume has been satisfying in that it has given me reason to illustrate the skeletons of almost all Mesozoic marine reptile species for which nearly complete material is available. These have been used to construct the most extensive library of side-view life studies of these sea creatures to date in print. An advantage of producing large sets of rigorous skeletals is that it can reveal information that would not otherwise arise. The overall result is a work that covers what is already well over two centuries of scientific investigation into the groups of tetrapods that inhabited the seas for up to 186 million years. Enjoy the travel back in time.

## Acknowledgments

Thanks to Kenneth Carpenter, Michela Johnson, Judy Massare, Hilary Ketchum, Mark Young, Sven Sachs, Asier Larramendi, Marcela Gomez Perez, Leslie Noe, Michael Taylor, Michael Everhart, Nicholas Gardner, Ben Creisler, Wafa Alhalabi, Sarah Chapman, Jane Davidson, John Schneiderman, Cornelis Hazevoet, Vanessa Rhue, Mallory Theurer, Patrick Druckemiller, Stephen Poropat, Serjoscha Evers, David Cerny, and Robert Telleria. I would also like to thank all those who worked on this book for Princeton University Press: Robert Kirk, Megan Mendonça, Kathleen Cioffi, Wanda España, Steven Sears, Matthew Taylor, Caitlyn Robson, and Laurel Anderton.

# 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, crocodilians, marine mammals, or preflood 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 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.

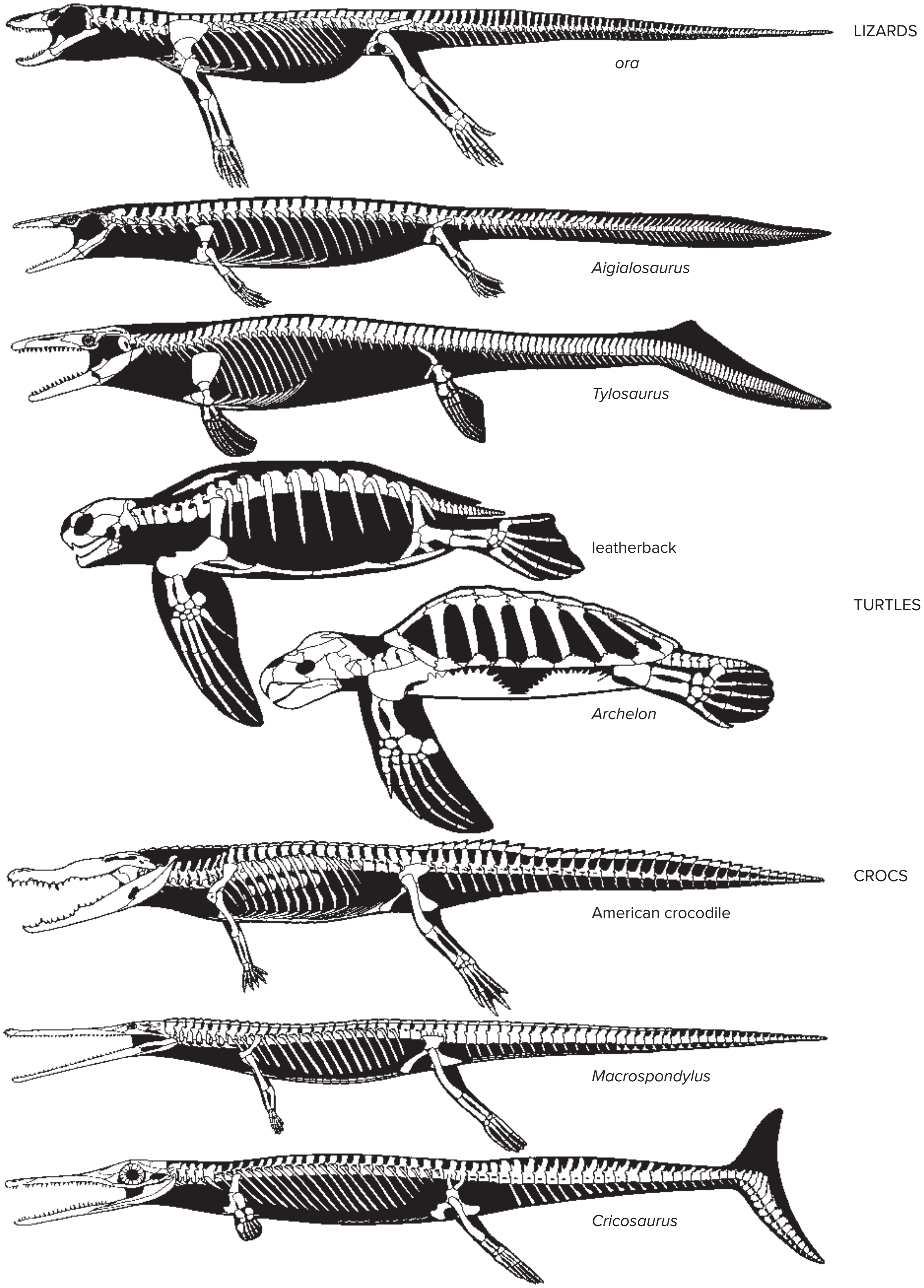
Although tetrapods appeared as the result of the vertebrate conquest of land, and amniotes secured it, the latter have been repeatedly prone to returning to water-immersed lifestyles. The sea reptiles we will be examining are the thalattosaurs; helveticosaurs; sauropterygians, which in turn include atopodentatians, placodontiformes, saurosphargians, pachypleurosaurs, nothosaurs, pistosaurs, and plesiosaurs; ichthyosauromorphs, which include hupehsuchians and ichthyosaurs; aigialosaur-mosasaur sea lizards 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 helveticosaurs were two small groups of early sea swimmers whose relationships to other diapsids remain obstinately unclear.



**Mesozoic sea reptiles with living relatives**

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.

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 ashfalls 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 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 semiaquatic. 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 claudiosaurs 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 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 comfortingly 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.

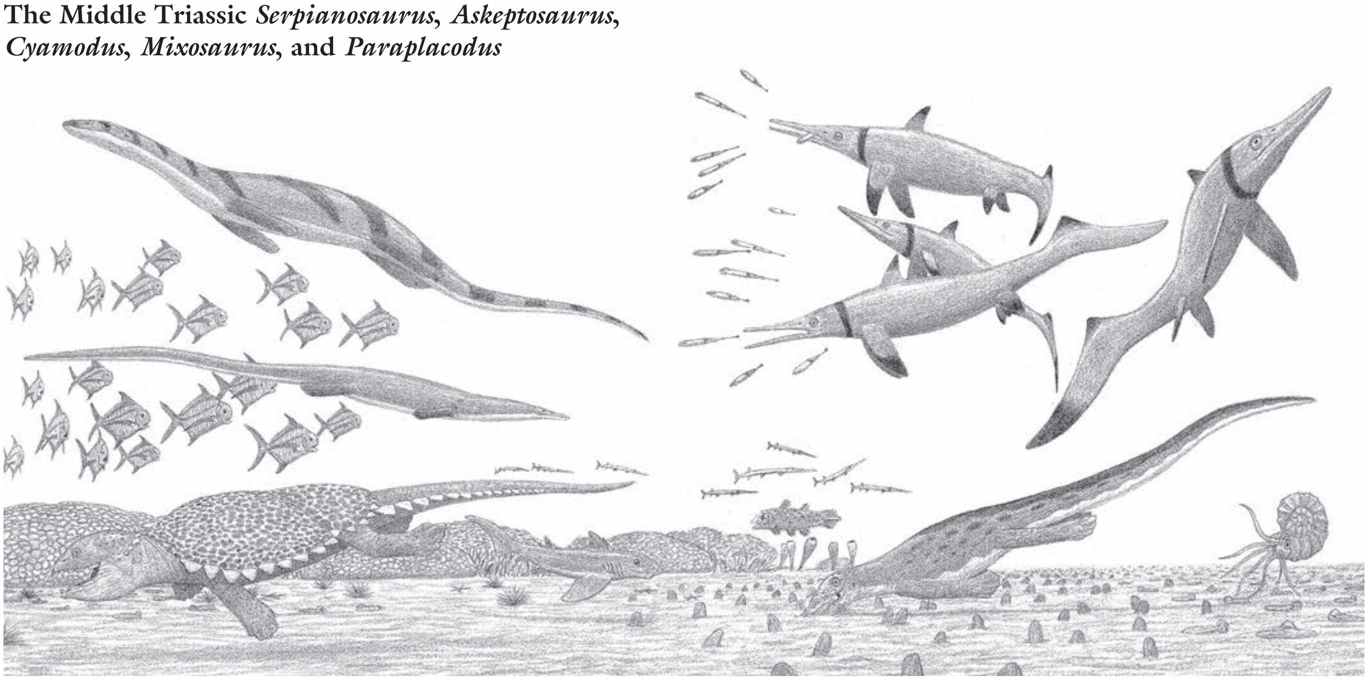
By the end of the Paleozoic the continents had joined into the great C-shaped supercontinent Pangaea, which straddled the equator and stretched nearly to both poles. As a result, there was no Atlantic. So at the beginning of the Triassic, 70 percent of the world consisted of the colossal Panthalassic 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 corosaurs. Also coming onto the scene for the first time were ichthyosauromorphs. Some 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-flippered, 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 protodinosaurs, 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 atopodentatians, 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 *Paraplacodus***



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 protoplesiosaur 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.

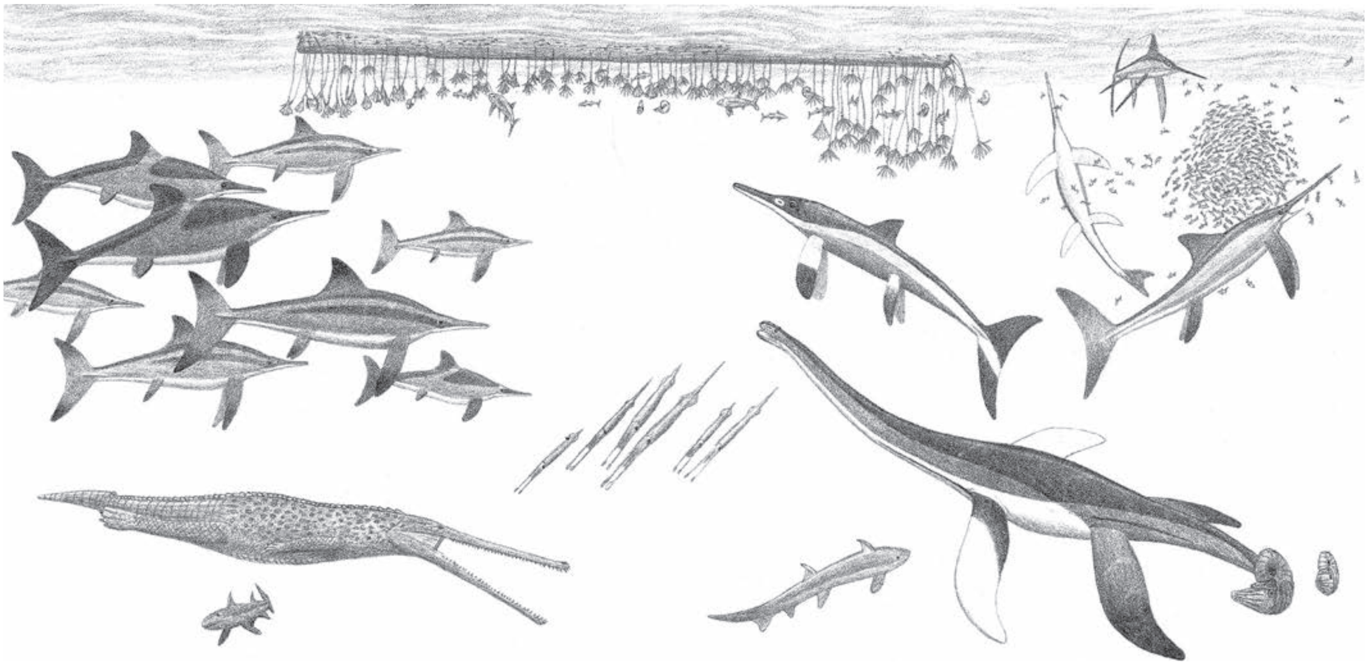
The marine reptile size rise took off in the early and middle Late Triassic, as shonisaur and megamarinasaur ichthyosaurs approached 17 m (55 ft) and ~20 tonnes. This early peak in sea reptile size was similar to sei whales but—contrary to claims by some researchers—fell well short of sperms, fins, blues, 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; atopodentatians 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 phytosaurs—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, phytosaurs 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



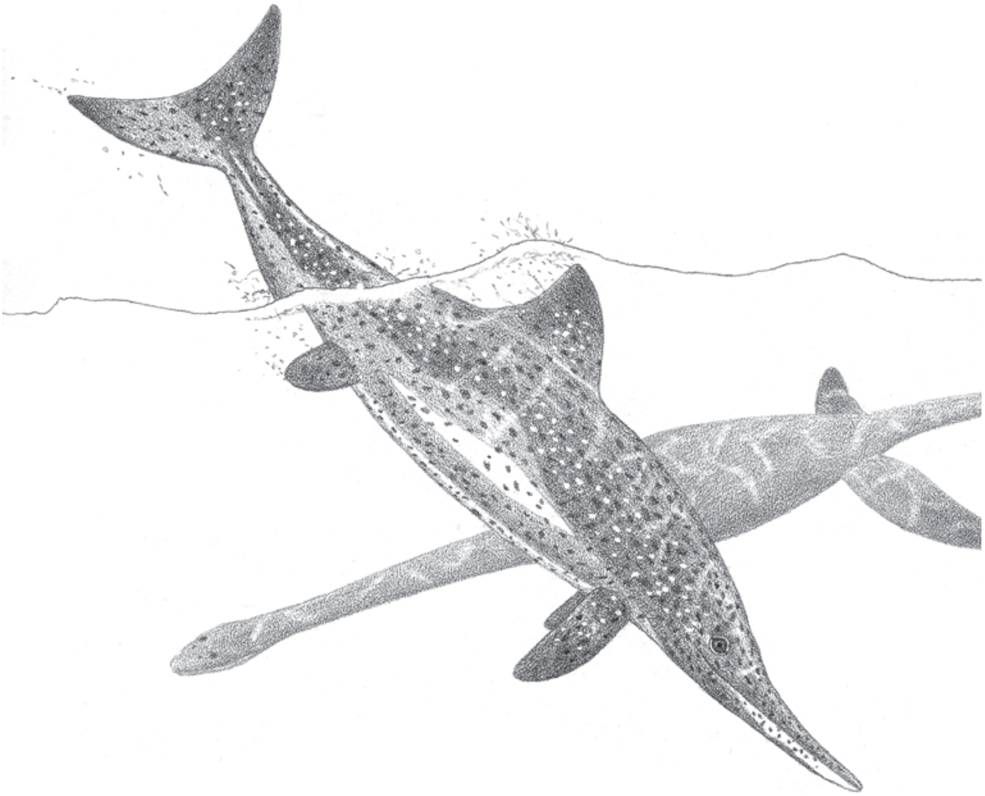
**The Early Jurassic *Stenopterygius quadriscissus*, *S. uniter*, *Macrospondylus*, *Suevoleviathan*, *Eurhinosaurus*, and *Seelyosaurus***

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 shonisaurs for reasons that are mysterious. In the early Jurassic, large, sleek leptonectid 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 pelagosaurs—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 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



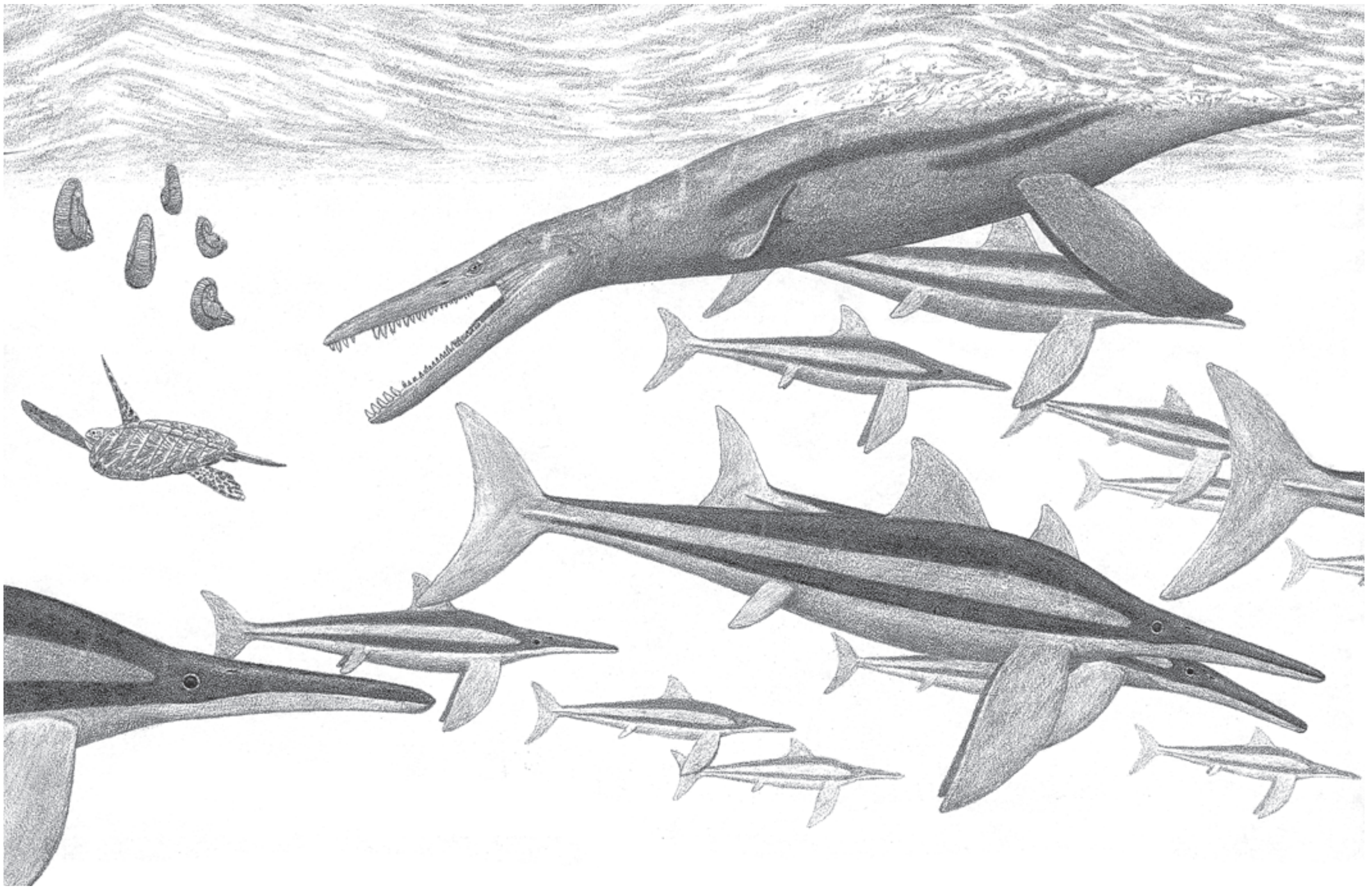
**The Late Jurassic *Cryopterygius* and *Ophthalmothule***

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 polycotylid plesiosaurs, which resembled but were not closely related to the similarly proportioned pliosaurs. 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 shonisaurs, 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.



**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 pterodactyloids 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.

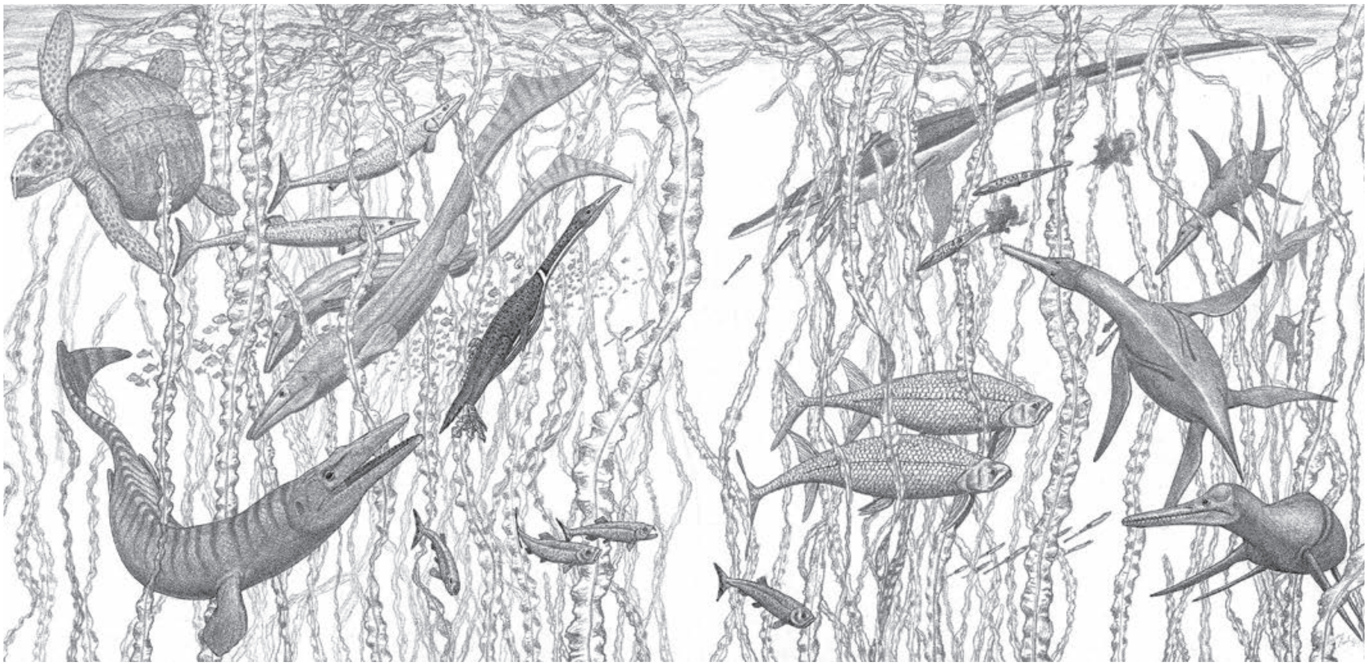
Starting in the late Jurassic as protobird dinosaurs and accelerating in the Early Cretaceous as birds with rapidly improving aerial abilities, some early, toothed avians became shorebirds on fresh and salt waters, then semiaquatic fliers, and then fully marine flightless birds, the loon-like diving 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 titanosaur 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 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 pliosaurs also went extinct during the Cenomanian-Turonian anoxic event—why they did not make it when the similarly short-necked polycotylids paddled through is not known; the latter did not become as huge as the pliosaurs. 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 crocodilians, 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, crocodilians 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 become 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 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 crocodilians 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 pliosaurs 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.

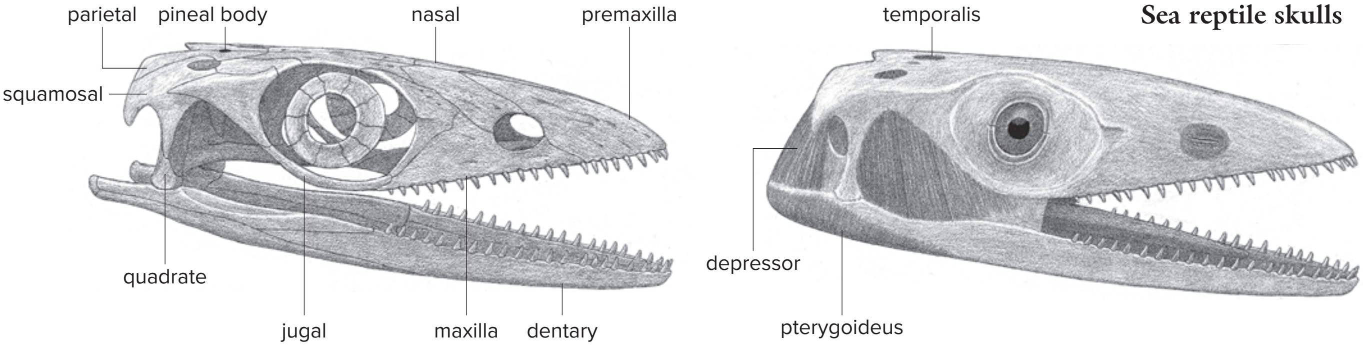
Chelonioidean sea turtles remain a significant, albeit not major, component of ocean faunas. Most are hard-shelled cheloniids limited to warm waters. But the big leatherback is an unshelled dermochelyid reminiscent of some of the lightly armored chelonioideans of the Cretaceous. It can dwell in chilly 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.

# BIOLOGY

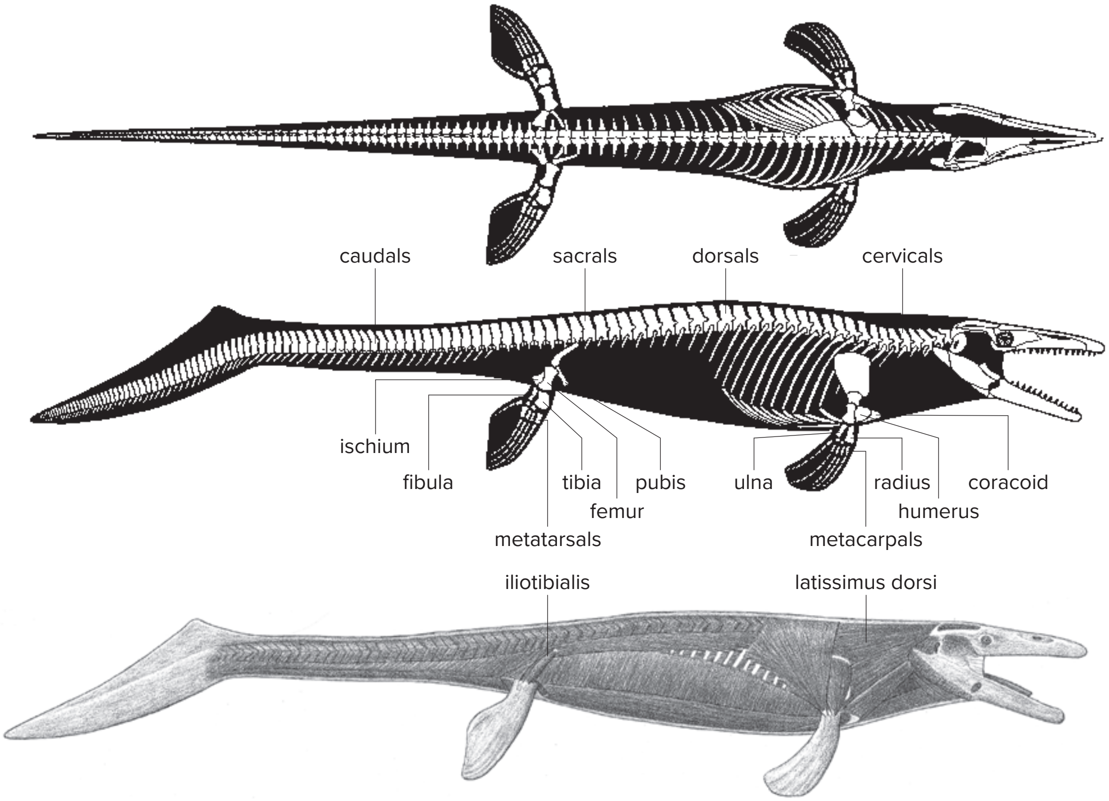
## General Anatomy

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.



**Sea reptile skulls**



**Sea reptile skeletal structure and muscles**

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, Atopodentatians, 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 gastralia 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, atopodentatians 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.

## Mosasaurs

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

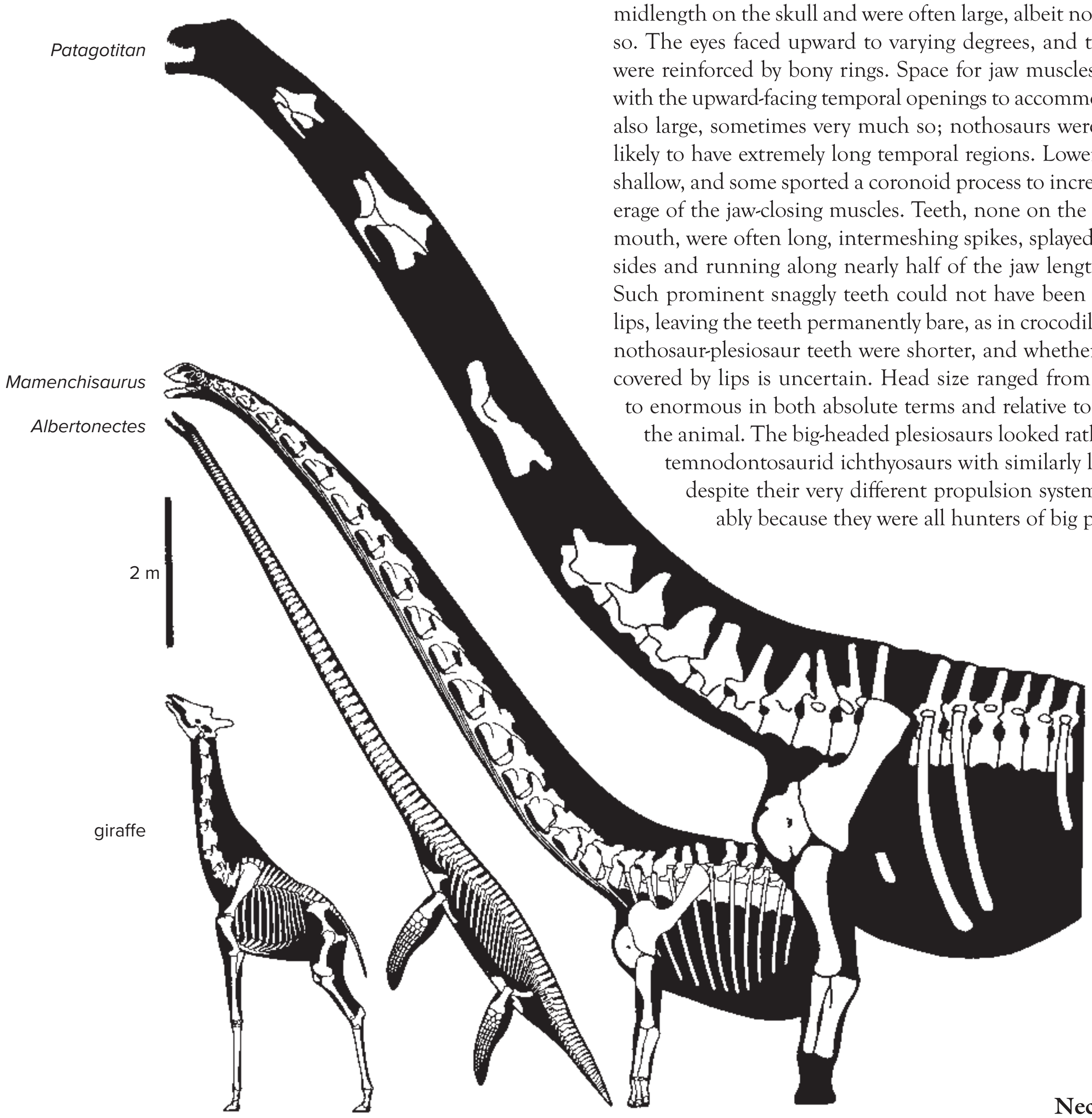
In at least some mosasaurs the skin consisted of small, well-ordered, diamond-shaped scales, which were keeled fore and aft on top of the body, and smoother on the underside. These overlay a sheath of fat deposits that hydrodynamically streamlined the animals.

## 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 arced 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 crocodilians. 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 was 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 pistosaur 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.

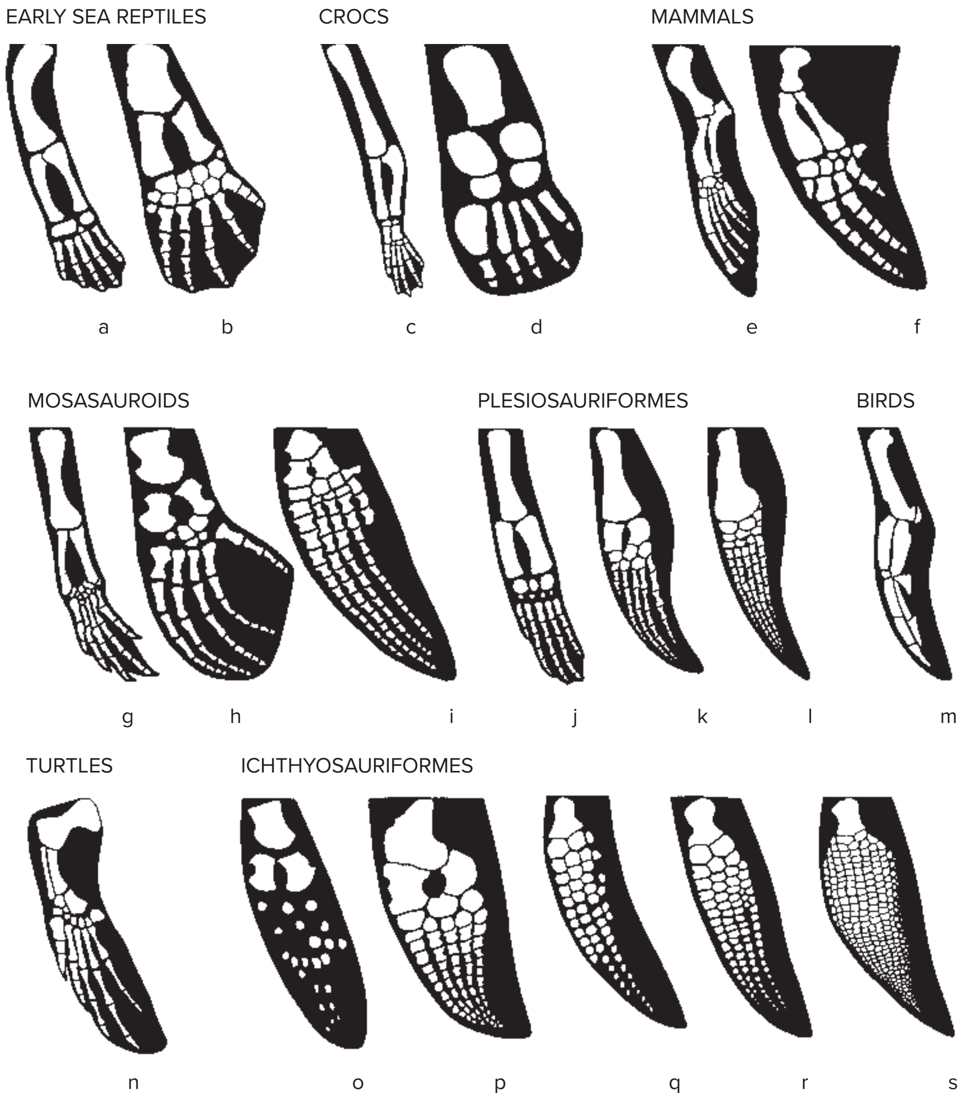
## Tanystropheids

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



**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*

fluke. 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 gastralia were slender, swept backward, and restricted to the belly region; in the pelvis, which was attached to the sacrum, the pubis was mobile.

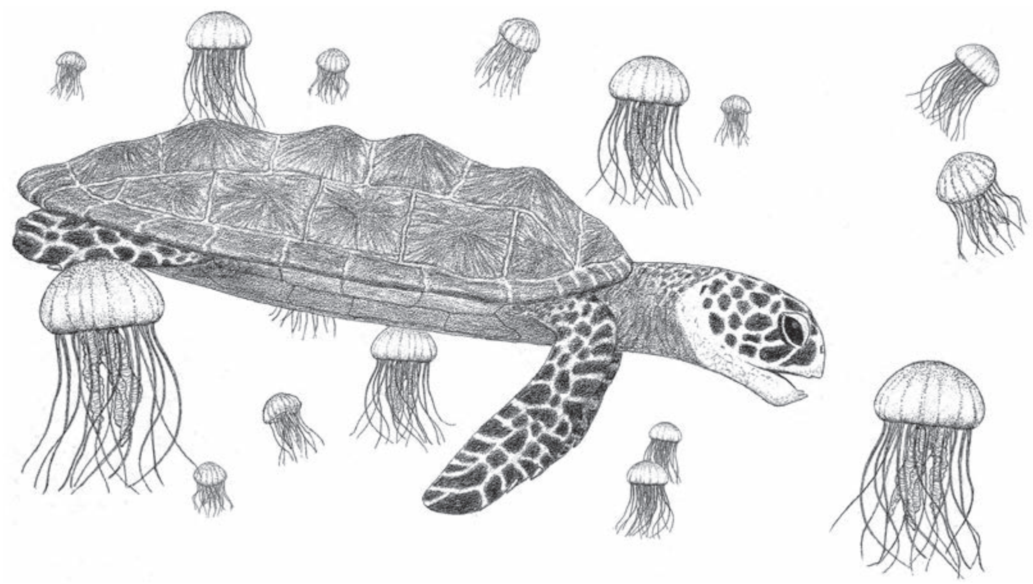
## Turtle-like Placodonts and Saurosphargids

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**

## 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 vacuous 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.

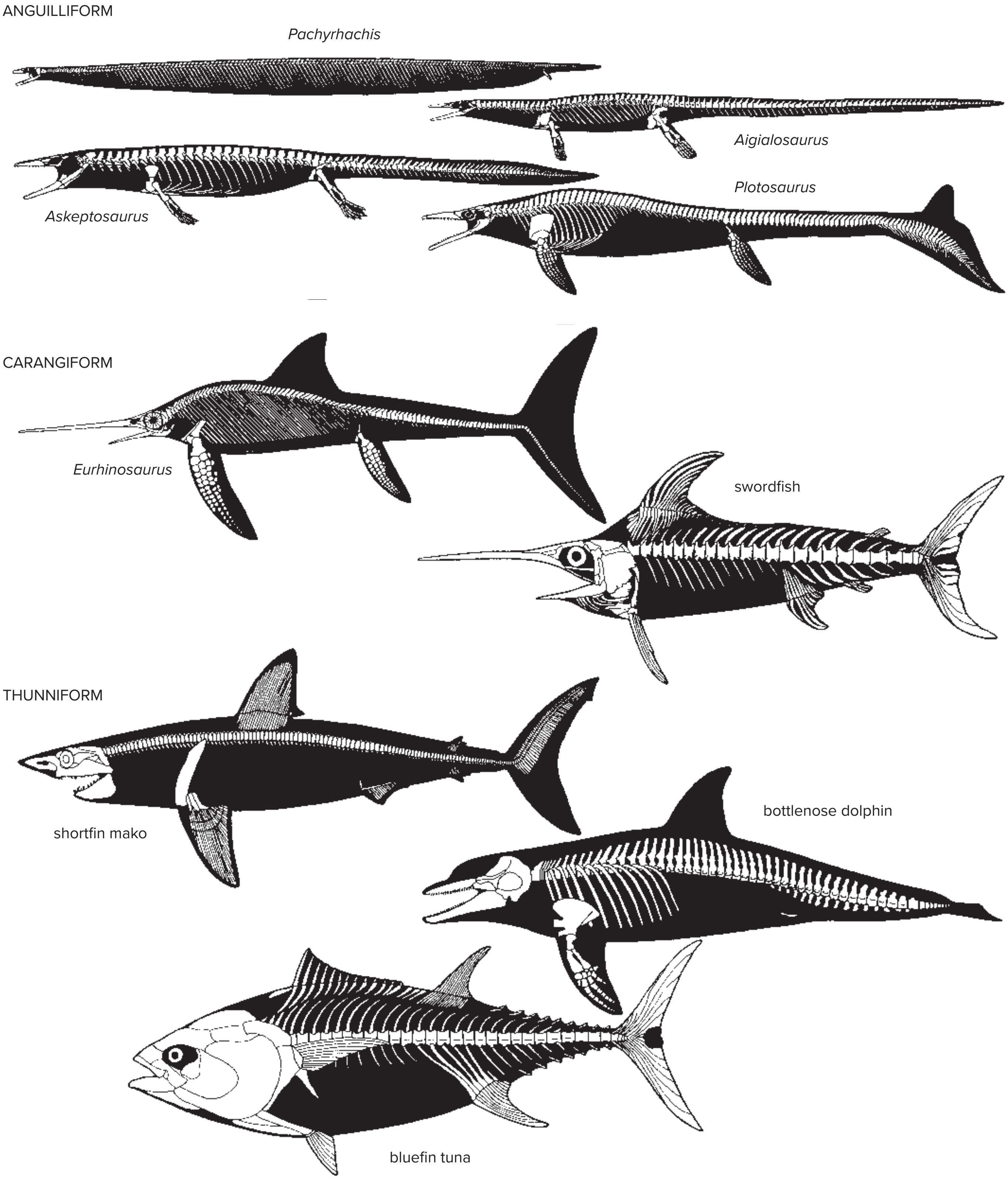
Fish are often up to 70 percent swimming muscles, which is one reason they are often good eating; dolphins are up to 60 percent. Muscles come in two general types. White-fibered muscles are specialized to produce short bursts of very intense anaerobic power, so they are best suited for sprints but cannot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



**Hydrodynamic body forms**

to minimize the drag they create, as in cruising crocodilians. In snakes the limbs are nearly or entirely absent. Anguilliformy 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, atopodentatians, basal placodontiformes and hupehsuchians, pachypleurosaurs, aigialosaurs, mosasaurs, dolichosaurs, sea snakes, marine crocs, and ichthyosaurs were body-undulating swimmers.

Of those undulators, the thalattosaurs, helveticosaurs, atopodentatians, 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

**Flipper-flapping**
*Hydrotherosaurus*

thin edge cutting forward in the water and the blade then retracted flat onto the water to generate thrust. Doing this creates some drag during the forward stroke, which produces no thrust, and the power stroke is inefficient because it produces lots of turbulence. Highly hydrodynamic flippers are used more like propellers, except instead of constantly rotating in one direction like the screws of vessels, they are flapped up and down like the wings of birds. On the downstroke the leading edge of the flipper is well below the level of the trailing edge, and on the upstroke the opposite is true. This means that whether the flipper is swinging up or down, it meets the water with the angle of attack needed to generate the vortex that flapping wings and spinning propellers use to produce the aft-directed flow of gas or liquid that provides the forward thrust. Flippers are symmetrical in cross section, so their shape will produce the same amount of thrust relative to available muscle power on both the downstroke and upstroke—note that the soft tissue cross section of the flipper trailing the bones can have a thin, slightly concave profile on both sides. In sea turtles, the downstroke produces more power and thrust than the upstroke, with the end of the downward flap being the most powerful moment. Because flippers are made of multiple pieces of bone, and elastic soft tissues are flexible, and because the flipper is thickest and most reinforced near its leading edge, the flipper will twist along its long axis under the pressure of water, reducing the angle of attack of the outer flipper—this can be seen in video of the foreflippers of swimming marine turtles. This is advantageous because it replicates the helical shape used by propellers to keep the angle of attack optimal along the length of the blade to account for the increasing rotation speed progressing outward—if the blade or flipper is uniformly pitched, the inner section will be too flat to the flow of water, and the outer portion so steeply angled it will risk stalling out.

Because powered flippered animals do not row but instead use hydrofoils to flap their way through water, it is often said that they fly though water. This analogy should not be taken too far. Actual wings are very large relative to a heavier-than-air animal flier because they have to generate lots of lift to maintain altitude in gas hundreds of times less dense than the flier's body, as well as thrust during powered flight. Because aquatic vertebrates are buoyant, their flippers need to produce only thrust, so the fins are not nearly as large as wings—contrast the surface area of the forelimbs of flying birds to that of flippered penguins—and act as propellers rather than wings. In essence, flipper-propelled creatures are more like buoyant airships with thrusters mounted in pods along the sides than they are like heavier-than-air planes. Top speeds in extant flipper swimmers are around 30 km/h (20 kts). Modern marine flipper swimmers include penguins and sea turtles, the latter of which have not changed significantly since they first appeared in the Cretaceous. Both groups use only forward flippers for propulsion, and the comparatively weakly developed aft fins of nearly tailless turtles are used predominantly as rudders.

With their somewhat turtle-like, broader-than-deep, rigid trunks sporting big flippers with plenty of bony area for muscle attachments, and their short tails lacking big tail flukes, plesiosaurs were predominantly or entirely flipper propelled. Anchored on the big plates of the lower portions of the pectoral and pelvic girdles as well as the robust gastralia, the ventral flipper muscles were more powerful than the upper sets. So the downstroke would have generated most of the propulsive thrust. Because the foreflippers were elevated by well-developed upper shoulder muscles, and the latissimus dorsi shoulder muscle could have been spread over much of the back, the disparity between the power of the downstroke and upstroke was not as great as it was with the aft flippers. That was most true in some plesiosaurs with unusually large vertebral spines that probably helped anchor especially large upper shoulder muscles. The upper pelvic muscles were not very large, so the upstroke of the aft flipper was much less than the downward sweep. If the tail fins were horizontal flukes, then the small surfaces would have been at best minor propulsive factors, perhaps most useful at slow speeds. According to some research, the very long necks that adorned some plesiosaurs would have produced significant surface drag even when held in the posture best suited to minimize it, in which case they were presumably rather slow swimmers that used high-speed neck motions to snap up prey. Other research indicates that long necks made surprisingly little drag difference. In any case, swinging the neck could also help rapidly turn the animal, enhancing maneuverability during ambush attacks. Short-necked plesiosaurs were presumably faster swimmers that made direct assaults. If a big-headed, short-necked plesiosaur was attacking a long-necked plesiosaur, it could have been like a Luftwaffe Me-109E engaging a slower but harder-turning Hawker Hurricane Mk 1 during the Battle of Britain in 1940. The latter would try to survive by turning inside the former so the aggressor could not get in proper attack position. Only small, short-necked plesiosaurs had the potential to porpoise, but whether any did so is very uncertain.

A major question about plesiosaurs is how they flapped their fore versus aft flippers. Because the aft flippers were about as well developed as the foreflippers, it is very probable that all four were used for propulsion. Having fore and aft propellers working in tandem can increase the efficiency of using a given frontal area of the water that passes through the system, as in contraprops that spin in opposite directions on the same shaft. It is also possible that plesiosaurs used their flexible ribs to elastically store locomotion energy, increasing the power-to-thrust ratio. Because shell-less, biflippered plesiosaurs had twice as many fin propellers as uniflippered sea turtles and were able to tap into more muscle power and elastic energy storage via the thrust efficiency of tandem action, it is likely that plesiosaurs were faster than the latter. According to some researchers' calculations, the most hydrodynamic plesiosaurs may have been about 80 percent as fast as thunniform ichthyosaurs, being able to achieve 45 km/h (30 kts).

Hotly debated is whether the fore and aft flippers were used in synch like butterfly wings, or flapped in an alternating pattern like dragonfly wings, or some combination. Because they lacked modern fore and aft flippers, it is not obvious what the tandem-flippered plesiosaurs were doing. During slow swimming, fully alternating fore-aft flipper flapping would have the disadvantage of pitching the trunk strongly up and then down with each opposing stroke of the front versus aft flipper. But at high speed, such motion would be suppressed by the smoothing power of the water streaming fast around the trunk and rendering it more stable. To maximize the hydrodynamic efficiency of the aft flipper required minimizing the time that the trailing flipper was operating in the disruptive turbulent wake of the forefin, and timing the fore and aft strokes to do that would in turn depend on stroke rates and forward speed, and whether the creature was turning, and if so how tightly. It is very likely that the way in which plesiosaurs stroked their fore and aft flippers relative to one another depended on the circumstances, sometimes alternating, sometimes moving in synch, and sometimes with the aft fin lagging only partly behind the foreflipper.

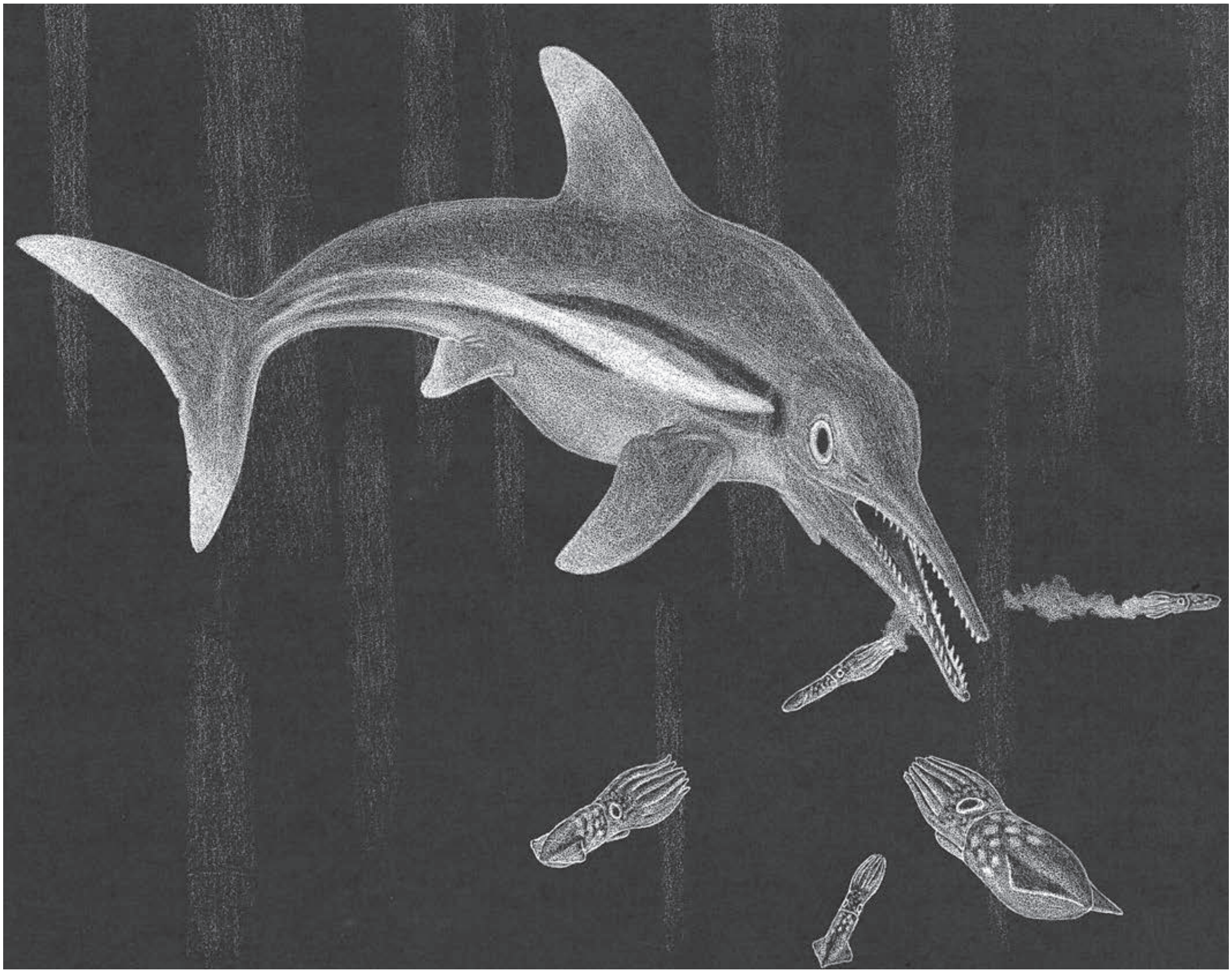
With short, moderately muscled limbs and short-webbed hands and feet suited only for inefficient paddling, and hindered by their turtle-like carapaces that were not all that streamlined, cyamodontoid placodonts would have been mediocre swimmers along the lines of freshwater aquatic turtles. The paddles of some were so short that they may not have met even that standard.

Elasmosaur plesiosaurs have been illustrated lofting their long necks and heads far above water level. This is problematic for a number of reasons. Having a long section of neck above the waterline would entail a considerable amount of forward mass unsupported by water, causing the front of the body to pitch strongly downward; the longer the neck relative to the body, the more pronounced this would have been, to the degree that it may not have been physically possible for plesiosaurs to loft their heads high for more than a few moments or minutes as they used their foreflippers to dog-paddle. Another problem has to do with the circulatory system. Pumping blood high above heart level against the gravity well of the planet requires very high pressure—in giraffes it is well over twice as high as is typical for mammals—which in turn requires an exceptionally powerful heart. Having no normal need to push blood up against 1G, aquatic animals inherently have fairly low circulatory pressures, insufficient to keep a brain held meters above sea level oxygenated—a plesiosaur with its head held high would faint after a few moments. Nor is it entirely clear that the necks were muscled powerfully enough to be lifted high into the air.

For reasons that are obscure, most sea reptiles did not have nostrils on the tops of their heads like cetaceans, even when the nostrils were well back on the skull. So the reptiles had to lift more of their heads above the waterline to engage in gas exchange. In that regard, the marine reptiles were more like penguins and pinnipeds, whose nostrils are not set high either. Low-set nostrils were not a problem for long-necked plesiosaurs, which could easily lift their small heads above surface level, and low nostrils would have encouraged porpoising in those reptiles that could do it. Some marine reptiles, among them small-headed plesiosaurs and lots of ichthyosaurs, had for unclear reasons nostrils too small to handle breathing needs, especially when exercising, so they must have breathed through their mouths. One item Mesozoic reptiles of the sea did not have to deal with is surface ice—except perhaps possibly in some polar seas in the Cretaceous winters—which seals deal with by maintaining breathing holes that they risk not being able to reach in time, and that might freeze over. Nor did ancient marine reptiles have to fret about being ambushed by marine bears when surfacing at any such holes.

At the opposite extreme from surface breathing, while air breathers are highly dependent on it, is diving. It would at first seem that animals that have to get oxygen from above the water surface would not be able to dive anywhere close to as deep as fish can go. It would also seem that animals with high metabolic rates that demand lots of oxygen would be especially tied to staying near the surface so they can breathe every few minutes. And there is the danger of getting the potentially injurious or lethal bends, caused by expanding nitrogen bubbles in the blood and tissues when a body returns too rapidly to the surface after a dive of 30 m (100 ft) or more. Tremendous water pressures and near-freezing temperatures must also be dealt with. Yet some seals and whales can stay under for over two hours and dive down nearly 3 km (2 mi). Superdiving is made possible by a host of extreme adaptations to the respiratory and circulatory systems. The lungs are emptied of air at the beginning of the dive to keep the nitrogen that causes decompression sickness to a minimum, and they further collapse under increasing pressure. Lung collapse also aids the dive rate by reducing buoyancy. Oxygen is instead stored in the blood, which is unusually abundant in volume and in hemoglobin content, as well as in the muscles. Heart rates drop dramatically. Tissues are unusually tolerant of anaerobiosis. Note that no living thunniform tetrapod is a truly deep diver, perhaps because these fast swimmers use too much energy per unit time to stay under so long.

Many sea turtles cannot deep dive, perhaps because their inflexible shells prevent their lungs from collapsing, and they are not able to handle cold water. The softer-carapaced, more cold-tolerant dermochelyid turtles can submerge down to 1.3 km (0.75 mi), and the same may have been true of softer-carapaced Cretaceous species, the fossil bones of which show signs of damage from the bends. So do bones of plesiosaurs, ichthyosaurs, and mosasaurs, indicating that they dived at least fairly deep on a regular basis. Long-necked elasmosaurs appear to have preferred coastal waters, where their fossil remains are most abundant. More often found in open-ocean sediments and resembling the body form of deep-diving seals and whales, the big-headed, short-necked plesiosaurs look well suited for quite deep dives. Among mosasaurs the carangiform-bodied examples were best adapted for going deep, and their bones sometimes record evidence of



***Stenopterygius* in dark waters**

the bends. Among ichthyosaurs the same pattern applies, and the thunniform species should have been less prone to deeper diving. On the other hand, the enormous eyes of the compact-bodied ichthyosaurs imply that they commonly fed in low-light conditions, but whether that was a result of feeding at depth or at night is not known. Night feeding may have been especially important to species that dwelled near the poles if they did not migrate away from the long winter nights.

Although swimmers and fliers both have to constantly deal with moving through three-dimensional fluids while paying neural attention and addressing muscle action to pitch, yaw, and roll, swimming is less challenging than heavier-than-air flying in many regards. There is no need to deal with the problems and dangers involved in taking off or landing, especially if a swimmer does not alight upon rocky shores. Stalling out and plummeting to the ground cannot happen. There are no trunks or branches to run into underwater, though some may float on the surface. The maneuvering of a flying animal in the air is a complex, dynamic process in which the animal must deal with the substantial loss of lift that occurs while banking into a turn, but this is not the case in water. Even so, swimming does have its control issues. There is the risk of collision with other sea creatures, whether in schools or during feeding frenzies with other fast predators dashing hither and about. Near the sea bottom there may be rock pinnacles and reefs to impact, and coming ashore on rocky coasts often pounded by big waves entails serious potential for injury. For axial flipper flappers to turn hard, and especially fast, flippers and perhaps tails must be used in complex dynamic ways to produce thrust while rolling the body to bank into the turn.

Many swimmers leap and breach—swim subvertically at high speed to break the surface and loft the body entirely or largely out of the water—and drop back down into the water without making significant lateral progress. For many smaller swimmers this is an escape tactic intended to throw off predators. It may also occur during mating disputes or displays. The loud underwater sound generated by a breach may be a form of sonic communication. Knocking off parasitic growth is another possible function. Yet swimmers sometimes seem to breach for no particular reason; a swimmer may enjoy using its power to throw itself out of the water briefly into the thin gas above and them slam back down into the dense liquid, in which case it is a form of play.

## On the Beach

Cetaceans are entirely unsuited for progressing on land, and strandings are often lethal. Female sea turtles, with their flat-bottomed carapaces and strong foreflippers bearing claws to improve traction, can struggle onto sandy beaches well enough to dig nests and lay their eggs, and the hatchlings can later scramble across the sand into the water. Pinniped bodies and flippers are supple enough to allow the animals to flop fairly well across beaches or on ice, where they breed.

Small- to medium-sized anguilliform marine reptiles that had fairly well-developed girdles and limbs had the potential to come onto land—these would include thalattosaurs, helveticosaurs, atopodentatians, basal placodontiformes and hupehsuchians, pachypleurosaurs, aigialosaurs, dolichosaurs, and marine crocs, although the latter could use only their hindlegs, their arms being too reduced. It would seem that sea snakes should be able to slither across bare sand and rocks, but apparently they lack the specific serpentine body coordination needed to readily progress on terra firma, so they limit activities on the latter if they do go ashore at all, and the same may well have been true of the Mesozoic examples. The rigid and broad-carapaced cyamodontoid placodonts should have been able to scramble onto land like freshwater turtles, although the limbs of some may have been too small to get them onshore.

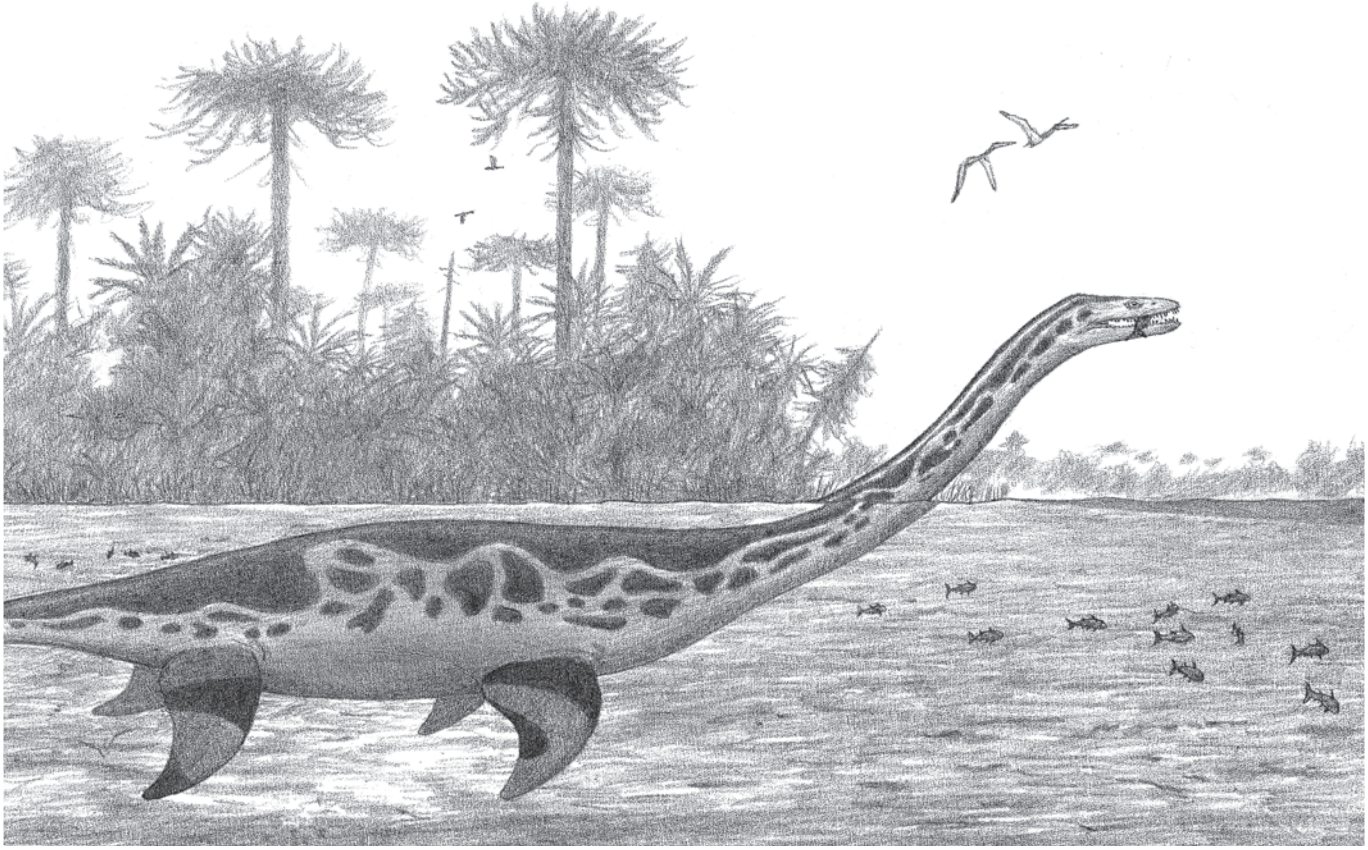
The most anguilliform of the early ichthyosaurs may have been able to wiggle onto beaches, but most of these fishlike reptiles were clearly no more suited to being on land than are cetaceans Also lacking large, well-muscled propulsive flippers, mosasaurs too appear poorly configured to get onto land, although they should have been better able to maneuver on the wave line than ichthyosaurs and cetaceans. Plesiosaurs are more problematic. On the one hand, their somewhat sea turtle–like flat-bottomed bodies and well-muscled flippers imply that they could get around on beaches well enough to reproduce. On the other hand, their flippers were more rigid, and many plesiosaurs appear to have been too large to have safely beached. It is possible but by no means certain that smaller plesiosaurs could beach, while larger ones could not.

## The Salt Problem

Many think that the salt content of blood and cells is about the same as that of seawater, but if that were true then it would be fine for land creatures such as ourselves to drink seawater. With oceans about 3.5 percent sodium chloride, and blood actually just 0.9 percent, blood does not taste as salty as a drink at the beach. If drinking lots of salt water raises the salt content of blood much higher than that in cells, osmotic pressure causes the water in the cells to leak into the blood in a chemical effort to dilute the latter, dehydrating the cells to death. In order to survive perpetually drinking ocean water, creatures must have an effective means of removing salt from their blood. That is achieved by salt glands, which in reptiles that spend lots of time in salty seas tend to be located somewhere between the orbits and the nostrils—the exact position varies among groups because they each evolved salt-removal glands independently; ichthyosaurs, for instance, had unusual complex bony nostrils that accommodated the salt glands. Problems for aquatic animals that switch from marine to freshwater habitats are less severe, and some ancient sea reptiles appear to have dwelled in rivers and lakes. Particularly interesting is that sea snakes appear to prefer to drink low-sodium water, including the sheen left on the surface of seawater after rains. Tooth isotope analysis indicates that the marine lizard relations of snakes, the mosasaurs, frequently visited freshwaters for chemical regulation. If so, then at least some mosasaurs may have been prevented from dwelling in the deep open oceans.

## Respiration and Circulation

The hearts of turtles, lizards, and snakes are three-chambered organs incapable of generating high blood pressures. Crocodilian hearts are incipiently four chambered but are still low pressure. Reptile lungs, although often large in terrestrial examples, are internally simple structures with limited ability to absorb oxygen and exhaust carbon dioxide. Although internally dead end, the lungs of some lizards and crocodilians may have unidirectional airflow in certain portions. Lizard and snake lungs are ventilated by straightforward rib action. Turtle and crocodilian lungs are ventilated by the action of the liver being pulled fore and aft, the muscles that move the liver being anchored on large bones in the abdominal and pelvic regions. An unusually mobile pubis is part of the liver pump system in crocodilians, and the marine versions had such mobile pubes. Birds and mammals have fully developed four-chambered, double-pump hearts able to propel blood in large volumes at high pressure. Mammals retain fairly large dead-end lungs, but they are internally very intricate, greatly expanding the gas exchange surface area. The lungs are operated by a combination of rib action and the vertical, muscular diaphragm. The presence of the diaphragm is indicated by



**Freshwater** ***Brancasaurus***

the well-developed, rib-free lumbar region, preceded by a steeply plunging border to the ribcage, on which the vertical diaphragm is stretched. Bird lungs are ventilated unidirectionally by large air sacs, a system that first appeared in preavian dinosaurs.

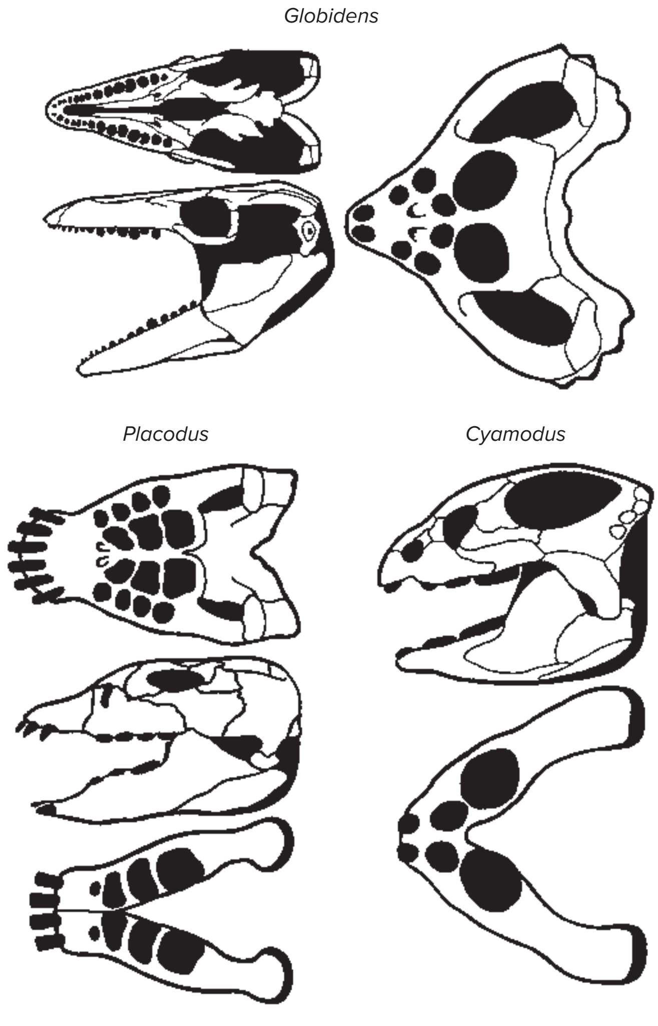
Because archaic marine reptiles did not need to pump blood at high pressures, it is plausible that few if any had fully evolved four-chambered hearts. And, not being birds and being about as dense as water, sea reptiles lacked air sacs, but some groups may have had some degree of unidirectional airflow. All marine reptiles should have had rather small lungs in order to avoid being overbuoyant. One might presume that mosasaurs had rib-ventilated lizard lungs like land lizards, but unlike the latter the marine lizards had a lumbar region intriguingly suggestive of the presence of some form of diaphragm. The turtle-like configuration of plesiosaur ribcages and pelvises implies that they had a similar mode of lung operation, perhaps liver driven. Ichthyosaurs had neither a large lumbar region for a diaphragm nor large abdominal and pelvic bones to anchor liver-pulling muscles, so they appear to have used their ribs to expand their lungs. Modern sea snakes are distinctive in that they can absorb up to a third of the oxygen they need through their skin while unloading most of their excess carbon dioxide, reducing but not eliminating their need to surface for fresh air. Presumably the same was true of their Mesozoic relations, including perhaps the dolichosaurs.

Mammalian red blood cells lack a nucleus, which increases their gas-carrying capability. The red blood cells of reptiles retain a nucleus, so those of the ancient marine reptiles should have as well. Posing a respiratory challenge were the high carbon dioxide levels of the Mesozoic. Although not high enough to be directly lethal, the carbon dioxide would have have had toxic effects unless the animals were physiologically adapted to deal with the excess.

## Feeding Apparatus and Digestive Tract

The beaks and the conical, often spiky but not bladed teeth of most marine reptiles were adapted for grabbing onto and holding food items, which they would have had to then swallow whole, or tear into large pieces for swallowing. The roots of sea reptile teeth were often bulbous. This may have allowed maximal attachment of the teeth to the jaws via pliable connective tissues yet still allowed the flexibility that enhanced gripping power on squirmy, slippery prey. Direct evidence of maritime reptile attacks is found on the famed fossil shells of ammonoids that bear the marks of mosasaur teeth. The apparent stomach contents of a large-headed plesiosaur included ammonoid beaks, similar to the giant squid beaks common in sperm whale bellies. Exceptions to the general spike-toothed pattern include those placodonts, basal ichthyosaurs, and mosasaurs that had large, flat, pavement-forming teeth well suited for pulping what they ate, whether plant or animal, into small, readily digestible bits. Other saltwater reptiles had mouths configured by natural selection to filter out, dabble up, or suck in small, easily digested food items—these reptiles included a few placodonts, hupehsuchians, ichthyosaurs, and turtles.

The ancient sea reptiles with the biggest and most powerfully muscled mouths of the underwater Mesozoic world were the short-necked pliosaur plesiosaurs, the broad-mouthed, large-toothed heads of which reached around 2.8 m (9 ft) as far as is known. In comparison, the head of the biggest living crocodilian, the saltwater crocodile, is well under 1 m (3.3 ft) in length, and the crania of the biggest extinct nonmarine crocodilians approach 2 m (6.5 ft). Although the largest ichthyosaur heads were around 2.8 m (9 ft) long, they were slender snouted and small toothed, with smaller jaw muscles than the big pliosaurs, the mouths of which easily surpassed those of the biggest predatory dinosaurs, including the tyrannosaurs. But the biting power of the greatest pliosaurs that swam Cretaceous seas would be markedly exceeded in the late Cenozoic by the big-toothed livyatan sperm whale's relatives, and perhaps even more so by the supershark megalodon. Attempts to calculate absolute bite forces of big extinct predators have produced inconsistent results.



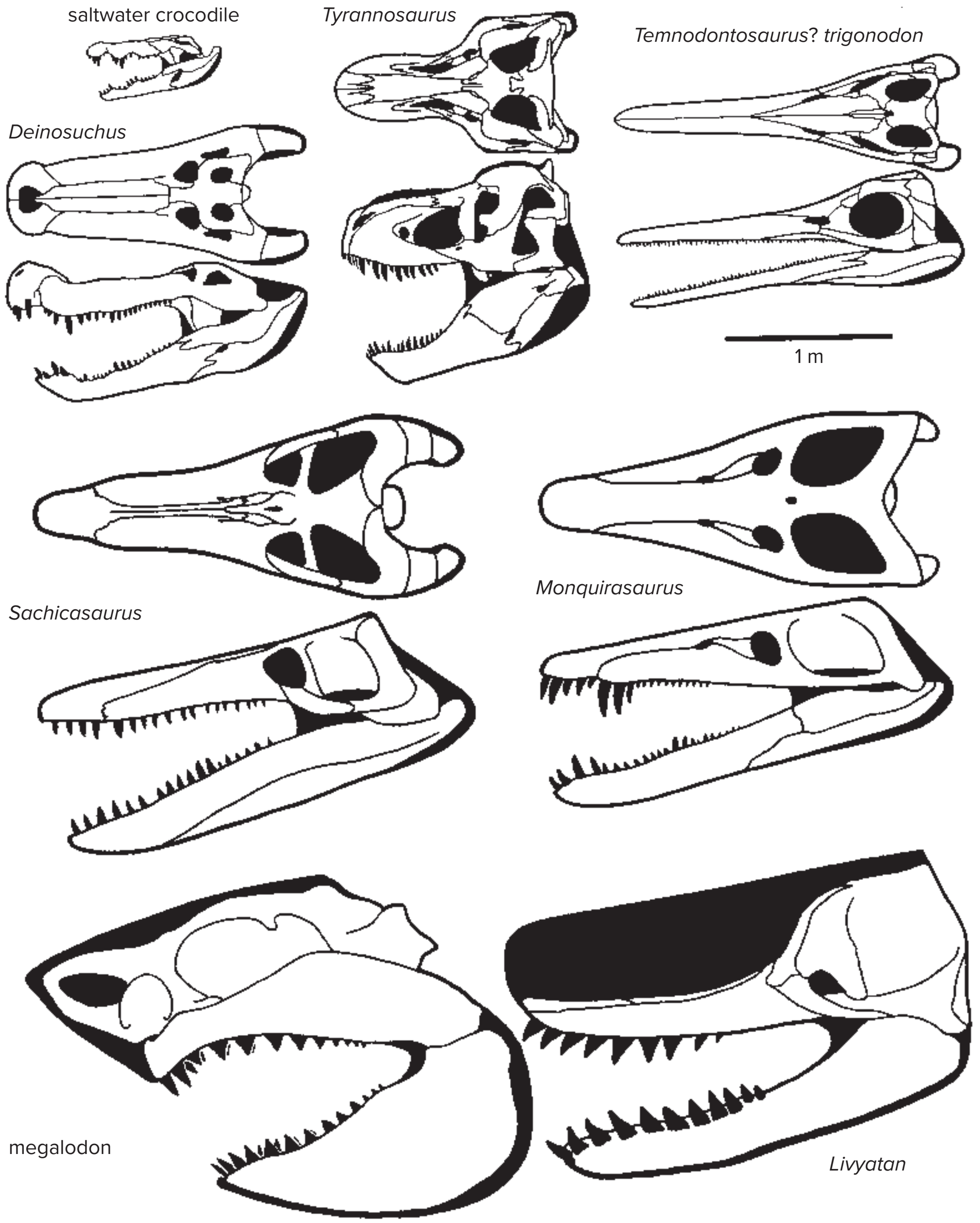
**Crushing teeth in mosasaurs and placodonts**

Terrestrial herbivores generally need to operate very long, bulky, elaborate digestive tracts in order to break down, often via fermentation, the tough tissues of the vascular plants that cover much of the land and inhabit some freshwaters. No such vascular plants dwell in salt waters, where all plants are algae-based, soft, water-saturated seaweeds that consist of much less resilient materials. As a result, saltwater vegetarians do not need extra-large, sophisticated digestive complexes. All predators, terrestrial and aquatic, have short, simple digestive systems, animal flesh being easily digested by creatures that are made of the same stuff.

Stone gastroliths have been found within the ribcages, and therefore the digestive tracts, of a variety of marine reptiles. The degree to which they helped grind up food items or acted as ballast, or both, is poorly understood. What is apparent is that the reptiles probably had to go to some effort to seek out sources of appropriate stones.

## Sea Reptiles as Food

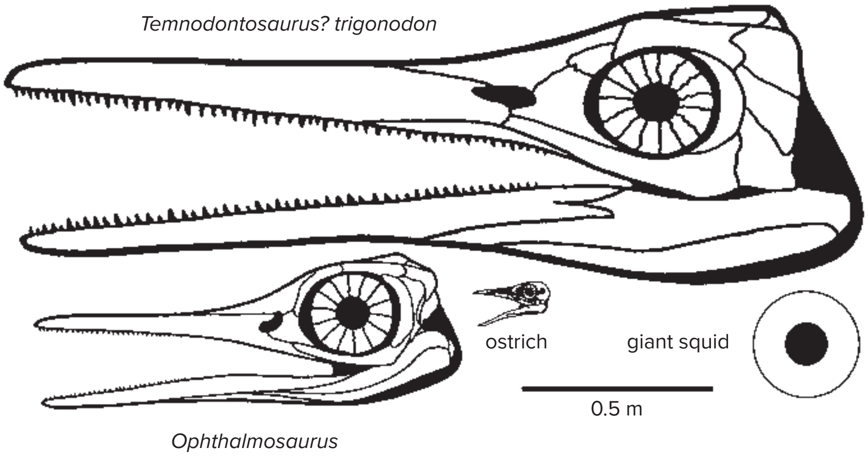
As for what ate marine reptiles, their often well-developed muscles and internal organs would have been appealing meals for Mesozoic oceanic eaters of flesh, and a number of their skeletons show evidence of being bitten by large fish, sharks, and fellow sea reptiles. Whether these particular specimens record scavenging versus predation is not determinable—unless the bones show signs of healing—but it is likely that both were involved. It is also likely that large predaceous oceanic reptiles attacked smaller species and juveniles, in some cases perhaps of their own species. Sea reptiles were very likely to have stolen food from other marine reptiles, again of their own species when the opportunity arose. On the menu of Mesozoic land predators such as dinosaurs—including birds—pterosaurs, land reptiles, and mammals would have been the eggs and hatchlings of aquatic reptiles that nested on land, which is one reason many sea reptiles nested in isolated locations where there were few stealers. Shore-stranded marine reptiles, whether living or not, would have been sources of flesh for any ground predators that came across them.



**Big jaws compared**

## Senses

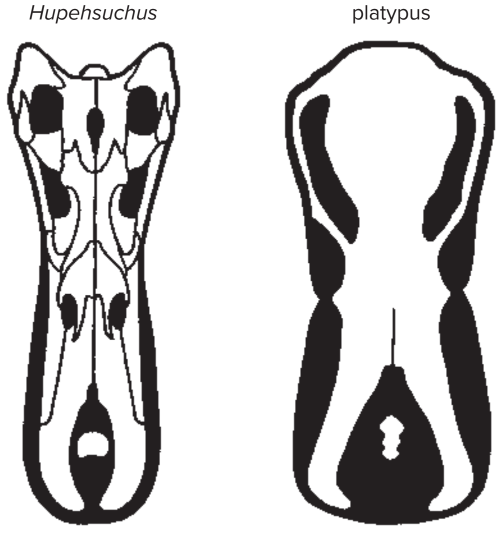
Marine tetrapods use an assortment of senses. Vision is common, ranging from poorly to quite well developed—that of ancient sea reptiles was optimized for seeing underwater, so vision above the waves would have been blurry because of the very different optics of air. Color vision is well developed in reptiles and birds, but not in sea mammals—one complication is that color is strongly skewed toward blue at the expense of red with depth, so the visual complexes of marine reptiles were presumably adapted to deal with this situation—human eyes are optimized toward green because plants were such an important part of our primate diets. The great majority of Mesozoic sea reptiles were highly visually oriented, with large eyes as indicated by the size of their orbits and the bony scleral rings that most of them possessed. Eye size was taken to such an extreme in some ichthyosaurs—approaching a 0.3 m (1 ft) in diameter, larger across than a dinner plate—that the eyes were larger than those of any other vertebrate and matched those of giant squid. This is compatible with the reptiles operating at the great depths at which squid normally dwell, up to 300–600 m (1000–2000 ft), where daylight is very dim. But whether these high-energy fast swimmers could hold their breath long enough to get down so far is an open question. Ichthyosaurs' big eyes may have been an adaptation for feeding at twilight or in



**Gigantic eyes**

moonlight. None of the other Mesozoic ocean reptiles had such tremendous eyes, suggesting that they were not sight adapted for extreme depths. Ichthyosaurs also had a modest degree of overlapping fields of vision, as did sea turtles and a few mosasaurs. Like the ichthyosauromorph mosasaurs, dolichosaur and sea snake eyes were directed sideways, as they typically are in lizards. Thalattosaurs and the assorted sauropterygians could look upward with their dorsally directed eyes. This was most useful for swimmers in shallow waters, where it was more important to keep track of what was above than what was below when the viewer was already close to or at the bottom.

Most sea reptiles—the marine turtles and crocs excepted—had a small opening atop the skull roof midline in the temporal region that accommodated a parietal "eye," sometimes called a third eye. Not true eyeballs that provide full vision, parietal structures are simpler light-sensitive photoreceptors that, in conjunction with the pineal organ they are connected to, help control an animal's thermoregulation and/or circadian rhythm with hormones such as melatonin. Parietal eyes tend to not be visually prominent, as they are often hidden by translucent skin.



***Hupehsuchus* and platypus skulls in top view**

One reason that most ancient marine reptiles were so visually oriented is that they did not always possess the alternative senses found in other ocean vertebrates. Particularly absent was the echolocation common in cetaceans. Nor did the reptiles have the lateral lines that fish use to detect vibrations in the water. Crocodilians, however, have dome pressure receptors in their scales that are highly sensitive to pressure, temperature, and chemicals, and presumably these were present on the marine crocs. There is evidence, via small-scale pitting of snouts, that similar sensors were present on the heads of a wide array of sea reptiles, perhaps most. Some of these pits may have accommodated electric mechanoreceptor sensors, which may have been especially well developed in the hupehsuchians with their platypus-style heads.

Some marine reptiles have basic hearing, a sense that is not as well developed as in mammals because only the latter have the extremely complex, multielement middle ear, rather than just a single stapes bone between the eardrum and the inner ear as in other tetrapods. Ears adapted for hearing in air are of little use in water, so auditory systems need modification for underwater hearing or are lost. Modern sea turtles can hear in the range of 200–500 Hz, compared to 100 Hz to 20 Khz for humans, and 1–160 KHz in marine mammals. Marine reptile hearing was probably best developed in the mosasaurs with their particularly prominent ossified eardrums. At the opposite end of the auditory spectrum, ichthyosaurs and plesiosaurs had a reduced hearing apparatus that was lost in elasmosaurs, and in at least that sense they were therefore deaf, although alternative sound detection systems may have been present.

The sense of smell may have been developed in plesiosaurs and ichthyosaurs more so than in mosasaurs, although exactly how this worked in aquatic air breathers is not well understood, and the very small nostrils of many species would seem to inhibit the sense of smell. Nasal olfaction was possibly used to help detect distant upwind food sources and items at the surface, as appears to be the case with sea turtles.

Some sea reptiles probably had sensors not present in other marine vertebrates. Turtles can smell via barbel bumps beneath the chin. The paired tongue tips of mosasaurs should have been used to deposit chemicals picked up in the air, or in this case water, onto the paired vomeronasal organs, with a resulting stereo sense of smell.

## Vocalization

Sea turtles are the least vocal of reptiles, there not being much opportunity for them to communicate via sounds created in their respiratory passages. The same is probably true of past marine reptiles, since they lacked echolocation systems that could have been used for underwater sound generation.

## Diseases, Pathologies, and Injuries

Mesozoic marine reptiles lived in a world filled with dangers to their health and well-being. The infectious disease problem was not as intense as it was for land animals, salt water being a considerable barrier to the transmission of microbes, and many sea reptiles were not prone to form long-lasting beach-based breeding colonies well suited for disease transmission.

Sea reptile pathologies are typically recorded in physical damage in the bones. These include mild damage from the bends, as well as age-related arthritis, bone fusion, and tooth puncture injuries from combat. The latter include flippers that are missing whole sections. In one case an ichthyosaur appears to have had its entire tail bitten off, and, unable to control its swimming, it drowned. The near-universal fate of a truly marine tetrapod is that the immediate cause of death, one way or another, is asphyxiation, usually via drowning. This can range from a failure to quickly reach the surface after live birth, to old age or disease weakening a sea tetrapod enough that it cannot get its nostrils into the air that one last time. Not getting back to sea level at the end of a deep dive in time is also a risk. Wounds suffered in predation or other combat will probably cause the damaged animal to be unable to surface before blood loss or other trauma kills it—orcas sometimes try to kill whales by keeping them from surfacing. At the opposite extreme of drowning is the rarer respiratory failure resulting from stranding among large marine forms that cannot properly respire out of water. Stranded ocean animals may be directly killed by predatory attack.

# BEHAVIOR

## Brains, Nerves, and Intelligence

Because they calculate what to do, brains are biocomputers that conduct analog/digital mass parallel processing over neural networks. In general, the larger—especially relative to body mass—and more complex brains are, the more capable they are likely to be. Sea reptile brains were (and are) consistently reptilian in being on the small side and not highly sophisticated. But this does not mean that small, simple brains have abjectly low performance. Fish and lizards can retain new information and learn new tasks. Many fish live in organized groups. Crocodilians care for their nests and young. Octopi are notorious schemers and escape artists. Social insects with tiny neural systems live in organized collections that rear young, enslave other insects, and even build large, complex architectural structures.

The great dimensions of some maritime reptiles, whether the result of sheer size or superlong necks, posed a potential problem in terms of the time required for electrochemical impulses to travel along the nerves. In the longest sea reptiles, a nerve input from the tail tip to the brain, and the responding command back to the tail, would have traveled 15 m (50 ft) or more. Synaptic gaps where chemical reactions transmit information slow down nerve impulses, so this problem could have been minimized by growing individual nerve cords as long as possible.

## Social Activities

Modern reptiles, including sea turtles and snakes, do not form organized social groups. Birds and mammals often do, but some do not—marine mammals range from solitary to highly social. Likewise, many fish swim in schools, and many do not.

Other than the presumption that Cretaceous oceanic turtles and snakes were nonsocial, as are the living examples, there is little direct evidence regarding the social activities or lack thereof among the marine reptiles of the Mesozoic. Obviously, they did not leave footprint trackways that could record herding and flocking activity. A few marine reptile bone beds may record social groups, but these may have formed during brief breeding aggregations or the like, or over time via the accumulation of individuals—the situations are not clear. It is quite possible that some ancient marine reptiles formed schools or pods, with the fast ichthyosaurs being the most likely to have done so. Such groups may have consisted of multiple species. It is plausible that like some modern social marine predators, schooling reptiles collaborated to improve hunting success by concentrating schooling prey fish into easier targets called bait balls.

## Reproduction

All reptiles reproduce via internal impregnation. If the result is eggs, they are produced in pairs via double ovaries and are small and soft shelled—only various archosaurs including crocodilians, and some or all dinosaurs including birds produce(d) hard-shelled eggs—and they are incubated by the warmth of the soil in the vast majority of species. Other reptiles give live birth, and the presence of oviparity versus viviparity can occur among close relatives. There are two basic reproductive stratagies, r-strategy and K-strategy. K-strategists are slow breeders that produce few young; r-strategists produce large numbers of offspring. One advantage of rapid reproduction is that it compensates for high losses of juveniles via genetic defects, accidents, survival incompetence during early independence, diseases, and especially predation. Producing large numbers of young also allows a species to quickly expand its populations when conditions are suitable, so r-strategists are "weed species" able to rapidly colonize new territories or to promptly recover their population after it crashes for one reason or another. Most fish are fast breeders, as are amphibians and many amniotes. A disadvantage of rapid reproduction is that it requires lots of energy to produce all the offspring, and animals that do not suffer high levels of juvenile predation are typically slower-breeding K-strategists. The latter include all marine mammals, which lavish attention on a typically single pup or calf that they nurse with highly nutritious milk. Sharks and rays include both r- and K-strategists; none are parental, and they may cannibalize their young.

The reproduction of Mesozoic sea turtles was presumably little different from what it is today. Males are smaller than females, and the former court the latter with elaborate sexual displays, with mating occurring in the water. The females lay the resulting numerous eggs in pits dug with their powerful clawed foreflippers into sandy beaches and covered with the sand. For reasons that are obscure, the sex of many reptiles including marine turtles is determined by the incubation temperature, with females becoming increasingly common the warmer the eggs are; presumably this seemingly dysfunctional scheme, which is vulnerable to producing skewed sex ratios depending on variation in environmental temperatures, was in force back in the Mesozoic. The r-strategist sea turtles provide no care to their progeny; they become independent at hatching, which takes about six to eight weeks.

Among many Triassic marine reptiles, direct evidence of egg laying versus live birth is scanty. Those that lacked full flippers may have been able to get onto land and nest, and this is very compatible with but does not disprove the idea that they bore their young live. Notably, there is plausible evidence that the marine tanystropheids were live bearers, but whether this was specifically because they dwelled in salt water cannot be assessed because we do not know how their more continental relations were reproducing.

A plesiosaur fetus has been found within the body of a moderate-sized specimen. The juvenile is solitary and a third the length of its mother. This indicates that at least some if not all plesiosaurs were K-strategists that bore a single, large baby, in which case it is possible that none beached themselves to deposit eggs in the sand. But it cannot be ruled out that plesiosaur reproduction was diverse in practice, and some of the early and/or smaller plesiosaurs may have been shoreline egg layers. Also open to question is whether a plesiosaur mother paid any attention to its calf, as do marine mammal mothers who spend years parenting their progeny. That the plesiosaur calf was single and large suggests that this was so, and that might have been of benefit to the juvenile if the adult was willing to provide some protection against predators. But a key reason juvenile marine mammals stick with their mothers is that the latter provide free and highly nutritious milk, which reptiles cannot do. Nor is it apparent how plesiosaur newborns could have kept up speedwise with the much larger adults—when dolphin mothers feed they may leave their charges under the protection of relatives, a behavior the small-brained sea reptiles were not likely to have been smart enough to practice. It would have made more sense for baby plesiosaurs to forage on their own in shallow coastal zones that offered some protection from predators. There is evidence, albeit less direct, that nothosaurs were live bearers. How much further back viviparity went in sauropterygians is not yet known, and it is possible that live birth versus egg laying was erratic among those able to clamber ashore.

Evidence regarding ichthyosaur reproduction is fairly abundant; a number of adult specimens containing fetuses, some apparently in the process of giving birth, have been discovered. The early ichthyosaurs were viviparous, so it is possible that even their terrestrial ancestors were live birthers. There is evidence that early species gave birth headfirst and later species tailfirst, the latter being the cetacean pattern. The fetuses are small, and in some cases the number of prebirth juveniles in a single female is high, up to nearly a dozen, showing that at least some species were r-strategists that probably directed little or no attention to their offspring. The progeny would have been hard pressed to keep up with their much larger and therefore swifter mothers, who may well have been prone to eat their own young unless they immediately fled as soon as they emerged. It is likely that birthing occurred in shallow waters where the newborns could immediately seek cover from that and other predation; an alternative location may have been drifting sargassum-style surface seaweed.

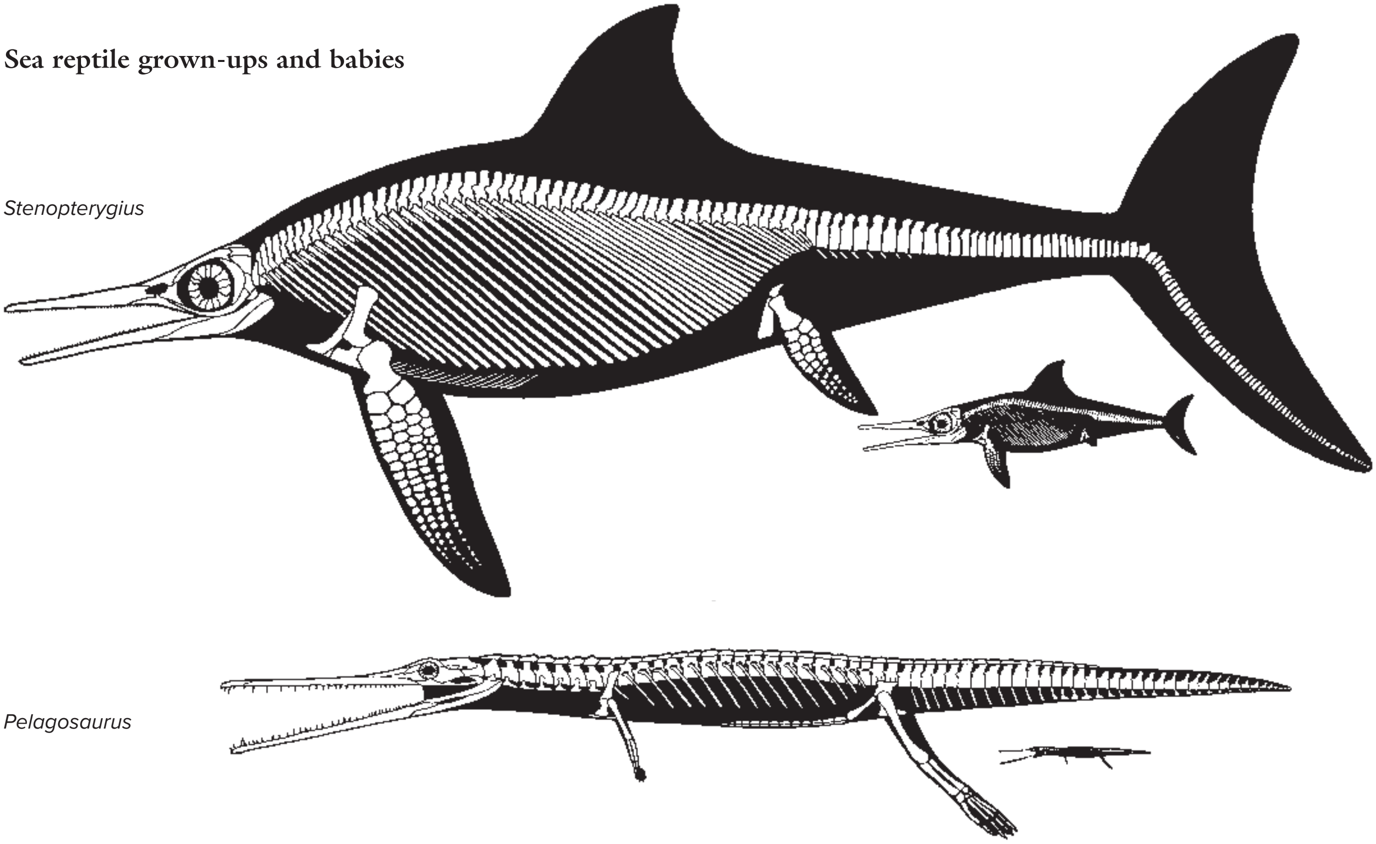
Evidence for the reproductive situation concerning mosasaurs is sparse. Neither eggs nor fetuses have been found in adult female skeletons. The remains of some juveniles about a fifth of adult size have been found well out from the shoreline in the western interior seaway. That is compatible with their being born in deep waters, but it is also possible that the 0.6 m (2 ft) youngsters swam out on their own, as some baby sea turtles do, perhaps in association with drifting seaweed, or they may have drifted there as carcasses from the coastline. It was widely thought that mosasaurs were viviparous r-strategists, like some modern lizards. But the discovery of a football-sized soft-shelled egg—one of the biggest eggs known—in shallow-water marine sediments suggests that at least some mosasaurs may have extruded eggs from which the babies quickly emerged and promptly headed to the surface for their first breath. It cannot, however, be ruled out that the egg belonged to a plesiosaur, or perhaps it is a dinosaur egg that drifted offshore. Some modern sea snakes are shoreline egg layers, and most give birth in salt water, so it is not known which of these the Cretaceous sea serpents were doing.

Nor is there direct information on the reproduction of marine crocs. That they all retained hindlimbs with at least some suitability for clambering ashore implies that they nested on beaches, although it is not impossible that the pelagic metriorhynchids gave aquatic birth.

## GROWTH AND AGING

All land reptiles grow slowly. This is true even of big and energetic (by reptilian standards) monitors, as well as giant tortoises. Most ocean turtles are slow growers, the exception being the leatherback, which grows fairly rapidly. Some marsupials and large primates, including humans, grow at the same rate or only a little faster than the fastest-growing land reptiles. Other mammals, such as other marsupials and a number of placentals, including some marine mammals such as dolphins, grow at a modest pace. Still others grow very rapidly; the biggest living birds, ostriches, grow up in less than a year, as do penguins and as did the hesperornithiformes. Horses are fully grown in less than two years, and blue whale calves put on a couple of hundred pounds a day and reach 100 tonnes or more in a couple of decades—the hyperrapid growth of megawhales being a result initially of their being supplied with enormous quantities of calorie-dense milk by their mothers. Most fish grow slowly, but giant sharks put on weight fairly fast, and the same appears to have been true of the biggest Mesozoic fish. Becoming gigantic requires quick growth in order to reach great dimensions and mass in a reasonable time. Growing fast can be easier in than out of water because the cost of swimming while obtaining the large amounts of food needed to grow rapidly—whether the nutrition is gathered by the juvenile itself or is provided by adults—is much less than the cost of moving on land in search of nutrition. But reproduction while still in the growth phase slows growth down, enough

**Sea reptile grown-ups and babies**



so that even high-metabolic-rate juveniles that are reproducing can have reptile-like growth rates. At the microscopic scale, the bone matrix is influenced by the speed of growth and can be used to estimate growth rates, especially if annual growth lines are deposited—although the alteration or reabsorption of the inner bone during growth and later can complicate counting the rings, similar to how the rotting of a tree core eliminates the record of its early years. As animals such as turtles, many fish, and cetaceans grow, they change form only a modest amount—the need to maintain hydrodynamic uniformity is involved in marine creatures' constancy of form—while others undergo radical changes, as in humans, fast-running ungulates, birds, and fish and amphibians that undergo dramatic lifestyle changes while maturing.

Growth in the hard-shelled turtles of the Cretaceous appears to have been at the same slow pace seen in their modern relatives. That of the softer-shelled species was apparently faster, as in loggerheads, and contributed to the gigantic proportions of *Archelon*. After fleeing the dangerously exposed beaches on which they hatch, the babies of some modern chelonioideans immediately swim far out to sea—using yolk sacs for energy—and seek refuge and food in surface-drifting seaweed, and such was probably true of some Cretaceous examples. Sea turtles become reproductive fairly late, after two or more decades, and life spans are similar to those of humans. The growth of most mosasaurs appears to have been more rapid than that of leatherbacks, albeit not especially fast paced. Basal mosasaurs apparently had more typically reptilian growth, so the group became increasingly like cetaceans as they became more marine. Except for the most basal members of the clade, plesiosaur growth appears to have been rapid, which would have been necessary for the achievement of enormous size in this group. The same applies to ichthyosaurs, and even the most archaic forms show evidence of fast growth.

While juveniles can outnumber adults in a habitat, they are often relatively scarce in the fossil record, perhaps because they survived to adulthood, or the small animals went down the gullet of something bigger, or rapidly decayed. Juvenile sea reptiles are not particularly common, and little is known about baby plesiosaurs, for instance.

Marine reptiles generally experienced significant changes in proportions as they grew. Hatchlings and newborns typically had oversized heads, often dramatically so, sporting big eyes and in many cases short snouts—these features are common in juvenile animals. Relative to the rest of the body the head became smaller, and the snout longer relative to the rest of the head, with maturity. The tanystropheids and plesiosaurs with very long necks did not start out with them; their necks elongated relative to the rest of the animal with growth. Relative head size in plesiosaurs may have been more stable during growth. More subtle proportional changes could occur with other parts of the body.

## ENERGETICS

Vertebrates can utilize two forms of power production. Aerobic metabolism involves the direct use of oxygen taken in via gills, skin, or lungs to power muscles and other functions. This system has the advantage of producing power indefinitely without intense fatigue but is limited in its maximum power output. An animal that is walking or swimming at a modest speed for a long distance, for instance, is exercising aerobically. The other scheme, anaerobic metabolism, involves chemical reactions that do not immediately require oxygen. This system has the advantage of being able to generate about ten times more power per unit of tissue and time. But it cannot be sustained for an extended period and produces toxins that can result in serious illness if sustained at too high a rate for too long, which can be well under an hour. Anaerobic power production also builds up an oxygen debt that has to be paid back during a recovery period. An animal that is running or swimming full tilt is exercising largely anaerobically.

Getting oxygen from water via gills is not easy because oxygen makes up only a very small fraction of 1 percent of the liquid. This is why one must be careful not to put too many fish in a tank, especially if the water is not aerated. In the latter case, and if the surface of the water is covered with a gas-impermeable sheet, the fish in the tank will run out of oxygen in short order. The warmer the water, the less oxygen it can contain. Absorption of atmospheric oxygen by an organism is not affected by temperature. Air is currently easy to get oxygen out of because it is one-fifth oxygen. Some research, however, indicates that atmospheric oxygen levels were half of today's levels in the first half of the Mesozoic and then gradually rose during the Cretaceous to near the modern percentage. If correct, this would have impacted the oxygen content of the water as well as the air. Other research disagrees, so this factor cannot be definitively analyzed at this time.

Most fish and all amphibians and modern reptiles have low resting metabolic rates and low aerobic exercise capacity. They are therefore bradyenergetic, and even the most energetic living reptiles, including the most aerobically capable monitor lizards, are unable to sustain truly high levels of activity for extended periods. Many bradyenergetic animals are, however, able to achieve very high levels of anaerobic burst activity, such as when a crocodilian or reef shark suddenly dashes toward and captures prey. Because bradyenergetic animals do not have high metabolic rates, they depend largely on external heat sources for their body heat, primarily the ambient water temperature for swimmers, so they are ectothermic. As a consequence, fully aquatic bradyenergetic animals usually have body temperatures that are barely above those of the water they are swimming in, and this is true even of the biggest sharks—fluctuating body temperatures are heterothermic. Ergo the temperature at which aquatic reptiles normally operate varies widely depending on their habitat. For marine forms, it can be as high as 32+°C (90°F), and most sea turtles are ectotherms and cannot function below 12°C (50°F), so it is incorrect to generalize reptiles as "cold-blooded." In general, the higher the body temperature, the more active an animal can be, but even warm reptiles have very limited long-term activity potential.

A number of marine fish are not bradyenergetic ectotherms. Some tuna and lamnid sharks have resting metabolic rates above those of reptiles, and they and some other fish are endotherms in that they can keep at least parts of their bodies much warmer than the surrounding water via special heat-exchanging retention complexes in their circulatory systems. So they are tachyenergetic in that they have metabolic rates and energy budgets above the reptilian level, and they are specifically mesoenergetic because they are in the lower tachyenergetic zone. These mesoenergetic fish are at least partially endothermic—in most, only parts of the body can be kept warmer than the surrounding water—but they are not homeothermic because they do not maintain their body temperature at the same level all the time. The low oxygen content of water impairs the ability of these gill breathers to achieve the higher levels of aerobic capacity possible in air-breathing swimmers. Leatherback turtles are bradymetabolic like other reptiles, but they combine constant high levels of activity, their large bulk—which means they have a low surface area relative to their mass—superficial fat deposits, and heat exchangers that leave the flippers unheated so that the thin appendages do not shed heat into the water, to keep their core temperatures up to 18°C (32°F) warmer than the water they are swimming in. This is mass or inertial endothermy—inertioendothermy—and it allows leatherbacks to cope with near-freezing water, whether at high latitudes or great depths.

Most mammals and birds have at least fairly high resting metabolic rates and high aerobic exercise capacity. They are therefore tachyenergetic to one degree or another and can sustain high levels of activity for extended periods. The ability to better exploit oxygen for power over time is probably the chief advantage of being tachyenergetic. Tachyenergetic animals also use anaerobic power to briefly achieve their highest levels of athletic performance, but they do not need to rely on this as much as reptiles, and since they can quickly take in a lot of oxygen, they can recover more quickly. The risk of death from intense anaerobic exercise is very reduced. Because tachyenergetic creatures have elevated metabolic rates, they produce most of their body heat internally, so they are largely or entirely endothermic, in particular tachyendothermic as opposed to inertioendothermic. As a consequence, tachyenergetic animals can achieve more stable body temperatures. Some, like humans, are highly homeothermic, always maintaining a nearly constant temperature throughout the body when healthy. So are some marine mammals, in particular those that dwell in warm waters or are well insulated at their surface by fur or fat. Those that dwell in cold waters but lack sufficient fur insulation are homeothermic when it comes to their core temperatures, but toward the skin their temperatures drop until they are only a little above ambient water temperature. Many birds and some mammals allow their body temperatures to fluctuate to varying degrees on a daily or seasonal basis. So they are heterothermic, albeit in a more controlled manner than reptiles because they can go into high temperature mode by ramping up internal heat production, which bradyaerobic reptiles cannot do. Helping many placental mammals keep their temperatures exceptionally steady is thermogenic brown fat; the absence of this special heat-producing tissue in other tachymetabolic creatures contributes to their lesser thermal stability. The basic ability to keep the body at or near its optimal temperature is another advantage of having a high metabolic rate. Body temperatures of pinnipeds and cetaceans are around 35°C–37°C (mid- to high 90s in °F). High levels of energy production are also necessary to do the cardiac work that creates the high blood pressures needed to be a tall animal. Typically, mammals and birds have resting metabolic rates and aerobic exercise capacity about ten times higher than those of reptiles, and differences in total daily to yearly energy budgets are even higher.

Not all mammals are so highly tachyenergetic. Some are mesoenergetic, with metabolic rates intermediate between reptiles on the one hand and most mammals and birds on the other. The egg-laying monotremes, some marsupials, sloths, anteaters, pangolins, hedgehogs, and sirenians are similar to mesoenergetic tuna and sharks in their resting metabolic rates. These low rates along with low activity levels leave manatees and dugongs without the heat production needed to cope with chilly water.

Bradyenergetic reptiles enjoy the advantage of being energy efficient, allowing them to survive and thrive on limited resources. Tachyenergetic animals can sustain higher levels of activity that can be used to acquire even more energy that can then be dedicated to the key factor in evolutionary success, reproduction.

Determining the energetics of ancient animals requires examining a set of bioindicators. If fossils represent a group that has survived with highly similar form, function, habits, and habitats until today, then the animals likely possessed similar metabolics and thermoregulation. So it is presumed that the hesperornithiform diving marine birds were tachyenergetic endotherms, a logical conclusion that is supported by other lines of evidence including their preserved feathers. A body ensheathed in blubber is evidence of at least elevated body temperatures. Isotopes in bones or teeth can record the internal body temperature at which a fossil animal was operating, and if it was markedly higher than that of its habitat, then it had some form of endothermy—via a high metabolic rate if in a small example, or because of bulk if in a large species—and if it was constant over time, it was homeothermic. Rapid growth tends to be associated with high metabolic rates, although this is less strongly correlated in energy-efficient swimmers than in nonaquatic creatures that have to work harder to find food. The presence of tetrapods in very cold habitats is strong evidence of some level of tachyenergy, as well as some level of endothermy, especially if bradyenergetic tetrapods are absent from the habitat.

Because ancient sea reptiles were reptiles, it was long presumed that they had reptilian energetics, a circular argument that was not scientifically tested. That Mesozoic oceans tended to be stereotyped as balmy and tepid subtropical and tropical seas reinforced this bias. The growing knowledge that some fish and leatherbacks are endotherms and even mesoenergetic helped open up consideration of the possibility that Mesozoic marine reptiles may not have been the bradyenergetic ectotherms that all modern terrestrial reptiles are. Techniques that showed that nonavian dinosaurs were tachyenergetic and endothermic to varying degrees contributed to the reconsideration.

Cretaceous hard-shelled sea turtles were presumably as bradyenergetic and ectothermic as the group is today, while the less armored of the chelonioideans were candidates for being bradyenergetic inertioendotherms in the leatherback mold. If so, the latter two groups had the potential to dive into the cold depths. It can similarly be presumed that Cretaceous dolichosaurs and sea snakes, with bodies too slender to retain heat, were classic reptilian bradyenergetic ectotherms like their living serpent relations. Other candidates for classic reptilian energetics include thalattosaurs, helveticosaurs, atopodentatians, placodontiformes, hupehsuchians, pachypleurosaurs, and aigialosaurs, which correspondingly favored warm shallows.

Sea crocs appear to have been a metabolically mixed bag. Examination of isotopes in their teeth indicates that the armored examples that were least dramatically modified from freshwater forms appear to have been bradymetabolic ectotherms that could use sun basking on shorelines to boost their body temperatures, which were in the range of 27°C–34°C (80°F–93°F). As a result of their reptilian energetics, they appear to have been successful during warmer periods, fading away when cooler waters became more predominant. Nor were they able to inhabit chilly polar waters. Isotopes indicate that the more highly marine metriorhynchoids were somewhat more energetic and endothermic than the crocodilian norm, freeing them from the need to bask, for which these more pelagic animals were ill suited, and making them more resistant to grand climatic shifts. They were not, however, sufficiently tachyenergetic to be highly homeothermic; their body temperatures were 29°C–37°C (84°F–98°F).

Tooth isotopes, bone structure including the fast growth it records, blubber, and the presence of some in cold polar waters support the idea that plesiosaurs of all sizes were highly tachymetabolic endotherms in the manner of pinnipeds and cetaceans. Body temperatures appear to have remained steady around 35°C (95°F), even in cold waters. The same evidence indicates that ichthyosaurs of all sizes were also full-blown tachyendotherms with body temperatures around 35°C. Although not especially fast growers, and with body temperatures that appear to have fluctuated a little, blubber-sporting mosasaurs, some of which were polar, appear to have been highly tachyendothermic, with body temperatures up to 39°C (100°F). There is some intriguing evidence that the gigantic paleophid sea snakes of the early Cenozoic were more energetic than the reptilian norm. Lacking the extra heat generation of placental mammal-style brown fat, the pelagic reptiles had to rely entirely on the heat churned out by organs and muscles doing their biological jobs, so the temperature stability of the tachymetabolic marine reptiles was presumably not as steady as can be achieved by sea mammals.

Until the 1960s it was assumed that high metabolic rates and/or endothermy were an atypical specialization among animals, being limited to mammals, birds, perhaps some therapsids that were the ancestors of mammals, and maybe the flying pterosaurs. The hypothesis was that being tachyenergetic and endothermic is too energy expensive and inefficient for most creatures, and these conditions evolved only in special circumstances such as the presence of live birth and lactation, or big brains, or powered flight. Energy efficiency should be the preferred status of animals, reducing their need to gather food in the first place. It has since been realized that varying forms of tachyenergy definitely are or probably were present in large flying insects, tuna, lamnid sharks, some basal Paleozoic reptiles, some sea turtles, plesiosaurs, ichthyosaurs, mosasaurs, paleophid snakes, brooding pythons, basal archosaurs, basal crocodilians and pelagic crocs, all dinosaurs including birds, some pelycosaurs, therapsids, and mammals. Energy-expensive elevated metabolic rates and body temperatures appear to be a widespread adaptation that has evolved multiple times in animals of the water, land, and air. This should not be surprising in that being highly energetic allows animals to do things that bradyenergetic ectotherms cannot do, and DNA selection acts to exploit available lifestyles that allow reproductive success, without caring a priori whether it is done with energy efficiency. Whatever works, works. So many animals do live on low, energy-efficient budgets, while others live by using more energy to acquire yet more energy that can be dedicated to reproducing the species.

A long-term debate asks what specifically it is that leads animals to be tachyenergetic and endothermic. One hypothesis proposes that it is habitat expansion, that only animals able to keep their bodies warm when it is cold outside can live in chilly places, whether near the poles, at high altitudes, in deep waters, or during chilly nights. The other proffers that only tachyenergetic animals with high aerobic capacity can achieve high levels of sustained activity regardless of ambient temperatures, whether at sea level in the tropical daylight or during polar winter nights, and that ability is critical to going high energy. Certainly the first hypothesis is true, but it is also true that all the many animal groups that feature high energy budgets and warmer-than-ambient body temperatures also thrive in warm and even hot climes where they beat out the bradyenergetic creatures in activity levels. So both hypotheses are operative.

**Highly energetic *Pteranodon* and *Platecarpus* feeding on fish and belemnite schools (mosasaurs and front pterosaur to same scale)**

## GIGANTISM

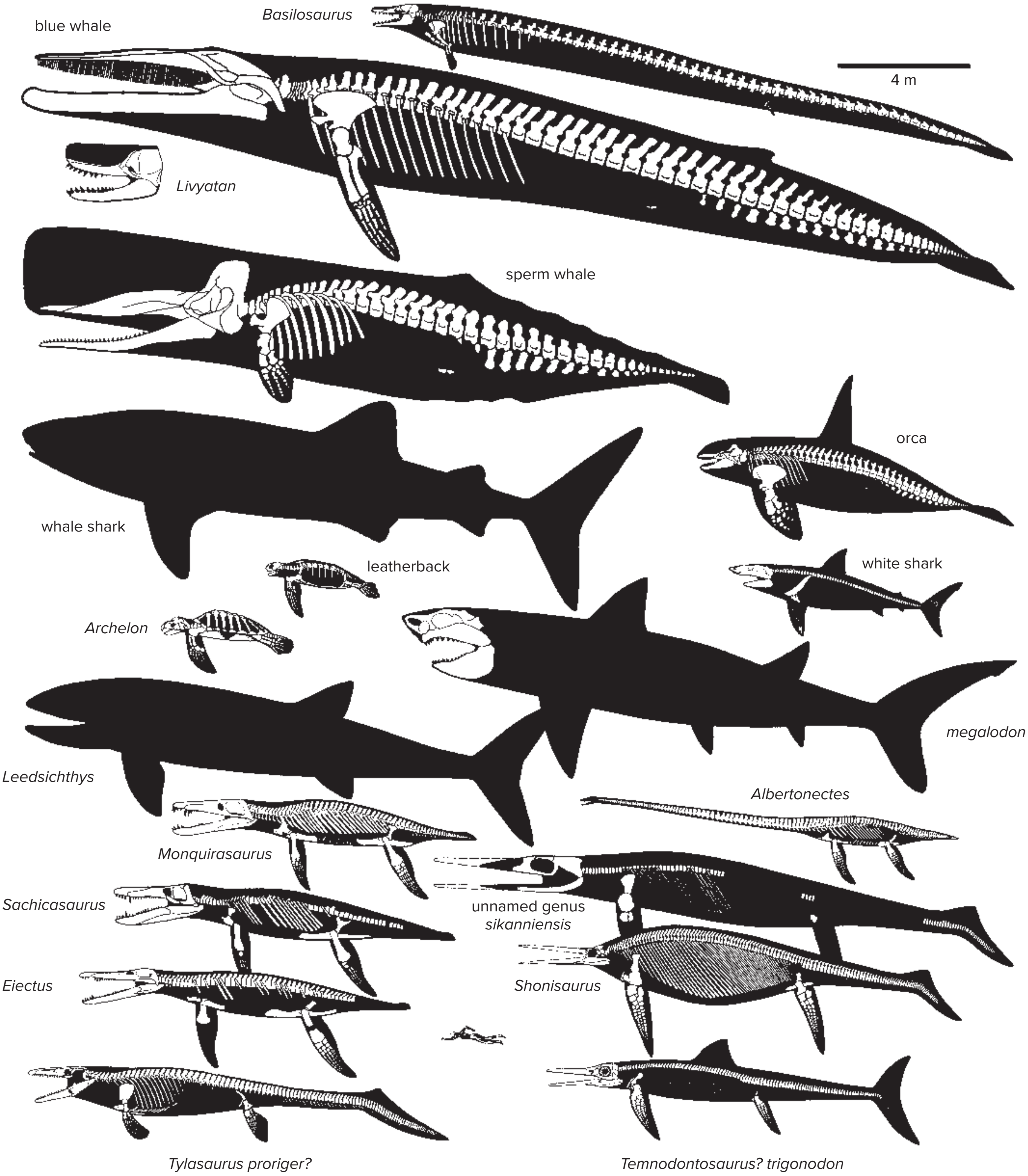
In the 1800s, Edward Cope, famed discoverer of giant plesiosaurs and mosasaurs, proposed what has become known as Cope's Rule, the frequent tendency of at least some animals in a group to evolve gigantism, as in the dinosaurs including birds, pterosaurs, and ancient mammals he also uncovered. Being really big has numerous advantages, including more successfully preying on other animals and a greater ability to resist being prey; energy efficiency per unit of mass, in metabolism as well as in cost of locomotion; resistance to fast starvation (water shrews have to eat as much as they weigh each day, which is why they are so frenetic, porpoises are much calmer because they down a small fraction of their own mass daily, and some megawhales normally go for months without feeding); easier internal thermal stability; and the ability to produce more and/or larger offspring (a blue whale calf weighs as much as a typical female Asian elephant). Downsides include greater sudden vulnerability to extinction over the long term because of population disruption during an environmental crisis, because of smaller adult populations resulting from larger individual food budgets and slower K-strategy reproduction, which is common among big beasts, and because of exclusion from many niches suitable for small animals such as shallows and reefs.

Among bony fish and whales, ancient and modern, the biggest examples have been filter feeders that deploy large mouth-straining arrays. Bioenergetic calculations indicate that aquatic creatures that can with relatively little effort sweep up the immense biomass of countless small invertebrates and fish that pack the oceans in some locations—such as where deep cold waters loaded over time with nutrients upwell into warm shallows where the nutrients feed sea life—are best able to acquire the immense amount of food needed to be enormous. Finding and chasing down large individual prey items burns more energy relative to biomass consumed and therefore limits maximum size. The largest sea reptiles did not sport big filter complexes. Why this is so is not apparent; a few of the small Triassic aquatic reptiles look like they were filter feeders, as were some of the late-appearing, small-headed plesiosaurs. The perplexing failure of any maritime reptiles to become big-mouthed water strainers may help explain why they never got nearly as big as the larger baleen whales, or even the greatest filter-feeding bony fish and sharks. In turn, the absence of a collection of big and slow, filter-feeding reptiles or fish for most of the Mesozoic may explain why no ocean-going flesh-eating reptile became as large as the megalodon shark. The absence of pelagic reptiles comparable to the big-toothed physeterids such as the deep-diving sperm whale can be blamed on their lack of the biosonar they would have needed to hunt the large deep-water squids of the late Mesozoic. Interestingly, the probable need of the lizard mosasaurs to go into rivers on occasion to refresh themselves with saltless waters would help explain why they never became truly titanic.

However it is achieved, being big has sufficiently powerful advantages that as early as the Triassic a number of sea reptiles were quite large. All the core Jurassic-Cretaceous marine reptile groups except marine crocs evolved gigantic examples, and even today some sea turtles are large. Even so, reptiles of the seas have never matched the great fish and whales in size. Known specimens record animals under 20 m (65 ft) long and 20 tonnes. Some size estimates of late have been extremely excessive, claiming lengths of up to 26 m (85 ft) and 80 or more tonnes, with some extrapolations of early ichthyosaurs even reaching the realm of blue whales. These fourfold-plus overestimates flow from repeated misreadings of the published dimensions of the largest known ichthyosaur, and from the use of overplump volumetric models. These major oversizings have led some to propose extremely rapid size expansions among the very early ichthyosaurs of the Triassic that far exceed those seen among any other vertebrate group and are almost certainly beyond what natural selection could produce. Still, it is possible that we have not found the greatest ancient marine reptiles. In the size comparison chart, note that the biggest living examples of oceanic giants that are illustrated represent rare world-record specimens, which can be a fifth to a quarter longer and two-thirds more to twice as massive as typical for the species—this includes the blue whale, in which females are the largest. Because the number of fossils known for each of the extinct taxa is small, they almost certainly represent average adult sizes. It is therefore quite possible that the largest marine reptiles reached 30–40 tonnes, about the size of big humpback whales. Similarly, the largest Jurassic filter-feeding fish and megalodon might have been 60 tonners, matching the biggest whale sharks. At the opposite size extreme, ancient sea reptiles could be quite small—some Triassic pachypleurosaurs were just 0.2 m (0.6 ft) in length and 20 g (0.7 oz).

## MESOZOIC MARINE EXPEDITION

Assume that a practical means of time travel has been invented, and, *The Princeton Field Guide to Mesozoic Sea Reptiles* in hand, you are ready to take a trip to those ancient times to swim in the sea reptiles' watery world. What would such a voyage of exploration be like? Here we ignore some practical issues that might preclude such an adventure, such as the problem of cross-contaminating different time periods with exotic diseases, though this would not be a terribly high risk in an ocean environment. Then there is the classic time paradox issue that plagues the very concept of time travel. What would happen if a time traveler to the era of thalattosaurs, ichthyosaurs, plesiosaurs, and mosasaurs did something that changed the course of events to such a degree that humans never evolved, which would mean that no time travelers would come into existence and abort their own existence? Fortunately,



**Mesozoic marine giants compared to Cenozoic marine giants**

dealing with marine life makes that awkward scenario less likely than being ashore where our ancient ancestors dwelled.

One difficulty that might arise could be the lack of modern levels of oxygen and the extreme greenhouse levels of carbon dioxide (which can be toxic for unprepared animals), especially if the expedition travels to the Triassic or Jurassic. Acclimation could be necessary, and even then, supplemental oxygen might be needed at least occasionally. All the work would be at sea level, so that would help. In tropical zones high levels of heat could pose a problem but should be tolerable, especially assuming the vessel that would be necessary for observing open-ocean life was air conditioned. A serious threat would be storms up to the size of hurricanes and typhoons. These would not be dramatically more severe than they are today, but a probable lack of reliable weather forecasting would make the danger of being caught in one significant. Having multiple vessels to aid one another if and when serious problems arose would be appropriate.

Open-ocean reptiles and other marine life could be observed from the main vessels, any light craft and drones they launched, small human-piloted subs, or robotic subs, or by snorkelers and scuba divers. Of these, only swimming among the marine creatures of the time would pose a potential threat via attack from predatory fish, sharks, and reptiles, some able to swallow a human whole. It is tempting to warn of the dire danger of swimming among such rapacious creatures, but how severe the danger would actually be is hard to assess. We once would have thought it reckless to swim among sharks and killer whales, but skilled divers frequently do so today, even with the biggest great whites. Apparently, sea creatures do not usually see humans as normal prey. Even so, sharks do on occasion attack humans, and big-headed plesiosaurs and mosasaurs would be real potential dangers. To be prudent, big predatory sea life would be most safely observed via remotely controlled submersibles—although it is possible that they could end up going down the gullets of the biggest sea reptiles!

## IF ANCIENT SEA REPTILES SURVIVED

Assume that no plesiosaurs or mosasaurs were killed off by the K/Pg impact and continued into the Cenozoic, or that the impact did not occur and such sea reptiles were not liquidated 66 million years ago. What would the evolution of animals of the water have been like in that case?

Certainly the extinct maritime reptiles, along with marine crocs and sea turtles, would have continued for millions of years, perhaps tens of millions, possibly even to today. How long and how well they would have done would depend in part in their diversity at that time. If only a handful of species made it to around 60 million years ago, then the groups would have been at high risk of extinction, and the more species flippering about, the more resilient they would have been.

Another variable is the situation with mammals. If the nonavian dinosaurs remained abundant, then they may well have continued to suppress the evolution of terrestrial mammals to the degree that they would have remained small creatures unable to spin off a host of big marine mammals. Without mammalian competition, it is very possible if not probable that reptiles would have remained a major component of the ocean fauna until today. In that case, plesiosaurs and mosasaurs, and perhaps sea crocs, would dominate the open ocean realm along with turtles, sharks, bony fish, and cephalopods—whether the latter would include ammonoids and belemnites is uncertain but plausible. The elevated metabolisms of the plesiosaurs and mosasaurs might have allowed them to continue to do well as the high-latitude oceans became colder in the late Cenozoic. Perhaps one or more of the plesiosaur groups would have gone extinct; it is also possible that ocean reptiles would have developed new forms. It is unlikely that any big reptiles would have finally gotten around to becoming colossal filter feeders like baleen whales; that niche would probably have been left to the sharks. Also not likely is that any reptiles would have reassumed a thunniform body like that of the ichthyosaurs; that role would be played by fish, both bony and cartilaginous. Also implausible are big-brained or echolocating marine reptiles, so deep-sea supersquids would be safe from them. Even if the archaic sea snakes persisted into modern times, it is quite possible that the venomous snakes would also have become dwellers of salt waters. It is possible that megalodon was a specialized whale killer and scavenger, and if so the absence of big cetaceans may have precluded the evolution of a predaceous megashark in reptile-filled seas. Or maybe something like megalodon would have chowed down on big pelagic reptiles. Penguins may well have evolved on a planet free of marine mammals, and they would not have posed serious competition for sea reptiles.

In the other scenario, nonavian dinosaurs do not make it into the Cenozoic, while plesiosaurs, mosasaurs, sea snakes, sea crocs, and marine turtles do make it through. In this case, the mammals of the continents take off evolutionarily and could potentially spin off sirenians, pinnipeds, and cetaceans. This situation leads to multiple plausible results. At one extreme the presence of a diverse marine reptile fauna aborts the movement of therians into the open seas of the world. But big-brained, social, parental mammals may have been able to overcome the reptile competition. If so, it is feasible that manatees, seals, dolphins, and whales, the latter two sporting sophisticated echolocation systems, may have driven their reptilian opposition to extinction. On the other hand, small-brained turtles and fish continued to do well in the face of the mammalian invasion, so nonturtle marine reptiles may have been able to deal with marine mammals, albeit perhaps in lesser numbers and diversity than they would have had in the absence of marine mammals.

## MESOZOIC MARINE REPTILE CONSERVATION, KEEPING, AND CONSUMPTION

If the last scenario above is taken to its extreme, assume that a diversity of sea reptiles beyond turtles and snakes managed to survive to modern times. And that we humans or something very like us had evolved and produced a technological civilization similar to the one we have. How would the assorted sea reptiles be doing?

The overall situation for modern sea reptiles would probably be serious, but just how serious is hard to calculate. We know this in part because the prognosis for the sea turtles we do have in the modern oceans is grim. They had little trouble surviving for tens of millions of years in good order, but they are currently in crisis in part because of human disruption of their nesting sites for a host of reasons. And for tens of millions of years large marine mammals remained diverse and actually increased in size to unprecedented dimensions in the recent geological record. The amazing collapse of whale populations has been largely the result of massive hunting that started in the 1700s, nearly extinguishing the right whales of the Atlantic, followed by the long-range Yankee sail- and oar-driven whalers that slaughtered whales in the 1800s, and culminating in the powered industrial whale ships of the 1900s that drove many species to near extinction. Not being filled with oils or other useful products, reptiles might not have been the target of an entire maritime industry. Nor would live-bearing marine reptiles have been afflicted by humans digging up their eggs for breakfast on beaches, or the beaches being developed for human use.

What would endanger the likes of modern plesiosaurs, mosasaurs, and so forth would be large-scale commercial net fishing, which would drown or otherwise afflict considerable numbers of reptiles, as it does sea turtles and mammals, and even big whales. Also a danger would be collision with ships. Another problem would be the plastic trash that is swamping the oceans. This would be ingested by some sea reptiles, interfering with their digestion—it kills some sea turtles. These threats would be serious but not critical to open-ocean reptiles. In the end it would come down the degree to which the reptiles were being hunted, presumably for their meat, which might or might not enjoy wide popularity—it is interesting that whale meat is not highly popular, many cuts being gamy. Because plesiosaurs were apparently slow breeders, they would be vulnerable to population collapse, just as sharks are proving to be if hunted at similar levels. Without knowledge of mosasaur reproduction, this aspect of their vulnerability is not assessable.

If a sea reptile fauna were extant, there is no doubt that marine reptile watching from boats would be popular. Those that would fit into big tanks would also be popular displays in public aquariums. Being small brained, they would not be as readily trainable as sea lions, dolphins, and orcas, so plesiosaur or mosasaur shows would be improbable. With the evolution of animal rights ethics, imprisoning sea reptiles for human viewing and other purposes would become increasingly controversial.

## WHERE FOSSIL SEA REPTILES ARE FOUND

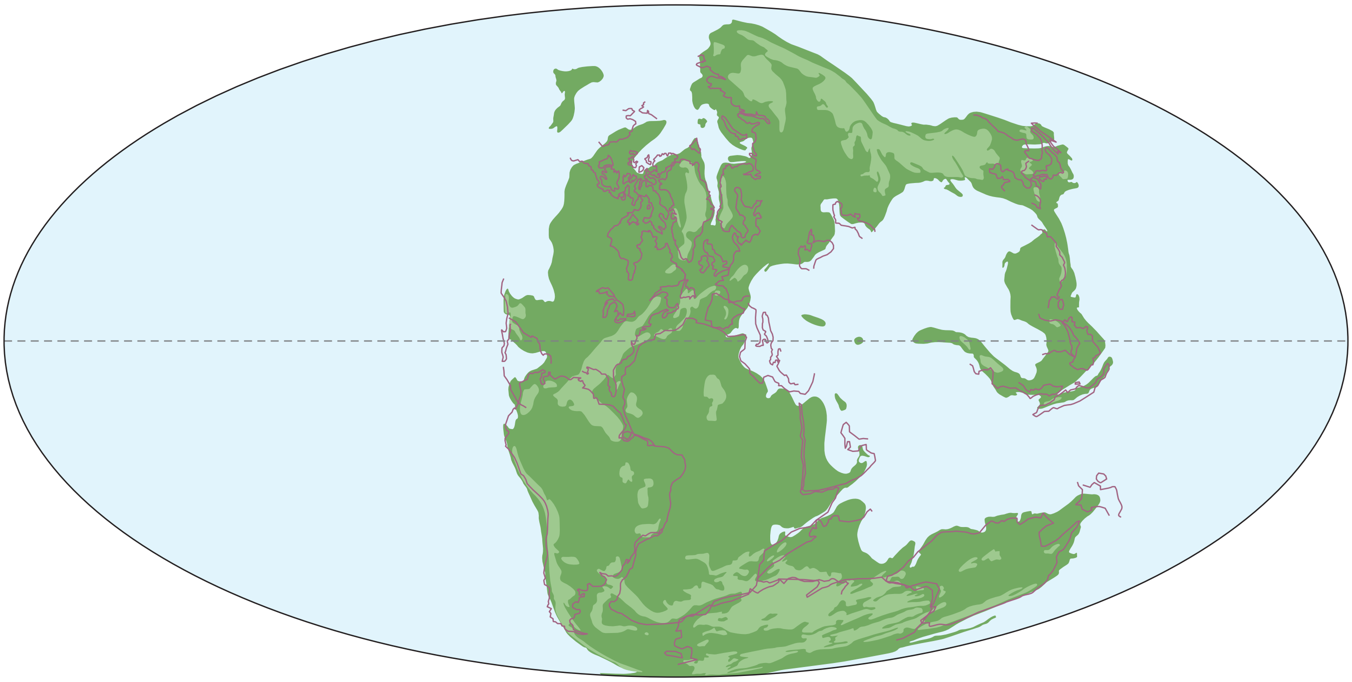
Because sea reptiles aside from turtles and snakes are in fact long gone and time travel probably violates the nature of the universe, we have to be satisfied with finding the remains they left behind. Mesozoic marine reptiles lived in all oceans, some of them shallow seaways that covered large portions of continents, so where they are found is determined by the existence of conditions suitable for preserving their bones and other traces, as well as by conditions suitable for finding and excavating the fossils. For example, if a sea reptile habitat lacked the conditions that preserved fossils, then that fauna has been totally lost. The same is true if deposits containing their fossils eroded away or were tectonically subducted into the mantle and melted. If fossils of a given fauna of marine reptiles are currently buried so deep that they are beyond reach, or on the bottom of watercourses, then they are not available for scrutiny.

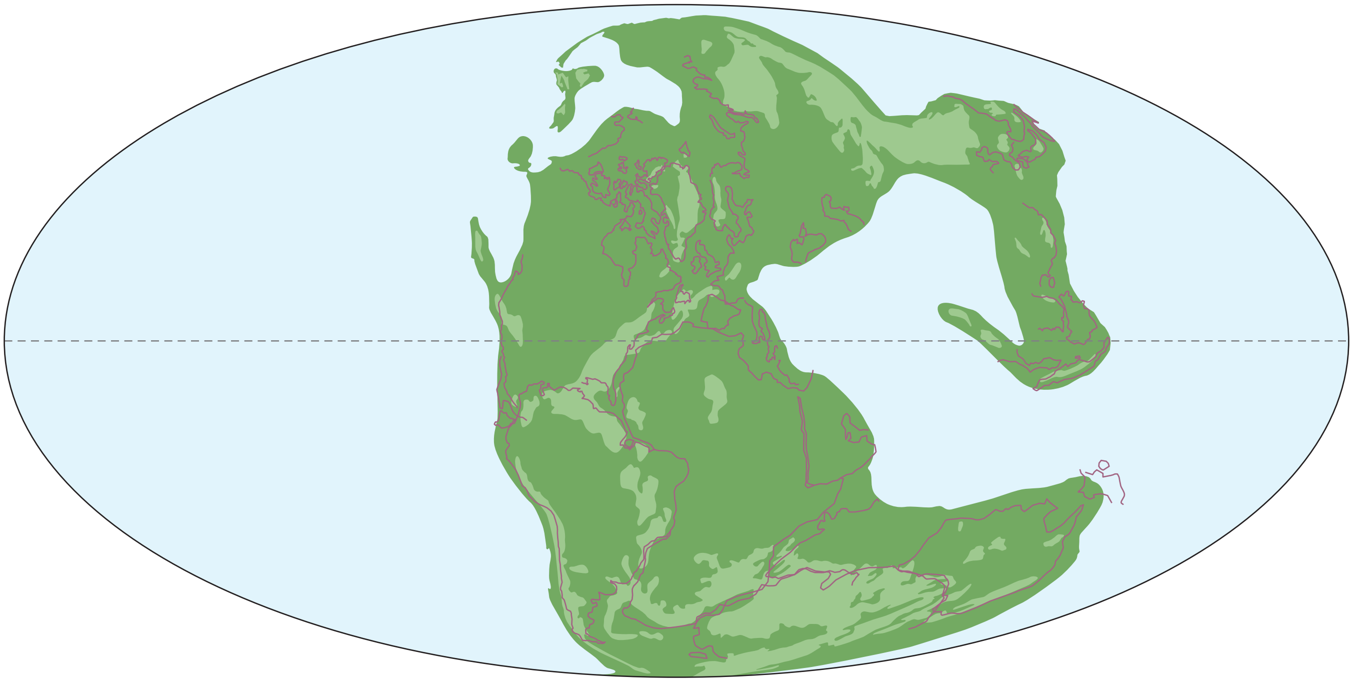
All but a very small percentage of carcasses are destroyed soon after death. Many are consumed by predators and scavengers, and others rot away. Even so, the number of animals that have lived over time is immense. Because at any given time from the beginning of the Triassic to the end of the Mesozoic many millions of sea reptiles were probably alive, amounting to many, many billions over the 186 million years they existed, most of them juveniles and small adults, the number of sea reptile fossils that still exist on the planet is large, probably including many millions of individual specimens.

Of these, only a tiny fraction of 1 percent have been found in or near the very small portion of formations that bear sea reptiles and are exposed on the surface where the fossils can be accessed, or in the deeper quarries that allow additional remains to be reached. Even so, the number of marine reptile fossils that have been scientifically documented to at least some degree is considerable. The question is where to find more of them.

As the moving continents constantly shed massive amounts of sediments via rivers and streams as well as by beach and cliff erosion, large tracts of the ocean build up layers of sedimentary sands, muds, and clays. This is especially true in coastal zones, but even the deep seas receive their share. Adding, sometimes massively, to sea bottom buildup are the tiny calcium carbonate shells of planktonic foraminifera that form limestones, including chalks, as exemplified by the White Cliffs of Dover.

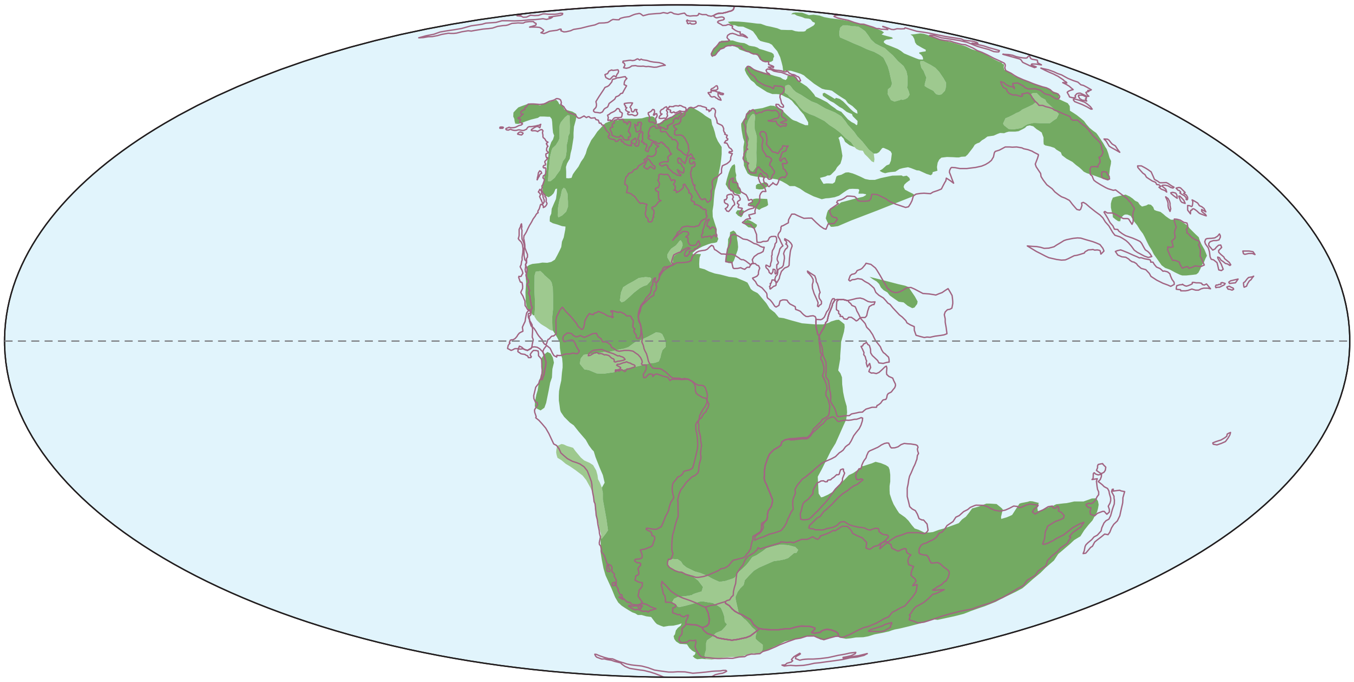
Early Triassic (Induan–Olenekian)

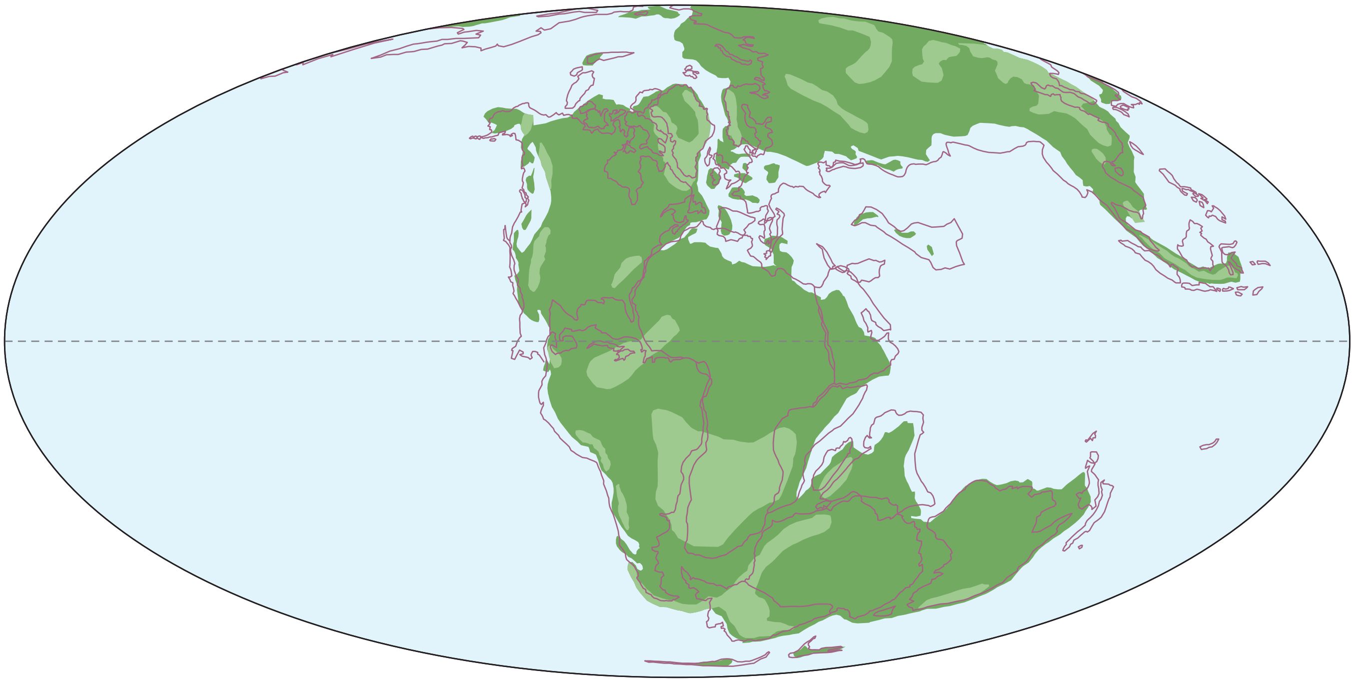




Middle Triassic (Anisian)

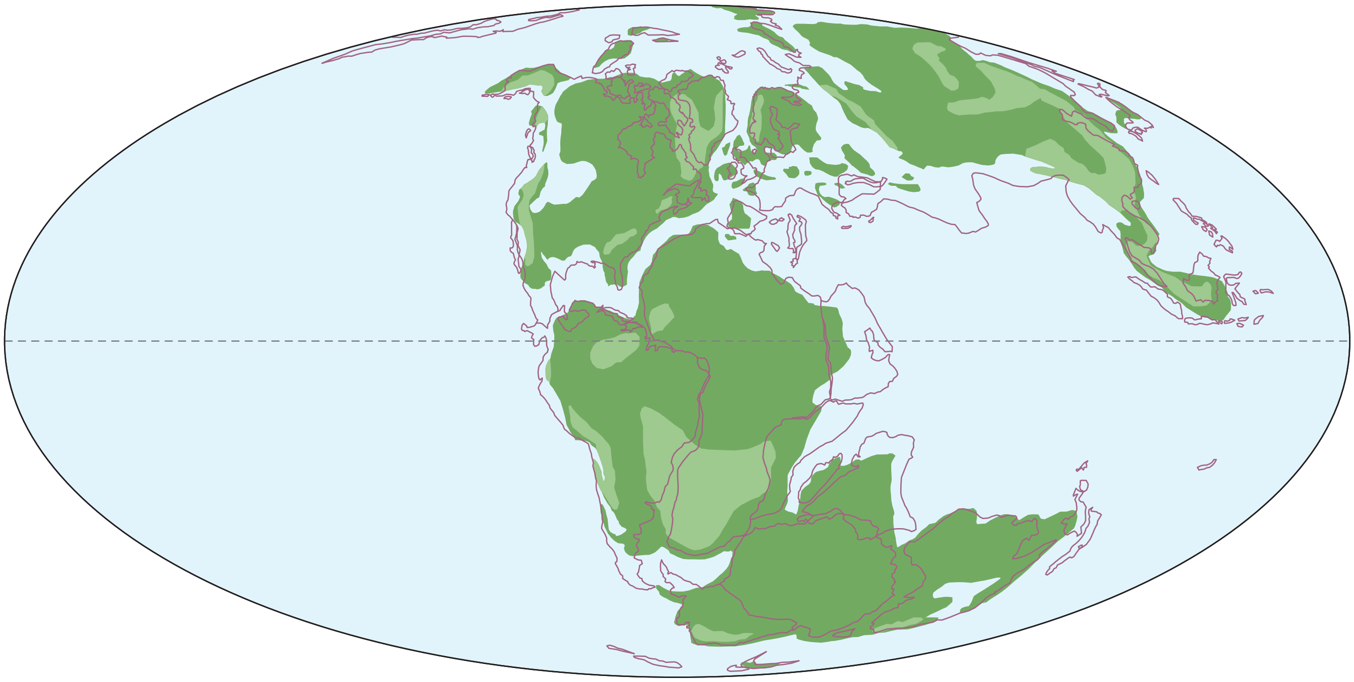
Late Triassic (Rhaetian–Norian–Carnian)

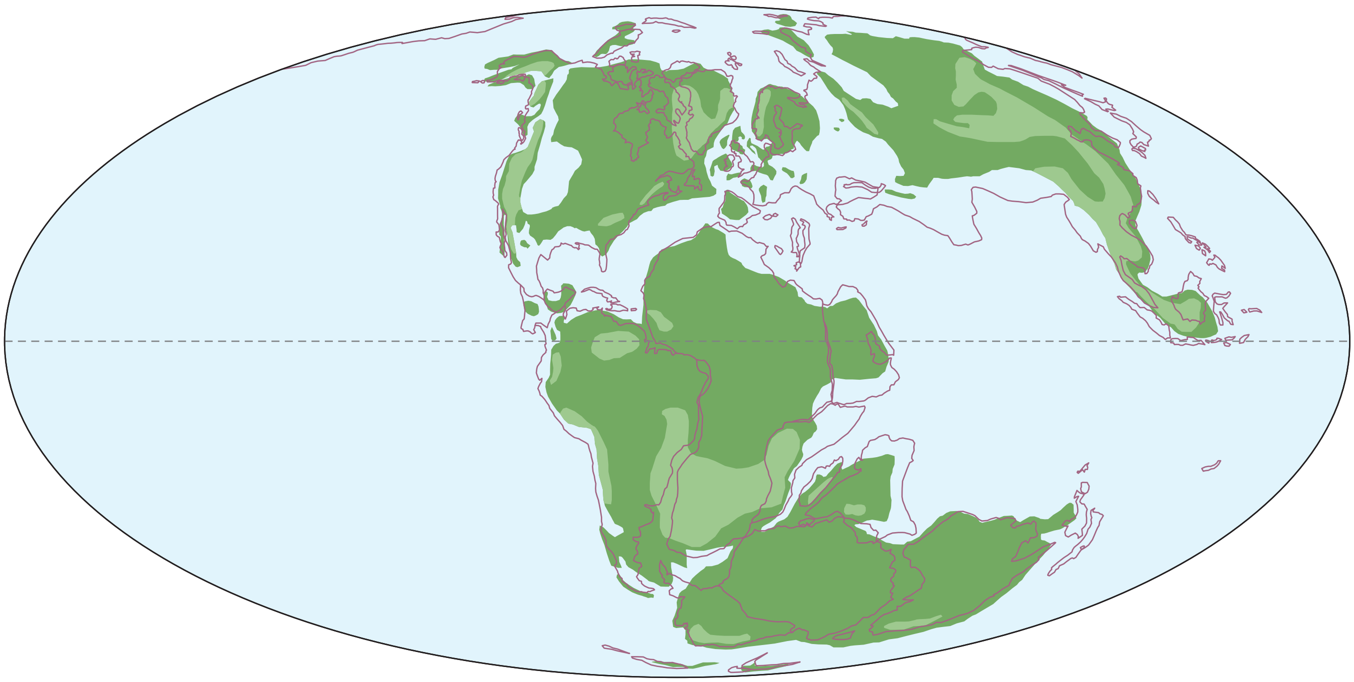




Early Jurassic (Sinemurian)

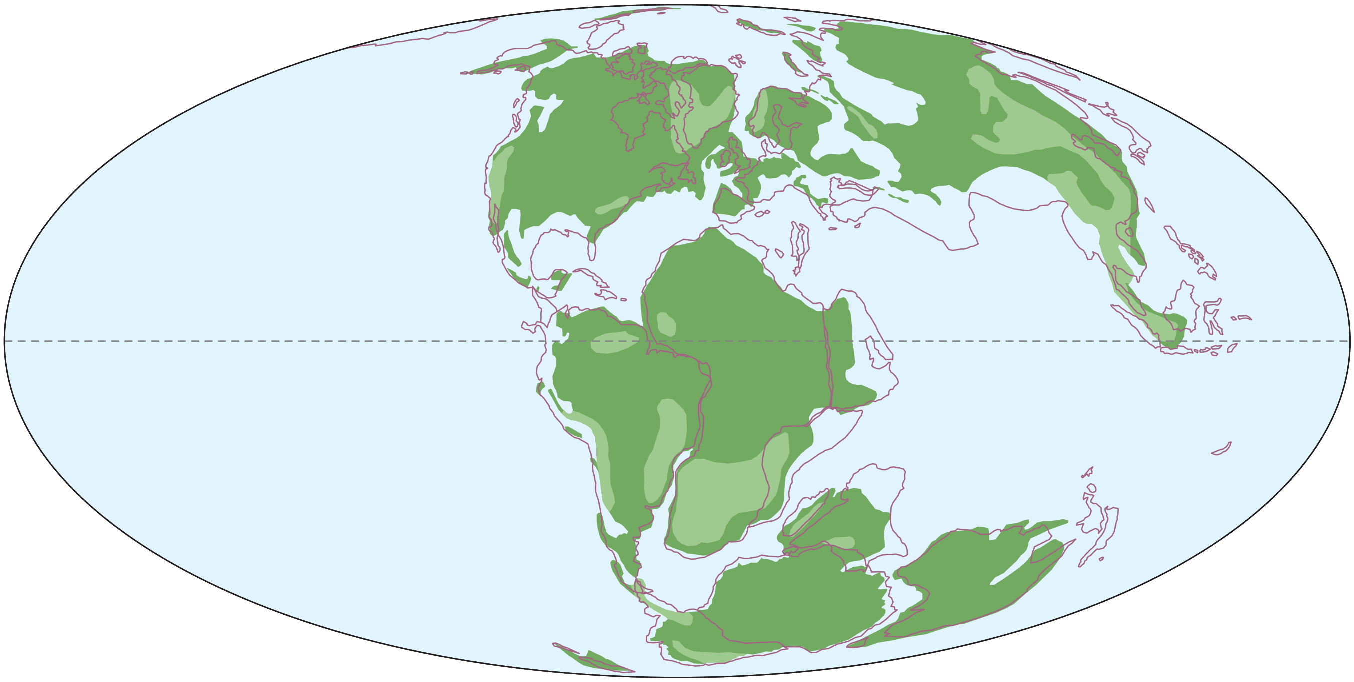
Middle Jurassic (Callovian)

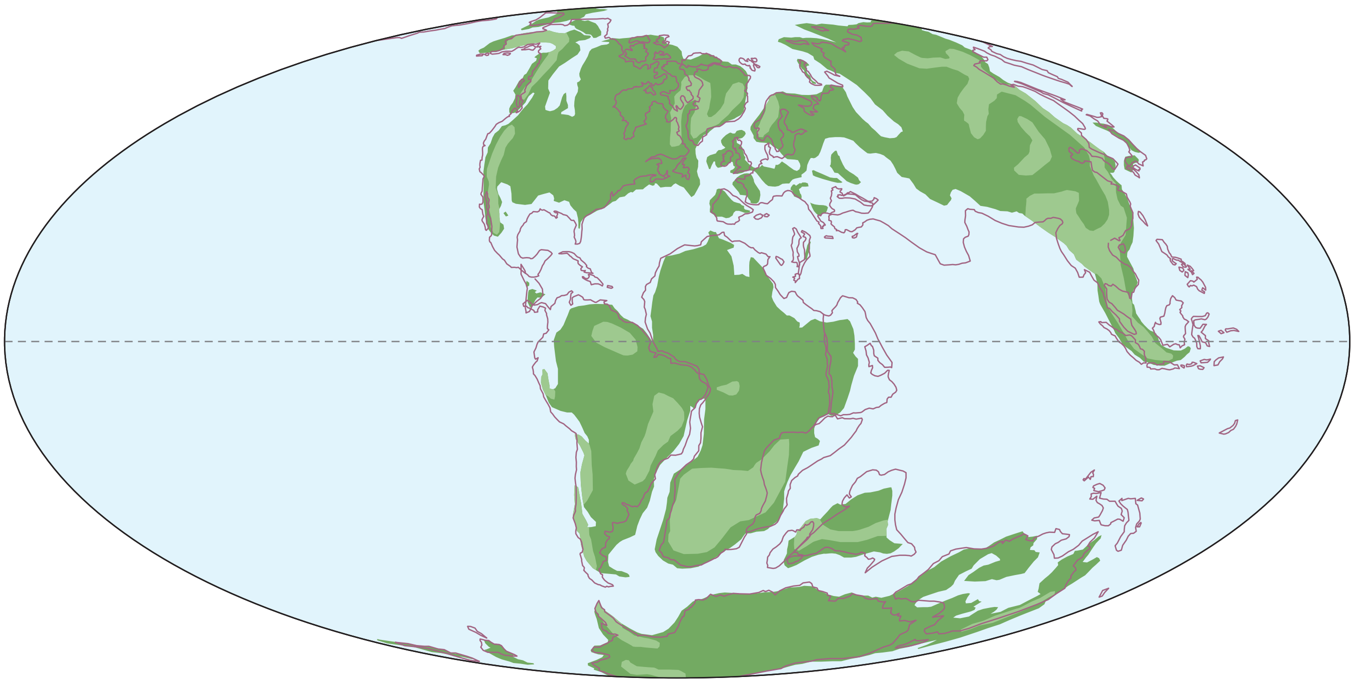




Late Jurassic (Kimmeridgian)

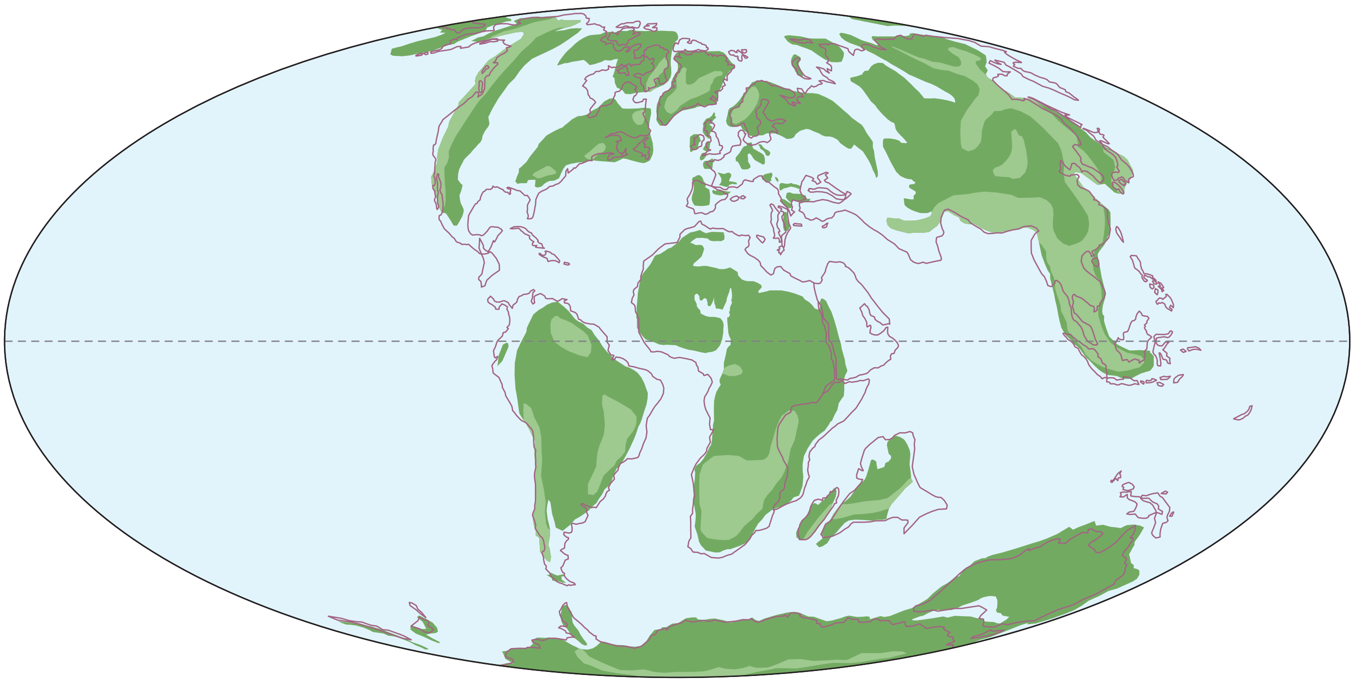
Early Cretaceous (Valanginian–Berriasian)

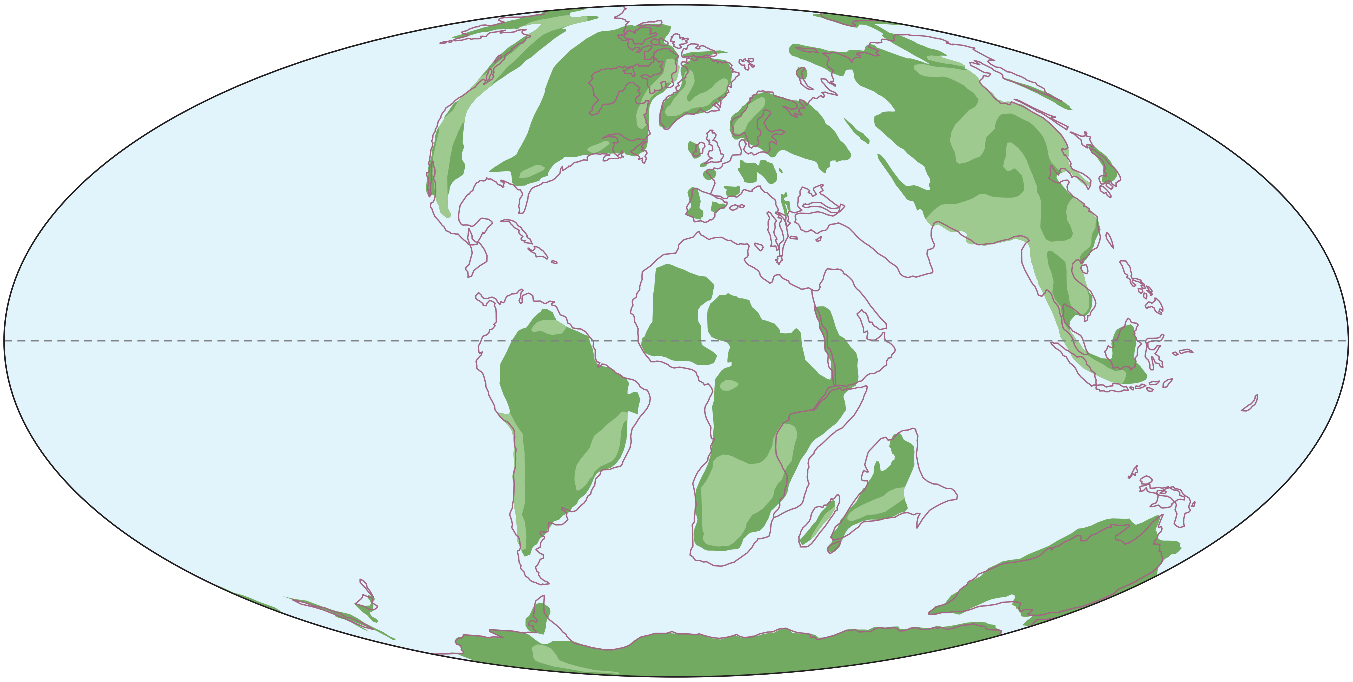




Early Cretaceous (Aptian)

Late Cretaceous (Coniacian)





Late Cretaceous (Campanian)

Depending on the circumstances, the sands, muds, clays, and limestones can be mixed in varying proportions. Volcanics in the form of ashfalls make a minor but important addition, and they are particularly useful for providing absolute dates as described earlier. Some of the sediments are fairly coarse sands, which may be suitable for preserving large skeletons. Other, extremely fine-grained deposits are laid down in calm, oxygen-depleted, sometimes toxic lagoon bottoms between beaches and reefs, and these can form the Konservat-Lagerstätten deposits, which preserve exquisite details, even soft tissues, usually of smaller creatures.

Among the sea sediments most likely to be preserved and later exposed are those laid down in shallow seaways covering continents. Thus we find plesiosaurs, mosasaurs, and marine turtles in Kansas. The deposits on the north and south sides of the English Channel were laid down in shallow seas surrounding what was then the archipelago of Euro-islands. Other sea reptile formations are continental coastal deposits that have been elevated above sea level since the Mesozoic. Not readily accessible are deposits laid down in the very deep oceans, beyond the continental shelves. Some are still far underwater. Others have been subducted into the mantle in superdeep trenches. The only way deep-sea sediments can become useful to paleozoologists is when an oceanic plate smashes into the edge of a continent and is thereby pushed up to at least a bit above the current low tide line.

Because sea reptile paleozoology is not a high-priority science backed by big financial budgets, and because the number of scientists searching for and excavating their remains in the world in a given year is only in the many dozens—which is markedly more than in the past—the number of Mesozoic marine skeletons that now reside in museums is still in the low thousands. In the lab, fine tools are often used to very meticulously eliminate some or all of the sediment from bones and any other remains. Acids can also remove dissolvable sediments such as limestones without mechanical disturbance. Slab mounts, in which a flattened skeleton is left half encased in a flat, hard plate that was first deposited as mud at the bottom of a lake, lagoon, or seabed, are common for marine reptile remains—in such cases the narrow-bodied helveticosaurs, basal placodontiformes and hupehsuchians, ichthyosaurs, and mosasaurs are usually preserved on their sides so that we see their bodies in profile, while thalattosaurs, atopodentatians, pachypleurosaurs, pistosaurs, plesiosaurs, aigialosaurs, dolichosaurs, sea turtles, and sea snakes are at least as likely, perhaps very likely, to be squashed top to bottom like roadkill. Most sea reptile fossil bones are left intact, and only their surface form is documented unless they happen to be broken open. Certain bones are increasingly being opened to reveal their internal structure for various purposes: sectioning allows researchers to examine bone histology and microstructure, to count growth rings, to search for traces of soft tissues, and to sample bone isotopes and proteins. It is becoming the norm to conduct CT scans on skulls and complex bones to determine the three-dimensional structure without invasive preparation, as well as to reduce costs. These scans can be published as conventional hard copies and in digital form. There is increasing reluctance to mount original bones in skeletons in display halls because delicate fossils are better conserved and more readily studied when properly stored. Instead, the bones are molded, and lightweight casts are used for display skeletons.

Landowners who allow researchers onto their land sometimes get a new species found on their property named after them, informally or formally. So do volunteers who find new ancient sea reptiles. Who knows, you may be the next lucky paleoamateur.

# USING THE GROUP AND SPECIES DESCRIPTIONS

Hundreds of maritime reptile species have been named, but a significant portion are invalid. Some are based on inadequate remains, such as one or a few bones, that are taxonomically indeterminate, although a number must represent real species when they are distinct from known species or are all that is known from formations that lack significant other remains. Because so many marine reptile species are based on at least fairly complete remains found in the fine-grained Konservat-Lagerstätten deposits, the ratio of valid to unsubstantiated species is much lower than for less often complete remains of dinosaurs. Other species are junior synonyms for species that have already been named. The plesiosaur species *Pliosaurus carpenteri*, for instance, is likely to be the same species as the previously coined *Pliosaurus brachydeirus*, so the first title is not usually used. In some cases small skeletons have been thought to be adults of small-bodied species. The unusual *Cartorhynchus lenticarpus* looks like the juvenile of the previously named and also atypical *Sclerocormus parviceps* from the same location, in which case the first name is not used. This guide includes species that are generally considered valid and based on sufficient remains. A few exceptions are allowed when a species based on a single bone or little more is important in indicating the existence of a distinct type or group of oceanic reptiles in a certain time and place.

The group and species descriptions are listed hierarchically, starting with major groups and working down to genera and species. Because many researchers have abandoned the traditional Linnaean system of classes, orders, suborders, and families, there is no longer a standard arrangement for the sea reptiles—many marine reptile genera are no longer placed in official families—so none are used here. In general, the taxa are arranged phylogenetically, with more derived groups nesting within more basal clades. There are a number of resulting problems. It is more difficult for the general reader to follow the various groupings without the traditional scheme. Worse, recent phylogenetic studies have often produced very different results, so there is no consensus on the detailed relationships of the groups, and some species are being placed in different clades by different analyses. This is not surprising considering that the incompleteness of the fossil record hinders a better understanding of their relations, the great majority of sea reptile species that lived are not known, many of those that are known are documented by incomplete remains, and it is not possible to examine their relationships with genetic analysis. Lacking a well-founded consensus to follow, I have used a degree of personal choice and judgment to arrange the groups, and the species within the groups. Some placements reflect my considered opinion, but most are arbitrary choices between competing research results. Most of the phylogeny and taxonomy offered here is not a formal proposal, but a few new group labels were necessary and were coined and defined for future use by others if they prove efficacious. Disputes and alternative placements of sea reptile groups and species are often but not always mentioned.

Under the listing for each group of sea reptiles the overall geographic distribution and geological time span of its members are noted. This is followed by the anatomical characteristics that apply to the group in general, which are not repeated for each species in the group. The anatomical features usually center on what is recorded in the bones, but other body parts are covered when they have been preserved. Anatomical details are used for general characterization and identification and are as much as possible what a marine reptile watcher might use; they are not extensive technical phylogenetic diagnoses. The type of habitat that the group favored is briefly listed, and this varies from specific in some types to very generalized in others. Also outlined are the restored habits that probably characterized the group as a whole. The reliability of these conclusions varies greatly. There is, for example, no doubt that pliosaurs with big spike teeth were archpredators of other sea life. But the diet of the pavement-toothed placodonts has been more controversial; most think they were shellfish crushers, but some think they mashed soft aquatic plants.

The naming of marine reptile genera and species is often problematic. In part this is because what were considered distinct genera and/or species at one time are now proposed to be juveniles or different sexes of another genus or species, or vice versa, by at least some, while others may disagree. Many species are based on very incomplete or otherwise poorly preserved remains that are problematic. In other cases there is disagreement on how much difference between species constitutes different genera, which are also based on phylogenetic relationships, and stratigraphic levels also play a role. Disputes and alternatives concerning the designation of genera and species are often but not always mentioned.

The entry for each species first cites the dimensions and estimated mass of adults; those for which juveniles alone are known are not cited. The total length is for the combined skull and skeleton, measured as a straight line from the tip of the snout to the aftmost tip of the tail—this is viable because the skeletals of these consistently low-slung sea swimmers are posed with the vertebral column as stretched out as it likely was in life. The values presented are general figures for the size of the largest known adults of the species and do not necessarily apply to the value estimated for specific specimens whose skeletons are restored. Because the number of specimens for a particular species is a small fraction of those that lived, the largest individuals are not on hand to be measured; "world record" specimens can be half again or twice as massive as is typical, and up to a quarter larger in dimensions. All values are, of course, approximate, and their quality varies depending on the completeness of the remains for a given species. If the species is known from sufficiently complete remains, the dimensions and mass are based on the profile-skeletal restoration. Skeletals set in profile of the body form can be used to estimate the volume of the animal. A difficulty in doing so is that the depth and especially the beam of the bodies of articulated skeletons that have been squashed flat on their sides, bellies, or backs can be signicantly altered from what they were in life, so approximations are often inevitable. Another complication is the presence of blubber in many examples, which made the body volumes somewhat larger than the skeleton and restored muscles would indicate. The volume estimate can then be used to calculate the mass, assuming that the overall density was close to that of water—marine animals tend to be solidly built, often with heavy bones, yet they have lungs that usually contain some air, so they are approximately as dense as water, with specific gravity close to 1; the value used herein is 1.025. When remains are too incomplete to directly estimate dimensions and mass, these are extrapolated from relatives and are considerably more approximate. In some cases the proportions of the species are too poorly known to produce mass estimates. The turtle-shaped cyamodontoid placodonts are especially incalculable because all the specimens are too flattened top to bottom to know how deep their carapaces were, so their body volumes are not reliably restorable—the depth-to-length ratios of teardrop-shaped sea turtle carapaces are fairly consistent in their side-view profiles, and volumes can be restored. Both metric and English measurements are included; all original calculations are metric, but because those are often imprecise, the conversions from metric to English are often rounded off as well.

The next line outlines the fossil remains, whether skull or skeletal material or both, that can be reasonably and confidently assigned to the species to date; the number of specimens varies from one to thousands. The accuracy of the list ranges from exact to a generalization depending on the information on hand. The latter sometimes results from recent reassignment of specimens from one species to another, leaving the precise inventory uncertain.

This book includes by far the most extensive sea reptile profile skull-skeletal library yet published—the specimens that have been restored and the masses that have been derived from them can be found at https://press.princeton.edu/the-princeton-field-guide-to-mesozoic-sea-reptiles. The profile-skull and profile-skeletal restorations in the species entries have been rendered for those species that are known from remains that were available as the book was being produced and that were sufficiently complete to execute a complete skull and entire skeletal reconstruction—the pace of discovery is so fast that some of the very newest finds may not have been included. The accuracy of the restorations varies somewhat depending on the quality and completeness of the available specimens. A few samples of top-view profile-skeletals of basic marine reptile types have been included, and top views of skulls are included when sufficient information is available. Ironically, a substantial number of sea reptile species that are known from complete specimens, in some cases in very large numbers, cannot be restored in side view because all the preserved skeletons are squashed flat top to bottom. Some species are known from a complete specimen but the skull is preserved on its side and the skeleton is crushed top to bottom, or the reverse; in either case a complete skeletal may not be possible, even if the skull can be restored. In other cases species are known only from a skeleton with a skull flattened on the sides, in which case a restoration is possible. Because many of the flat-trunked sea turtles and cyamodontoid placodonts are inherently not possible to reliably restore in side view, only top/bottom skeletals were prepared.

The skull and skeletal restorations show the bones and in some cases restored cartilage as solid white set within solid black profiles that include the restored muscles, tendons, digit pads, keratin sheaths, and other nonbony tissues, some of which have been preserved in a few cases, such as the famed dorsal-finned ichthyosaurs. All the skull and skeletal restorations in the species section are of mature specimens. The profile-skeletals are posed in a common basic posture in order to facilitate cross comparisons. Some representative examples of shaded skull restorations have been included with some of the major groups. The same has been done with a sample of muscle studies, whose detailed nature is no more or less realistic than are the particulars in full-life restorations, which, if anything, involve additional layers of speculation.

The color plates are based on fully or nearly adult skeletal restorations or skulls of those species deemed of sufficient quality for a full-life profile restoration. The more atypical a species is, the more likely a life profile was produced based on a less complete set of remains. Because the flattened carapaces of the cyamodontoid placodonts cannot be readily restored in side view, color life restorations were not produced. The colors and patterns are speculative to at least a certain degree, usually entirely so—the exceptions are those few cases in which preserved skin pigments give some idea of the color pattern, but even then artistic license cannot be avoided. The color patterns that adorn modern marine fish, reptiles, and mammals were often used as inspirations—interestingly, in some living species color patterns vary substantially on the left and right sides, and such asymmetry may have been present on occasion in the Mesozoic. The same basic color scheme has been applied to all life restorations of a given species in the guide. Because the presence and orientation of plesiosaur tail fins or flukes is poorly understood, they are not consistently illustrated. The same is true of dorsal fins of basal ichthyosaurs. Those who wish to use the skeletal, muscle, and life restorations herein as the basis for commercial or other public projects are reminded to first contact the copyright illustrator.

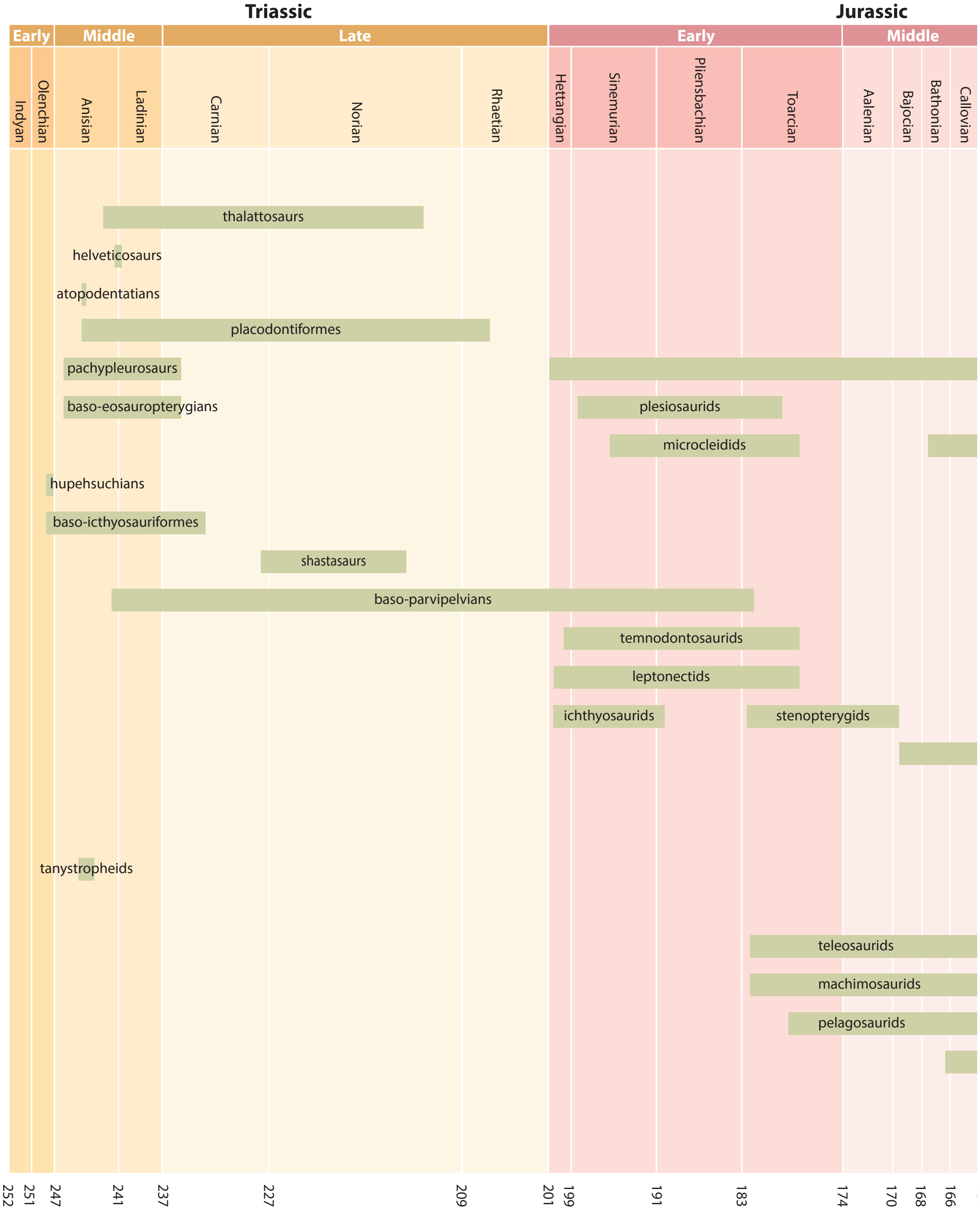
The particular anatomical characteristics that distinguish the species are listed, and these too are for general identification by putative sea reptile watchers and are not technical species diagnoses. These differ in extent depending on the degree of uniformity versus diversity in a given group as well as the completeness of the available fossil remains. In some cases the features of the species are not different enough from those of the group to warrant additional description. In other cases not enough is known to make a separate description possible.

Listed next is the formal geological period and, when available, the stage from which the species is known. As discussed earlier, the age of a given species is known with a precision of within a million years in some cases, or as poorly as an entire section of a period in others. The reader can refer to the time scale on the timeline chart to determine the age, or age range, of the species in years (see pp. 64–65). Most species exist for a few hundred thousand years to a couple of million years before either being replaced by a descendant species or going entirely extinct. It is sometimes not entirely clear whether a species was present in just one time stage or crossed the time boundary into the next one. In those cases the listing is “and/or,” as in late Santonian and/or early Campanian.

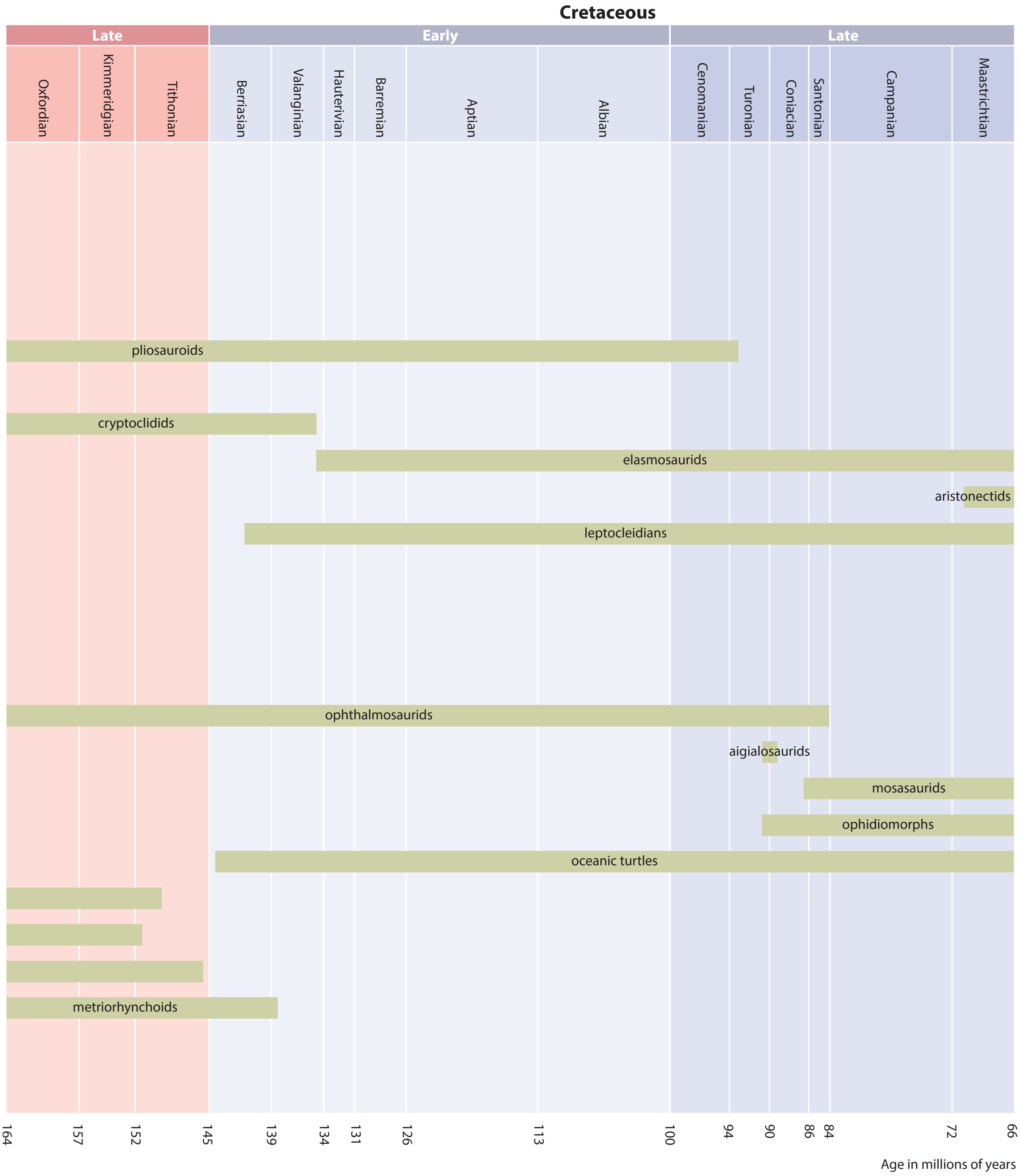
Next the geographic location and the geological formation that the species is known from so far are listed; in a few cases the information is absent or dubious, and not all sediments are in named formations. The paleomaps of coastlines (see pp. 56–60) can be used to geographically place a species in a world of drifting continents and fast-shifting seaways, with the proviso that no set of maps is extensive enough to show the exact configuration of the ancient lands when each species was extant. I have tended to be conservative in listing the presence of a specific species only in those places and levels where sufficiently complete remains are present. Some species are known from only a single location, whereas others have been found in an area spread over one or more formations. In some cases formations have yet to be named, even in areas that are well studied. Many formations were formed over a span that was longer than that of some or all of the species that lived within them, so when possible the common procedure of simply listing the overall formation a given species is from is avoided. For example, *Tylosaurus proriger* is known from the upper Niobrara and the slightly younger lower Pierre Shale Formations, while its close relative and possible descendant *Tylosaurus pembinensis* hails from the still younger middle Pierre Shale.

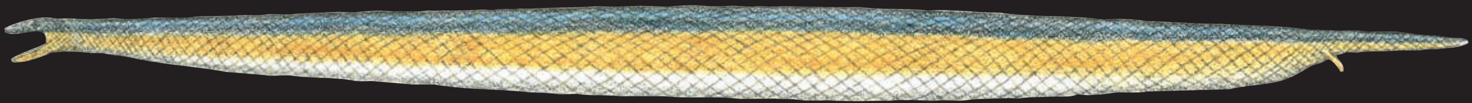
## USING THE GROUP AND SPECIES DESCRIPTIONS

Noted next are the basic characteristics of the marine reptile's known watery habitat specific to the species—because many swimmers can move far at low cost, their habitats may have been broader than indicated. Environmental information ranges from well studied in heavily researched formations to nonexistent in others.



Listed last are special notes about the species when they are called for. Other marine reptiles that the species shared its habitat with are listed. Possible ancestor-descendant relationships with close older or younger relatives are sometimes noted, but these are always tentative. This section also notes alternative hypotheses and controversies that apply to the species.





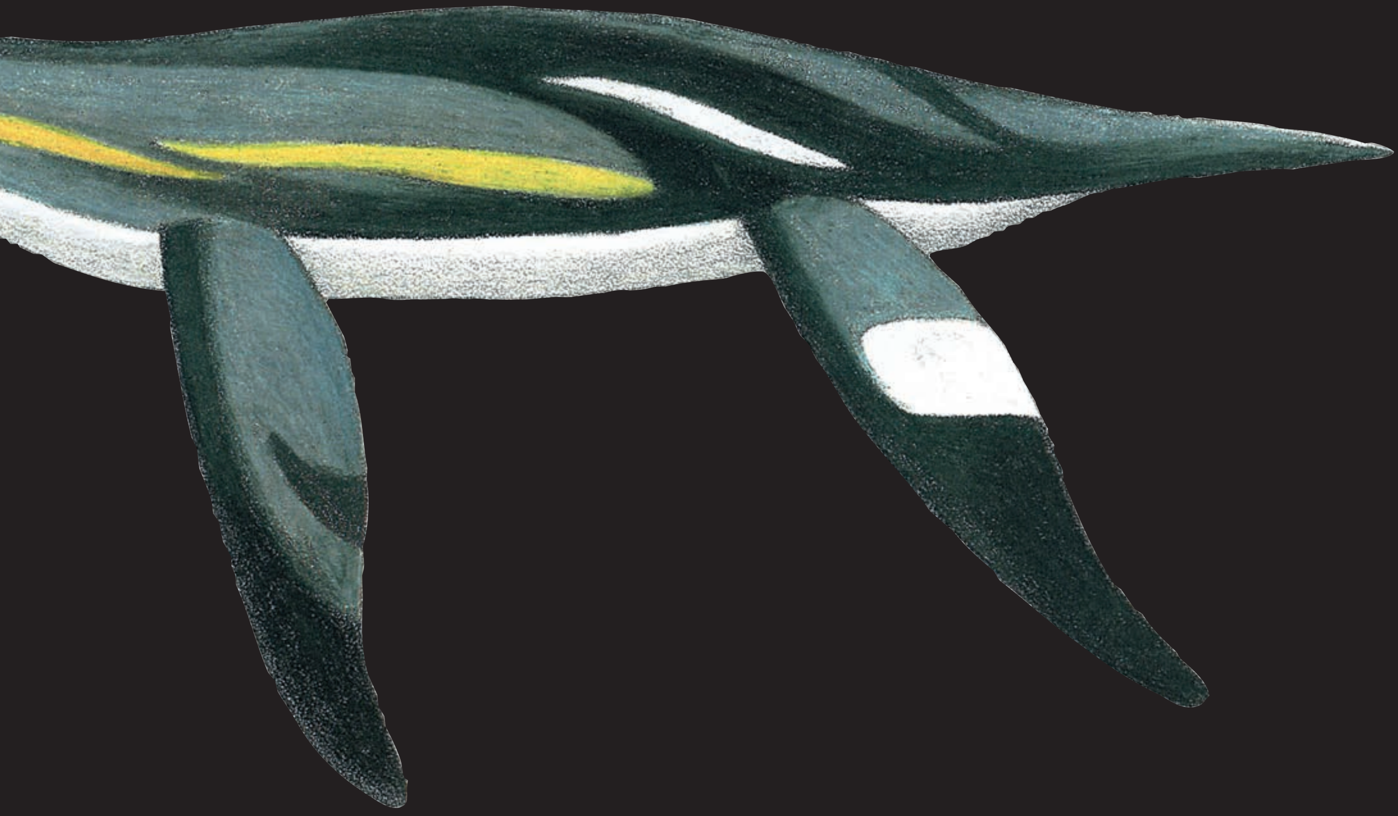
# DIAPSIDS

## SMALL TO GIGANTIC TETRAPODS FROM THE LATE PALEOZOIC TO MODERN TIMES, GLOBAL

**ANATOMICAL CHARACTERISTICS** Extremely variable. Two temporal openings in the skull, often lost by partial opening or by closure. Ribs usually swept backward.

**HABITAT AND HABITS** Extremely variable, marine to fully terrestrial to highly aerial, highly herbivorous to archpredatory.

**NOTES** One of the three great tetrapod groups, the others being the extinct anapsids, and the synapsids that include mammals.



# NEODIAPSIDS

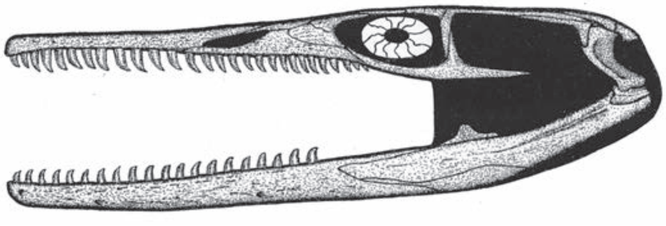
SMALL TO GIGANTIC DIAPSIDS FROM THE LATE PALEOZOIC TO MODERN TIMES, GLOBAL

**HABITAT AND HABITS Extremely variable, marine to fully terrestrial to highly aerial, from highly herbivorous to archpredatory.**
**NOTES The great bulk of diapsids.**

## THALATTOSAURS

SMALL TO LARGE NEODIAPSIDS FROM THE MIDDLE TO LATE TRIASSIC OF THE NORTHERN HEMISPHERE

ANATOMICAL CHARACTERISTICS Fairly uniform. Skulls akinetic, heads small to moderate sized, nostrils small, set just before orbits, eyes face at least somewhat upward, scleral rings often present, lateral temporal opening at least partly open at bottom, coronoid projection on lower jaw, teeth range from full set to absent, may be present on mouth roof. Necks very short to fairly long. Trunks moderately long, not very broad, gastralia present. Tails exceptionally long, highly flattened side to side along most of length, straight and not expanded aft. Pelvis attached to vertebral column. Limbs short, modified into stiff-jointed paddles, fingers and toes present but not highly elongated, presumably webbed. Moderately hydrodynamically streamlined, primarily axial undulators of anguilliform grade, limbs primarily for stability and maneuvering, pressed tight to body when hydrocruising.
HABITAT Coastal and brackish shorelines, lagoons, reefs, estuaries, freshwaters.
HABITS Shallow-water ambush and pursuit fishers of small to medium-sized game. Possibly bred and probably nested on beaches.
NOTES Relationships relative to other basal neodiapsids uncertain. Absence from Southern Hemisphere may reflect lack of sufficient sampling.



*Askeptosaurus* (Askeptosauroids)

## ASKEPTOSAUROIDS

SMALL TO MEDIUM-SIZED THALATTOSAURS FROM THE MIDDLE TO LATE TRIASSIC OF EURASIA

ANATOMICAL CHARACTERISTICS Necks moderate in length.

### ENDENNASAURIDS

SMALL ASKEPTOSAUROIDS FROM THE LATE TRIASSIC OF EUROPE

ANATOMICAL CHARACTERISTICS Heads subtriangular, snouts pointed, toothless. Neck length moderate. Trunk moderately broad. Shoulder and pelvic girdles fairly well developed, limbs including fingers and toes not very short.

***Endennasaurus acutirostris***
**1 m (3 ft) TL, 1.5 kg (3 lb)**
FOSSIL REMAINS Skull and majority of skeleton severely flattened top to bottom, partial skeleton.
ANATOMICAL CHARACTERISTICS Head medium sized. Hand smaller than foot.
AGE Late Triassic; Norian.
DISTRIBUTION AND FORMATIONS Italy; Zorzino Limestone.
HABITAT Island nearshore.

### ASKEPTOSAURIDS

MEDIUM-SIZED ASKEPTOSAUROIDS FROM THE MIDDLE TO LATE TRIASSIC OF EURASIA

ANATOMICAL CHARACTERISTICS Heads subtriangular, not large, coronoid projection not large, teeth subconical. Neck moderately long. Shoulder and pelvic girdles somewhat reduced, same for arms and legs, with short fingers and toes.

## *Askeptosaurus italicus*

**3.9 m (13 ft) TL, 85 kg (180 lb)**

**FOSSIL REMAINS** Several skulls and skeletons.

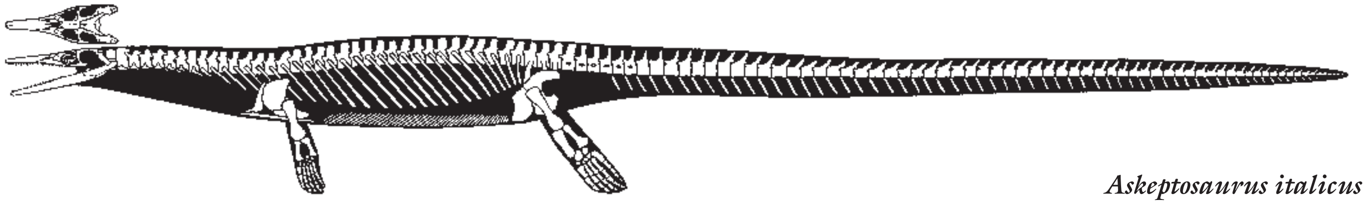
**ANATOMICAL CHARACTERISTICS** Head somewhat elongated, fairly narrow, teeth fairly sharp. Shoulder and pelvic girdles not strongly reduced, hand smaller than foot.

**AGE** Middle Triassic; latest Anisian and earliest Ladinian.

**DISTRIBUTION AND FORMATIONS** Switzerland-Italy border; Besano.

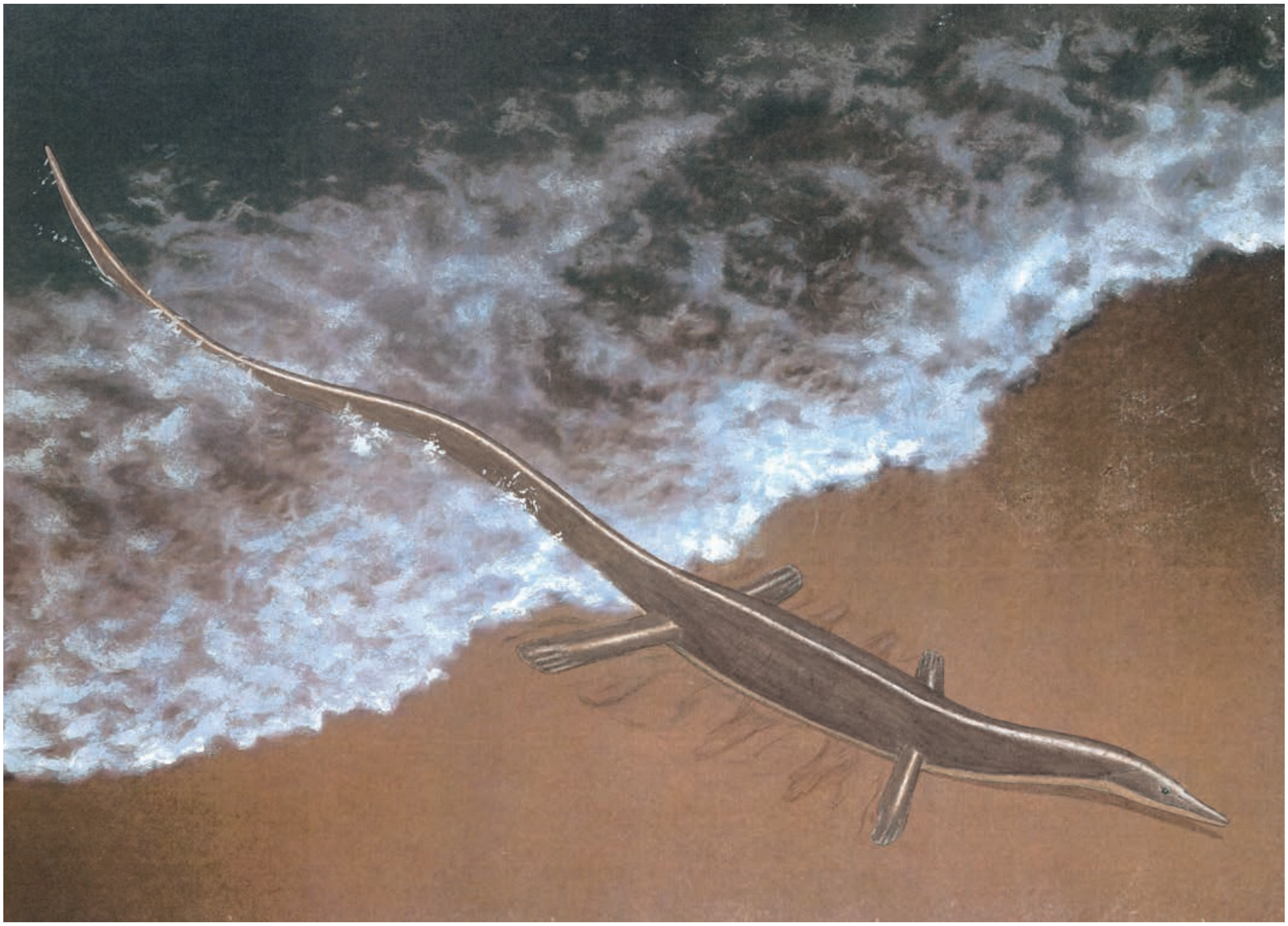
**HABITAT** Island nearshore.

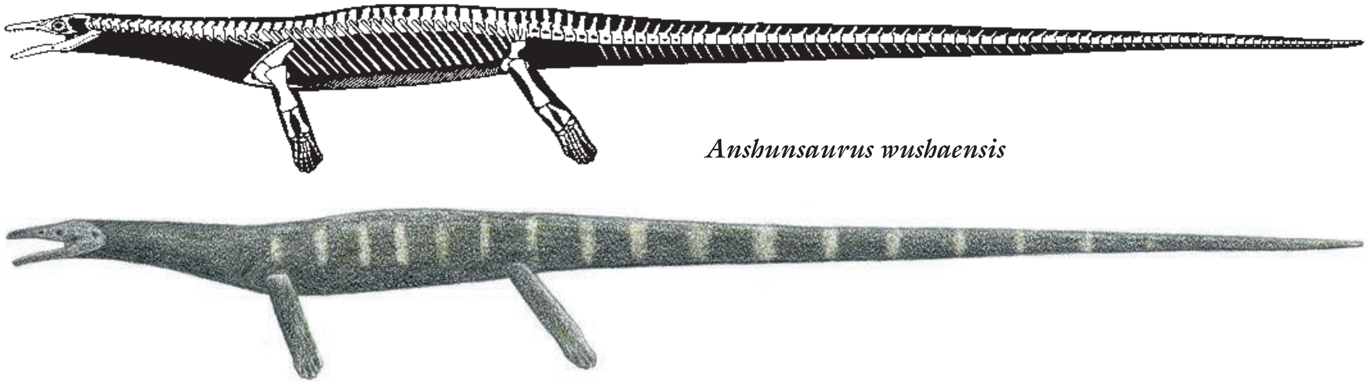
**NOTES** Shared its habitat with *Helveticosaurus*, *Paraplacodus*, *Serpianosaurus*, *Wimanius*, *Besanosaurus*, unnamed genus *buchseri*, *Mixosaurus cornalianus*, *M.? kuhnschnyderi*.



*Askeptosaurus italicus*

*Askeptosaurus italicus*





*Anshunsaurus wushaensis*

### *Anshunsaurus wushaensis*

**3.1 m (10 ft) TL, 35 kg (80 lb)**

**FOSSIL REMAINS** Nearly complete skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head rather small, nostrils very small, teeth fairly sharp. Shoulder and pelvic girdles reduced, as are arm and leg. Hand and foot similar in size.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Southeast China; middle Falang.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with *Xinpusaurus? xingyiensis*. May be direct ancestor of *A. huangguoshuensis*.

### *Anshunsaurus huangguoshuensis*

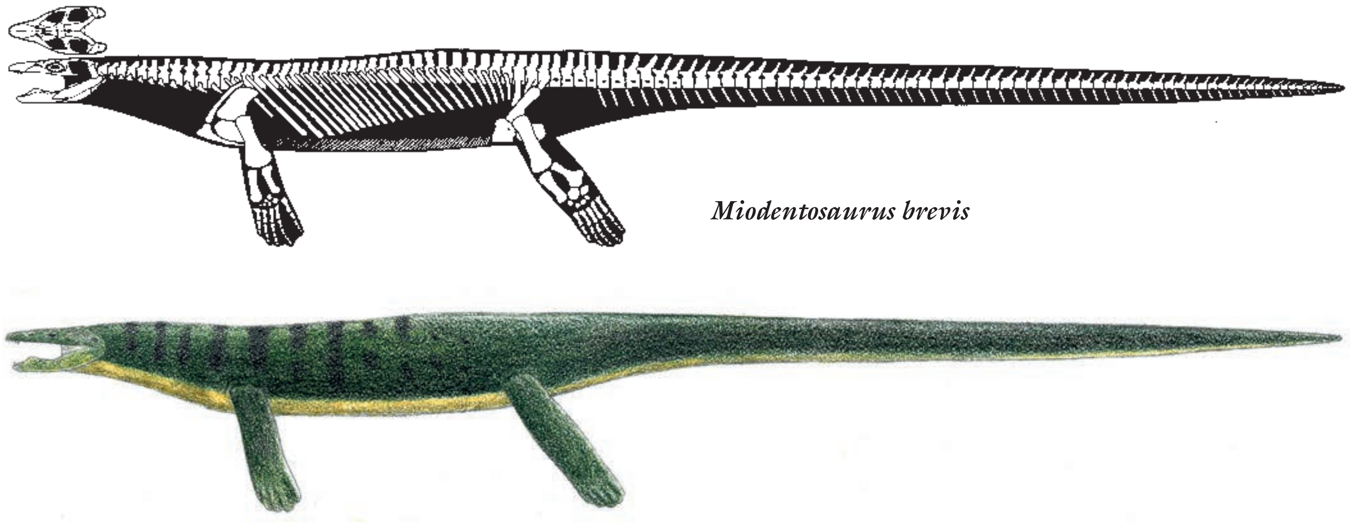
**3.5 m (11 ft) TL, 50 kg (110 lb)**

**FOSSIL REMAINS** Several skulls and skeletons, most severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Nostrils very small, teeth fairly sharp. Shoulder and pelvic girdles reduced, as are arm and leg. Hand and foot similar in size.
**AGE** Late Triassic; early Carnian.
**DISTRIBUTION AND FORMATIONS** Southeast China; upper Falang.
**HABITAT** Continental nearshore.
**HABITS** May include *A. huangnihensis*. Shared its habitat with *Yunguisaurus*, *Qianichthyosaurus zhoui*, *Guanlingsaurus*, *Guizhouichthyosaurus*, unnamed genus *orientalis*, *Miodentosaurus*.

### *Miodentosaurus brevis*

**5 m (16 ft) TL, 190 kg (420 lb)**

**FOSSIL REMAINS** Two skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head short, fairly broad, snout rather short, nostrils very small, lower jaw fairly deep, coronoid process shallow, modest upward projection at front of lower jaw, teeth few and limited to front of jaws, rather blunt. Neck stout. Shoulder and pelvic girdles fairly well developed, same for arm and leg. Hand and foot about same size.
**AGE** Late Triassic; early Carnian.
**DISTRIBUTION AND FORMATIONS** Southeast China; upper Falang.
**HABITAT** Continental nearshore.



*Miodentosaurus brevis*

## THALATTOSAUROIDS

**SMALL TO MEDIUM-SIZED THALATTOSAURS FROM THE MIDDLE TO LATE TRIASSIC OF NORTH AMERICA AND ASIA**

**ANATOMICAL CHARACTERISTICS** Snouts strongly modified, coronoid projections fairly large, teeth reduced. Necks very short. Shoulder and pelvic girdles strongly reduced, same for arms and legs. Radius in lower arms enlarged, projecting forward, fibula in lower leg enlarged, projecting backward, hands smaller than feet.

## NECTOSAURIDS

**SMALL THALATTOSAUROIDS FROM THE LATE TRIASSIC OF NORTH AMERICA**

**ANATOMICAL CHARACTERISTICS** Heads short and deep, subrectangular because snouts are deep, snout tips apparently sharply downturned, teeth few and limited to front of jaws, teeth medium sized, stout, subconical, and fairly sharp.

### *Nectosaurus halius*

**0.5 m (1.5 ft) TL**

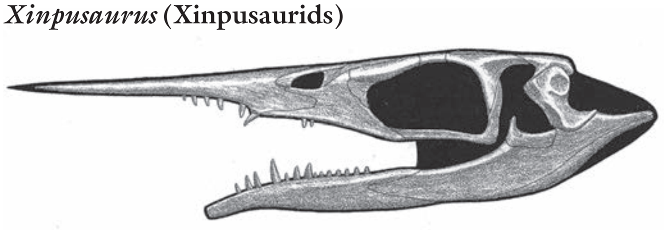
**FOSSIL REMAINS** Partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** As for group.
**AGE** Late Triassic; late Carnian.
**DISTRIBUTION AND FORMATIONS** Northern California; middle Hosselkus Limestone.
**HABITAT** Continental nearshore.
**NOTES** Not able to estimate mass because of insufficient skeletal material. Shared its habitat with *Thalattosaurus*, *Shastasaurus*, *Toretocnemus*?

## XINPUSAURIDS

**SMALL TO MEDIUM-SIZED THALATTOSAUROIDS FROM THE MIDDLE TO LATE TRIASSIC OF ASIA**

**ANATOMICAL CHARACTERISTICS** Snout elongated into a spike, lower jaw much shorter than upper, teeth reduced. Arms and legs reduced, arms smaller than legs.

***Xinpusaurus* (Xinpusaurids)**



### *Xinpusaurus? xingyiensis*

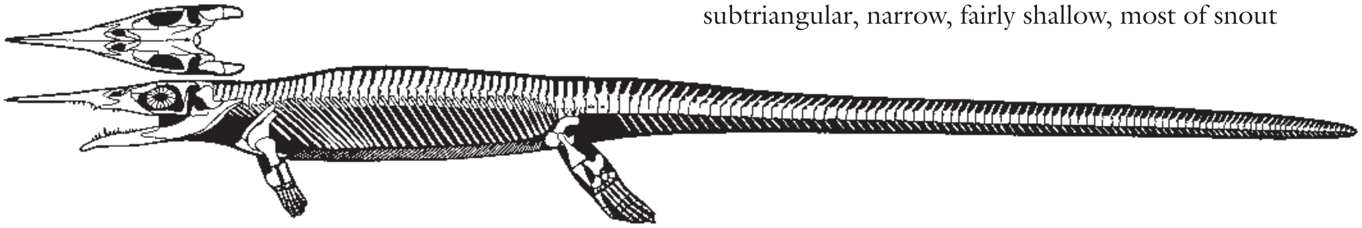
**3 m (10 ft) TL, 40 kg (90 lb)**

**FOSSIL REMAINS** Majority of skull and skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head subtriangular, snout elongated into toothed slender spike, lower jaw much shorter than upper.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Southeast China; middle Falang.
**HABITAT** Continental nearshore.
**NOTES** May not be the same genus and may be a direct ancestor of *X. suni*. Shared its habitat with *Anshunsaurus wushaensis*.

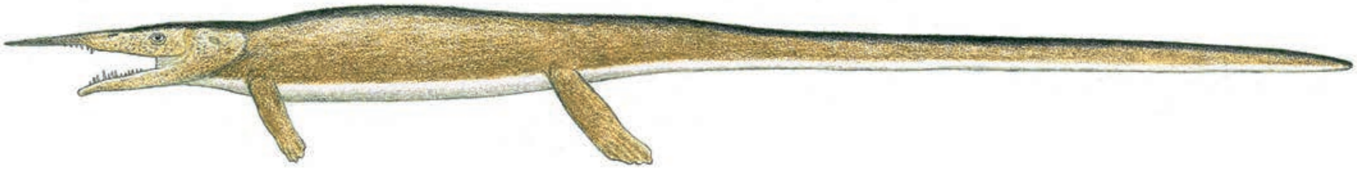
### *Xinpusaurus suni*

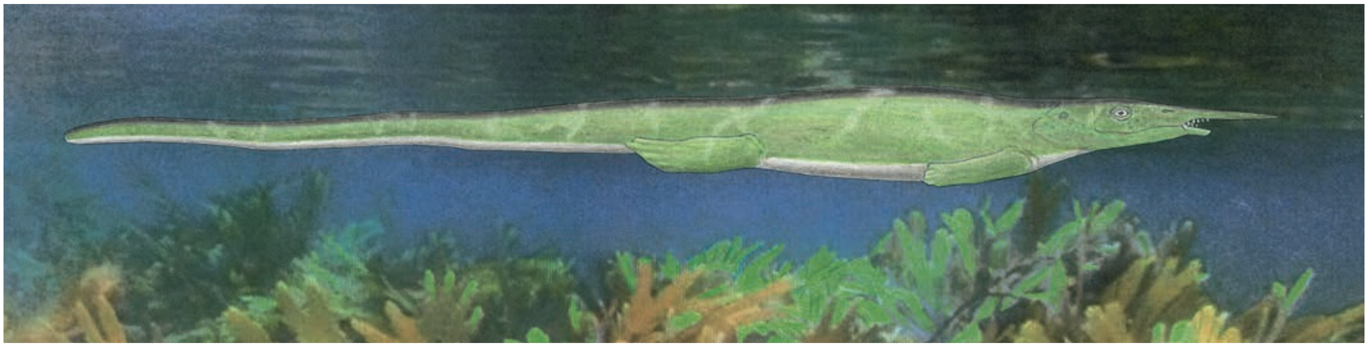
**1.3 m (4.3 ft) TL, 3.5 kg (8 lb)**

**FOSSIL REMAINS** Several skulls and skeletons, juvenile to adult.
**ANATOMICAL CHARACTERISTICS** Head large, subtriangular, narrow, fairly shallow, most of snout

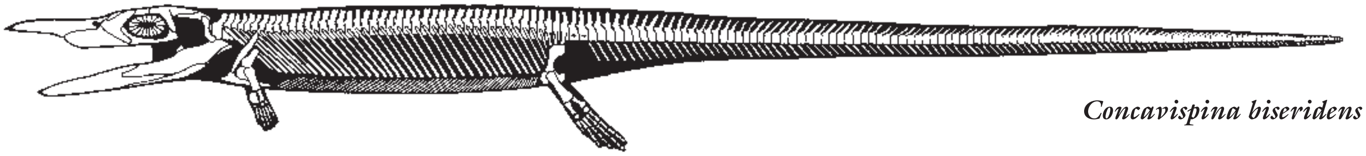


***Xinpusaurus suni***





*Xinpusaurus suni*



*Concavispina biseridens*

elongated into toothless slender spike, orbits large, lower jaw much shorter than upper jaw, slightly S curved, upper teeth limited to middle of upper jaw, lower teeth not at tip of lower jaw, otherwise more numerous and along much of lower jaw length, teeth fairly large, subconical, and fairly sharp.
**AGE** Late Triassic; Carnian.
**DISTRIBUTION AND FORMATIONS** Southern China; Xiaowa.
**HABITAT** Continental nearshore.
**NOTES** *X. kohi* and *X. bamaolinensis* are probably growth stAGEs of this species. Shared its habitat with *Concavispina*.

### *Concavispina biseridens*

**3.7 m (12 ft) TL, 75 kg (179 lb)**

**FOSSIL REMAINS** Nearly complete skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head large, robustly constructed, snout enlarged into possible spike, lower jaw shorter than upper, heavily built, teeth extremely reduced. Limbs quite small.
**AGE** Late Triassic; Carnian.
**DISTRIBUTION AND FORMATIONS** Southern China; Xiaowa.
**HABITAT** Continental nearshore.
**NOTES** Tip of snout broken so length uncertain.

## THALATTOSAURIDS

**SMALL THALATTOSAUROIDS FROM THE EARLY AND/OR MIDDLE TO LATE TRIASSIC OF NORTH AMERICA**

**ANATOMICAL CHARACTERISTICS** Head subtriangular, snout downturned.
**NOTES** Not able to estimate masses because of insufficient skeletal material.

### *Agkistrognathus campbelli*

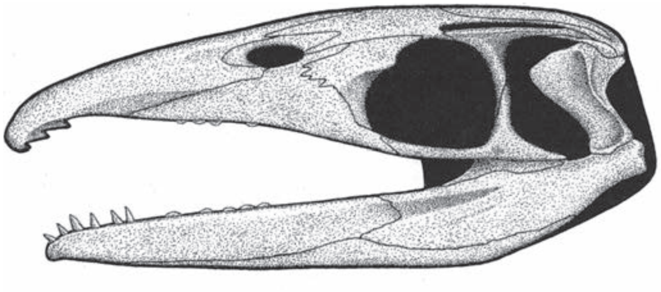
**1.5 m (5 ft) TL**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Teeth robust.
**AGE** Early or Middle Triassic.
**DISTRIBUTION AND FORMATIONS** British Columbia; Sulphur Mountain.
**HABITAT** Continental nearshore.
**NOTES** Fossil found downslope of original layer, therefore uncertain. Shared its habitat with unnamed genus *borealis*, *Paralonectes*.

### *Paralonectes merriami*

**1 m (3 ft) TL**

**FOSSIL REMAINS** Three partial skulls.
**ANATOMICAL CHARACTERISTICS** Head fairly deep, teeth modest in size.



*Thalattosaurus* (Thalattosaurids)

**AGE** Early or Middle Triassic.
**DISTRIBUTION AND FORMATIONS** British Columbia; Sulphur Mountain.
**HABITAT** Continental nearshore.
**NOTES** Fossils found downslope of original layer.

### Unnamed genus *borealis*

**0.75 m (2.5 ft) TL**

**FOSSIL REMAINS** Partial skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Snout fairly elongated, teeth robust.
**AGE** Early or Middle Triassic.
**DISTRIBUTION AND FORMATIONS** British Columbia; Sulphur Mountain.
**HABITAT** Continental nearshore.
**NOTES** Fossil found downslope of original layer. Is unlikely to be same genus as much later *Thalattosaurus*.

### *Thalattosaurus alexandrae*

**2 m (6.5 ft) TL**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head subtriangular, narrow, tip of upper jaw bears serrations, upper teeth limited to middle of upper jaw, low and blunt, lower front teeth conical spikes, middle teeth low and blunt.
**AGE** Late Triassic; late Carnian.
**DISTRIBUTION AND FORMATIONS** Northern California; middle Hosselkus Limestone.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with *Nectosaurus*, *Shastasaurus*, *Toretocnemus*?

*Thalattosaurus alexandrae*

## CLARAZIIDS

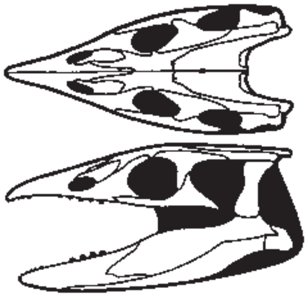
### SMALL THALATTOSAUROIDS FROM THE MIDDLE TRIASSIC OF EUROPE

**ANATOMICAL CHARACTERISTICS** Heads subtriangular, snouts not elongated, turned downward, nostrils set halfway between snout tip and orbit, lower jaws stoutly built, teeth reduced in number.
**NOTES** Not able to estimate masses because of insufficient skeletal material.

### *Clarazia schinzi*

**0.75 m (2.5 ft) TL, 0.6 kg (1.5 lb)**

**FOSSIL REMAINS** Skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head not deep, moderately broad, snout tip downturned slightly, teeth few in number, limited to jaw tips and middle of jaws, front sets small, low, and blunt.
**AGE** Middle Triassic; late Anisian and/or early Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; unnamed.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Hescheleria*.



*Clarazia schinzi*

### *Hescheleria rubeli*

**1 m (3 ft) TL**

**FOSSIL REMAINS** Majority of skull.
**ANATOMICAL CHARACTERISTICS** Head short and deep, snout tip strongly curved downward, upper teeth limited to tip of snout and middle of upper jaw, lower teeth to tip of lower jaw astride a toothlike conical projection of the jaw, upper front teeth small, middle upper teeth short and blunt, lower front teeth small.
**AGE** Middle Triassic; late Anisian and/or early Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; unnamed.
**HABITAT** Island nearshore.
**NOTES** Not able to estimate masses because of insufficient skeletal material.

## HELVETICOSAURS

### MEDIUM-SIZED NEODIAPSIDS FROM THE MIDDLE TRIASSIC OF EUROPE

**ANATOMICAL CHARACTERISTICS** Skulls akinetic, heads small, short, and deep, nostrils near tip of snout, teeth large, long spikes. Neck short, trunk fairly stout. Gastralia present. Tails straight and not expanded aft. Pelvis attached to vertebral column, shoulder and pelvic girdles fairly well developed, same for arms and legs, which are modified into stiff-jointed partial hydrofoils but are not full flippers,

fingers and toes present, not highly elongated but fairly long yet not ossified, presumably webbed. Moderately hydrodynamically streamlined, both undulatory and flipper swimmers.
**HABITAT** Island coastal and brackish shorelines.
**HABITS** Shallow-water ambush fishers of small game. Possibly bred and probably nested on beaches.
**NOTES** Relationships relative to other basal neodiapsids uncertain. Absence from at least some other seas may reflect lack of sufficient sampling.

### *Helveticosaurus zollingeri*
**2 m (7 ft) TL, 15 kg (50 lb)**

**FOSSIL REMAINS** Majority of skull and skeleton, badly damaged.
**ANATOMICAL CHARACTERISTICS** As for group.
**AGE** Middle Triassic; latest Anisian and earliest Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; Besano.
**NOTES** Shared its habitat with *Askeptosaurus*, *Paraplacodus*, *Serpianosaurus*, *Wimanius*, *Besanosaurus*, unnamed genus *buchseri*, *Mixosaurus cornalianus*, *M.? kuhnschnyderi*.

# SAUROPTERYGIANS

**SMALL TO GIGANTIC NEODIAPSIDS FROM THE MIDDLE TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Highly variable. Skulls akinetic, scleral rings often present. Gastralia present. Tails straight and aft vertebrae not expanded. Limbs at least partial stiff-jointed hydrofoils.
**HABITAT AND HABITS** Very variable, fully aquatic to fully terrestrial, highly herbivorous to archpredatory.

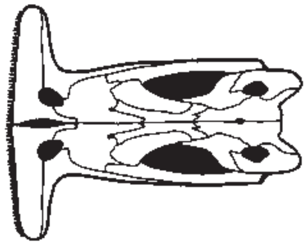
## ATOPODENTATIANS

**MEDIUM-SIZED SAUROPTERYGIANS FROM THE MIDDLE TRIASSIC OF ASIA**

**ANATOMICAL CHARACTERISTICS** Heads small, snout forms a hammerhead much broader than main skull, which is itself moderately broad, nostrils near tip of snout, teeth very numerous, slender pegs along front rim of hammerhead. Necks moderately long. Trunks fairly broad. Pelvis attached to vertebral column, shoulder and pelvic girdles fairly well developed, same for arms and legs, which are modified into stiff-jointed paddles, fingers and toes present but not highly elongated, presumably webbed. Moderately hydrodynamically streamlined, primarily axial undulators of anguilliform grade, limbs primarily for stability and maneuvering, pressed tight to body when hydrocruising.
**HABITAT** Island coastal and brackish shorelines.
**HABITS** Either filter feeder on small invertebrates, or algae eater by scraping sea bottoms. Possibly bred and probably nested on beaches.
**NOTES** Relationships highly uncertain. May be the earliest herbivorous sea reptiles. Absence from at least some other seas may reflect lack of sufficient sampling.

### *Atopodentatus unicus*
**3 m (10 ft) TL, 50 kg (100 lb)**

**FOSSIL REMAINS** Several skulls and skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Hand and foot about same size.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; middle Guanling.
**HABITAT** Continental nearshore. Shared its habitat with *Dianopachysaurus*, *Dinocephalosaurus*.



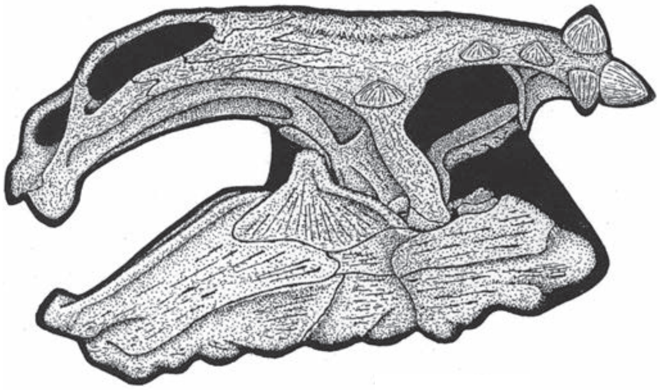
*Atopodentatus unicus*

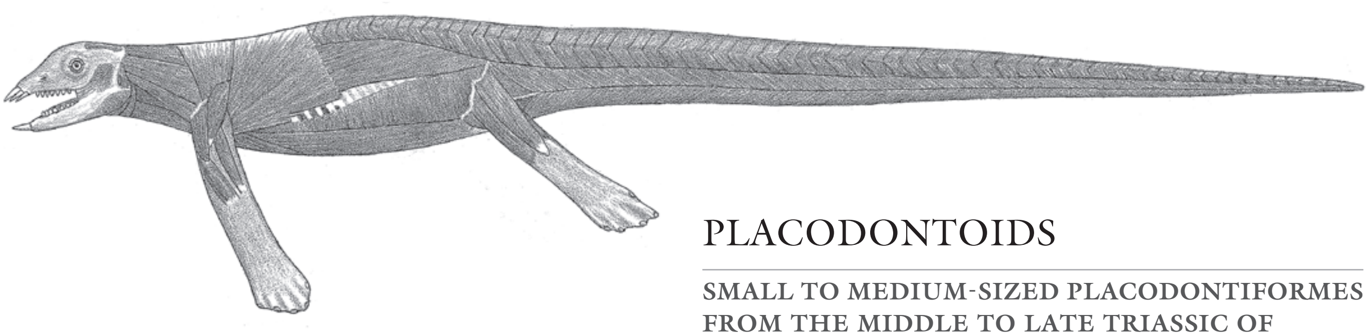
## PLACODONTIFORMES

**SMALL TO MEDIUM-SIZED SAUROPTERYGIANS FROM THE MIDDLE TO LATE TRIASSIC OF EURASIA**

**ANATOMICAL CHARACTERISTICS** Highly variable. Robustly built. Heads short and at least fairly broad,

*Henodus* (Placodontiformes)





***Paraplacodus* muscle study**

orbits face partly upward, coronoid process large. If present at least some teeth form a flattened pavement, teeth often present on mouth roof. Necks short. Trunks compact, moderately to extremely broad. Tails moderately long. Arms and legs rather short, narrow, modified into partial hydrofoils but not full flippers, fingers and toes present but not highly elongated, presumably webbed. Not highly hydrodynamically streamlined.

**HABITAT** Coastal and brackish shorelines, lagoons, reefs, estuaries.

**HABITS** Combination of tooth pavements and powerful jaw muscles anchored in large temporal region indicate were primarily hard shellfish crushers, a few were filter feeders. Some researchers argue that at least some were manatee-like herbivores. Possibly bred and probably nested on beaches.

**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

## PLACODONTOIDS

### SMALL TO MEDIUM-SIZED PLACODONTIFORMES FROM THE MIDDLE TO LATE TRIASSIC OF EUROPE

**ANATOMICAL CHARACTERISTICS** Heads small, subtriangular, teeth at tips of jaws procumbent, large, conical. Trunks not extremely broad, fairly deep. Armor if present limited to dorsal midline where it forms a serrated ridge. Primarily axial undulators.

## PARAPLACODONTIDS

### SMALL PLACODONTOIDS FROM THE MIDDLE TRIASSIC OF EUROPE

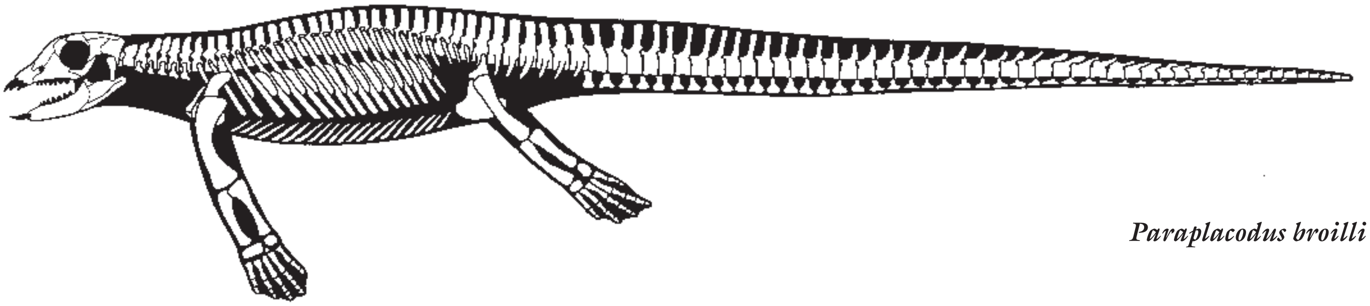
**ANATOMICAL CHARACTERISTICS** Only mouth roof teeth are flat plates.

### *Paraplacodus broilli*

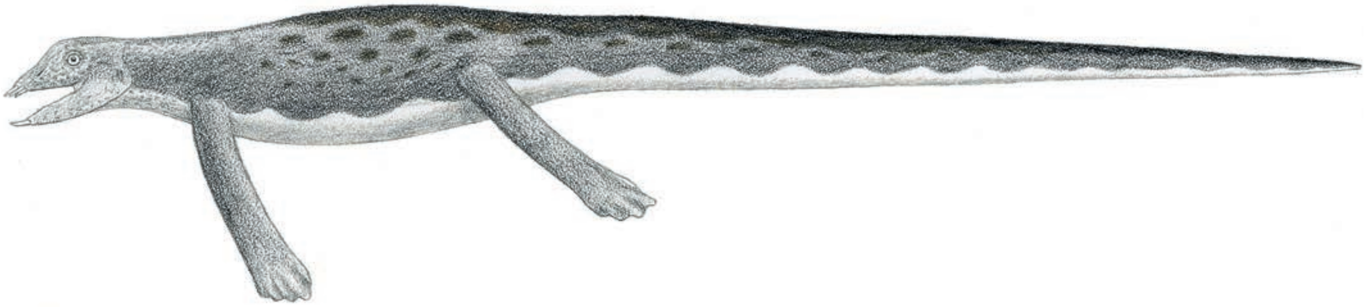
**1.25 m (4 ft) TL, 4 kg (12 lb)**

**FOSSIL REMAINS** Skull and minority of skeleton, partial skull and majority of skeleton.

**ANATOMICAL CHARACTERISTICS** Head medium sized, orbits large, teeth at tips of jaws very large, teeth at midjaws



***Paraplacodus broilli***



conical, very stout, blunt. Trunk robust. Tail very long. Limbs large.
**AGE** Middle Triassic; late Anisian and early Ladinian.
**DISTRIBUTION AND FORMATIONS** Northern Italy; Besano.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Askeptosaurus*, *Helveticosaurus*, *Serpianosaurus*, *Wimanius*, *Besanosaurus*, unnamed genus *buchseri*, *Mixosaurus cornalianus*, *M.? kuhnschnyderi*.

## PLACODONTIDS

### SMALL TO MEDIUM-SIZED PLACODONTOIDS FROM THE MIDDLE TRIASSIC OF EUROPE

**ANATOMICAL CHARACTERISTICS** Heads subtriangular, very heavily built, nostrils halfway between snout tip and orbits, lower jaw deep, teeth at tips of jaws procumbent, conical, large, teeth at midjaws flat, forming pavement.

### *Pararcus diepenbroeki*

**1.5 m (5 ft) TL, 10 kg (20 lb)**

**FOSSIL REMAINS** Minority of skeleton, possible juvenile skull.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Middle Triassic; early Anisian.
**DISTRIBUTION AND FORMATIONS** Netherlands; lower Muschelkalk.
**HABITAT** Island nearshore.
**NOTES** *Palatodonta bleeker* may be juvenile of this species. Shared its habitat with *Nothosaurus marchicus*, *Lariosaurus vosseveldensis*.

### *Placodus gigas*

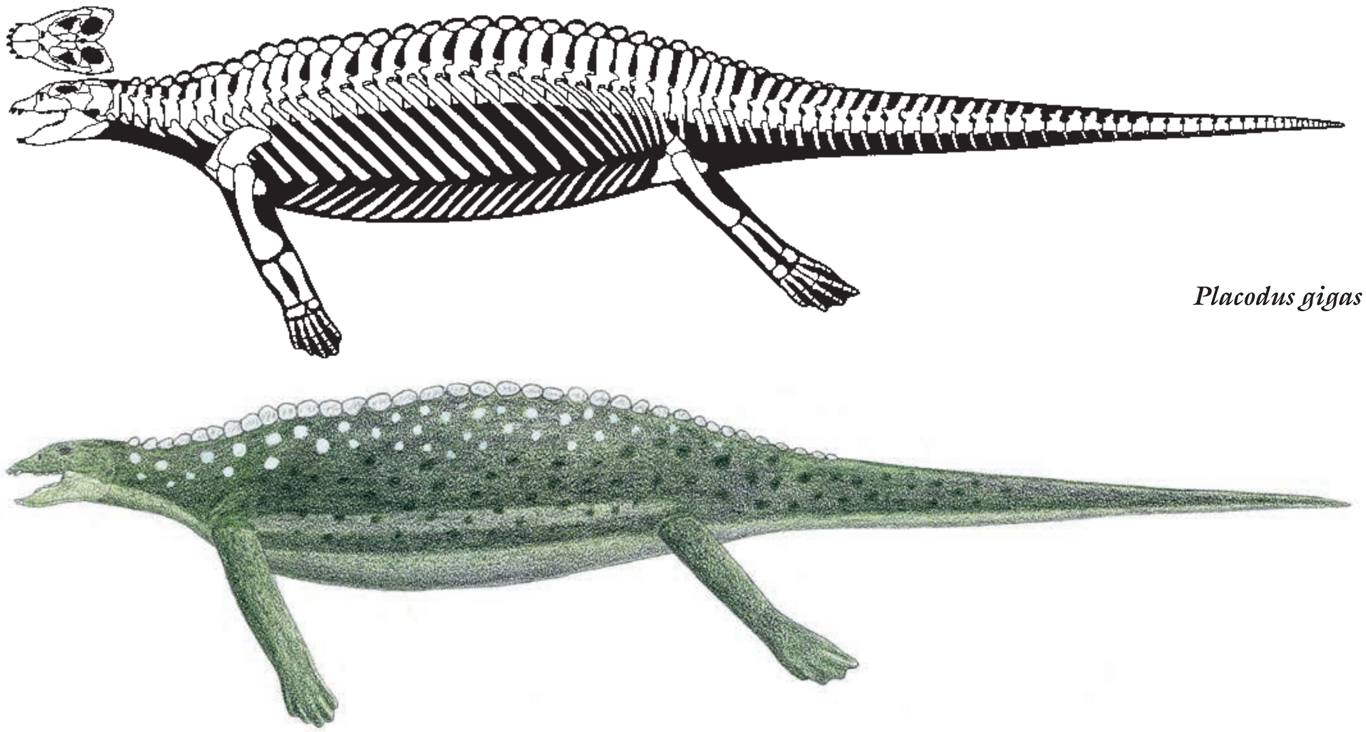
**3.2 m (10.5 ft) TL, 100 kg (220 lb)**

**FOSSIL REMAINS** Skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head broad. Trunk robust. Tail length moderate. Shoulder and pelvic girdles reduced, hand and foot same size.
**AGE** Middle Triassic; late Anisian.
**DISTRIBUTION AND FORMATIONS** Germany, Netherlands, France; upper Muschelkalk.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Nothosaurus mirabilis*, *N. giganteus*, *Pistosaurus*, *Phantomosaurus*.

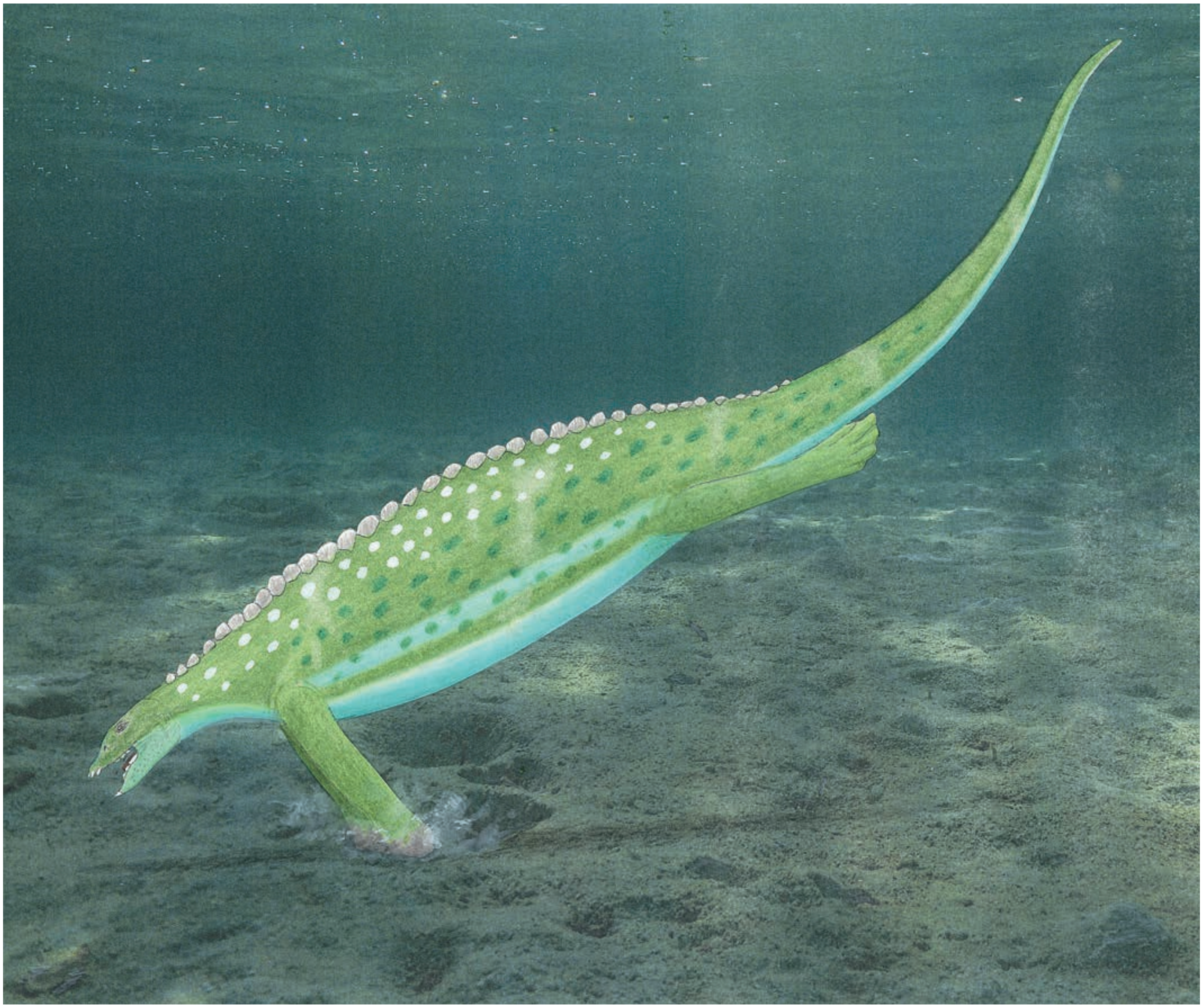
## CYAMODONTOIDS

### SMALL TO MEDIUM-SIZED PLACODONTIFORMES FROM THE MIDDLE TO LATE TRIASSIC OF EURASIA

**ANATOMICAL CHARACTERISTICS** Turtle-like, with flattened, very broad trunk. Hornlets adorn temporal



*Placodus gigas*



*Placodus gigas*

region of skull. Ribs not swept backward. Tails not very long. Poorly hydrodynamically streamlined, propulsion and maneuvering provided by tails and/or appendages. **NOTES** Severe top-to-bottom flattening of all specimens compromises mass estimates.

## CYAMODONTIDS

**SMALL CYAMODONTOIDS FROM THE MIDDLE TO LATE TRIASSIC OF EURASIA**

**ANATOMICAL CHARACTERISTICS** Heads large, deep, very broad at back because temporal region is very expanded, aft rim lined by hornlets, all teeth very blunted. Main trunk and distinct pelvic carapaces present. Tail armored by dorsal and lateral rows of hornlets, tail tip bare.

### *Cyamodus tarnowitzensis*

**Adult size uncertain**

**FOSSIL REMAINS** Partial skull, possibly immature.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; lower Muschelkalk.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Tholodus*, *Contectopalatus*. May be direct ancestor of *Cyamodus rostratus*.

### *Cyamodus rostratus*

**0.9 m (3 ft) TL, 5 kg (11 lb)**

**FOSSIL REMAINS** Skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** 7 pairs of upper teeth, 4 pairs of lower teeth.
**AGE** Middle Triassic; late Anisian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; middle Muschelkalk.
**HABITAT** Island nearshore.
**NOTES** May be direct ancestor of *C. munsteri*.

### *Cyamodus munsteri*

**1.4 m (4.5 ft) TL, 22 kg (50 lb)**

**FOSSIL REMAINS** Several skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** 7 pairs of upper teeth, 3 pairs of lower teeth. Main and pelvic carapace profiles rounded in top view, carapace pavements made of small irregular platelets, rimmed by modest-sized hornlets forming a serrated edge. Hand somewhat smaller than foot.
**AGE** Middle Triassic; early Ladinian.
**DISTRIBUTION AND FORMATIONS** Southern Germany, Switzerland, northern Italy?; upper Muschelkalk, lower Meride Limestone, Besano?
**HABITAT** Island nearshore.
**NOTES** Probably includes *C. hildegardis*. Shared its habitat with *Neusticosaurus*, *Ceresiosaurus*. May be direct ancestor of *Cyamodus kuhnschnyderi*.

### *Cyamodus kuhnschnyderi*

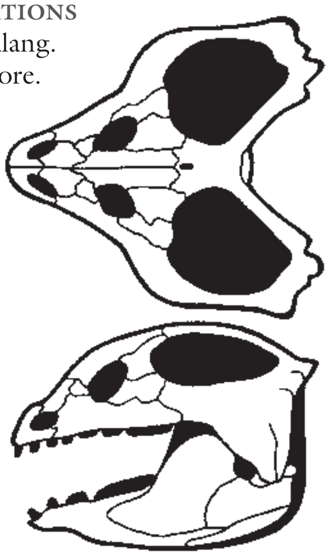
**1.5 m (5 ft) TL, 25 kg (60 lb)**

**FOSSIL REMAINS** Skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Front teeth further reduced, 5 pairs of upper teeth, 3 pairs of lower teeth.
**AGE** Middle Triassic; middle Ladinian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; upper Muschelkalk.
**HABITAT** Island nearshore.

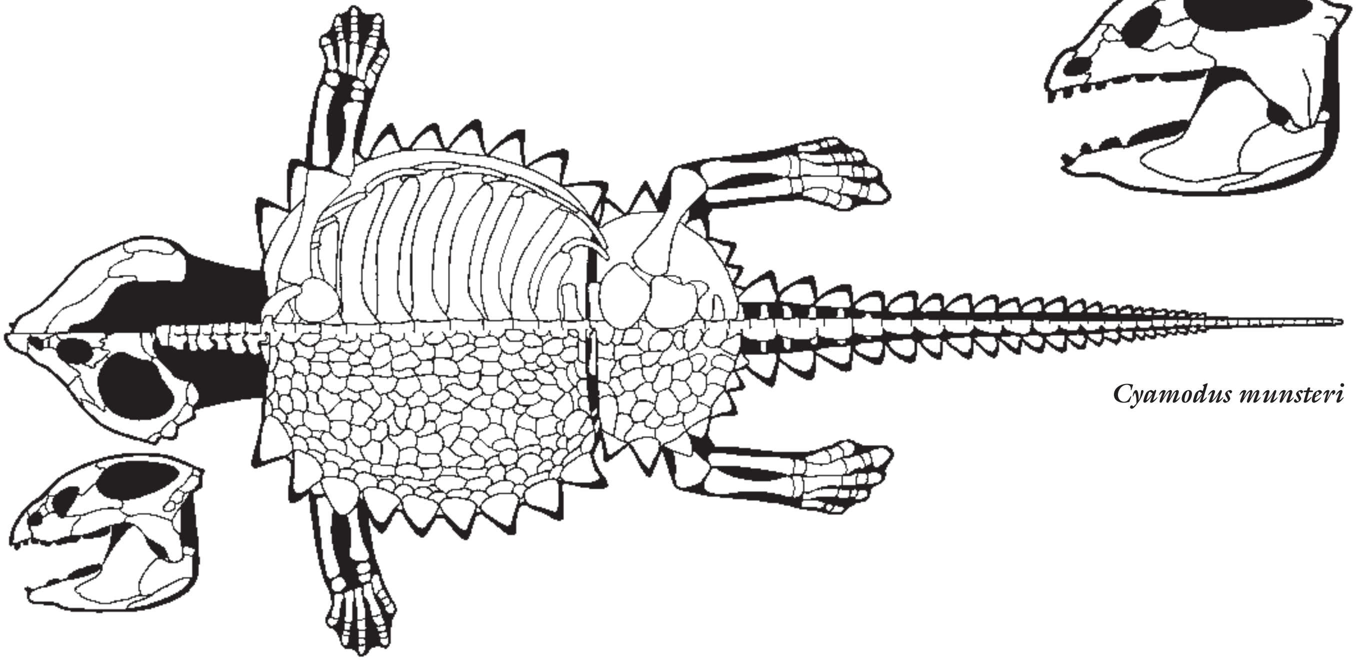
### Unnamed genus? *orientalis*

**1.5 m (5 ft) TL, 20 kg (45 lb)**

**FOSSIL REMAINS** Skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Aft rim of temporal region not lined by hornlets, tooth rows short with just 4 pairs of upper teeth, 2 pairs of lower teeth. Main carapace profile somewhat squarish in top view, consists of medium-sized irregular plates, pelvic carapace irregularly formed, neither lined by hornlets. Hand and foot similar in size.
**AGE** Late Triassic; early Carnian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; upper Falang.
**HABITAT** Continental nearshore.
**NOTES** Placement in earlier and European *Cyamodus* highly problematic.



*Cyamodus rostratus*



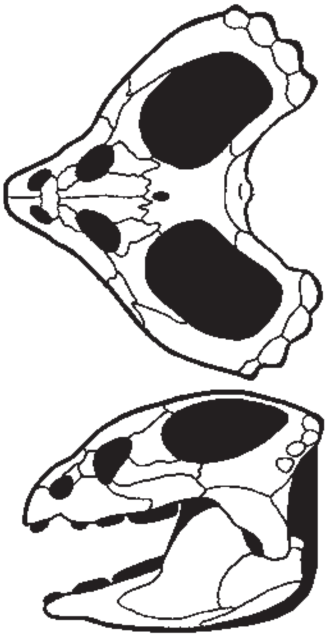
*Cyamodus munsteri*

Shared its habitat with *Anshunsaurus huangguoshuensis*, *Miodentosaurus*, *Yunguisaurus*, *Qianichthyosaurus zhoui*, *Guanlingsaurus*, *Guizhouichthyosaurus*.

### *Macroplacus raeticus*

**1 m (3.3 ft) TL, 8 kg (20 lb)**

FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic; early Rhaetian.
DISTRIBUTION AND FORMATIONS Southern Germany; Koessen.
HABITAT Island nearshore.



***Cyamodus kuhnschnyderi***

## PLACOCHELYIDS

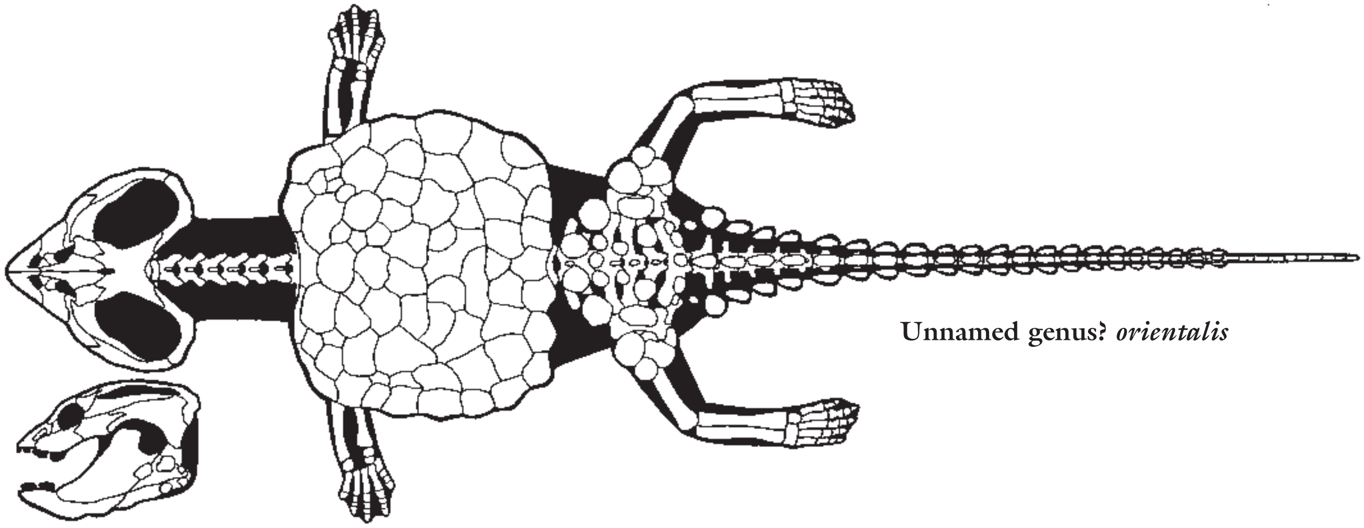
### MEDIUM-SIZED CYAMODONTOIDS FROM THE MIDDLE TO LATE TRIASSIC OF EUROPE

ANATOMICAL CHARACTERISTICS Heads not large, broad, somewhat flattened, snout square-tipped, toothless, elongated, and narrow, nostrils immediately in front of orbits, temporal region expanded, all teeth flat plates at middle of jaws. No hornlets rim carapaces.
NOTES Although the skulls of the two known genera are very similar, the major differences in their skeletons may warrant placement in different families.

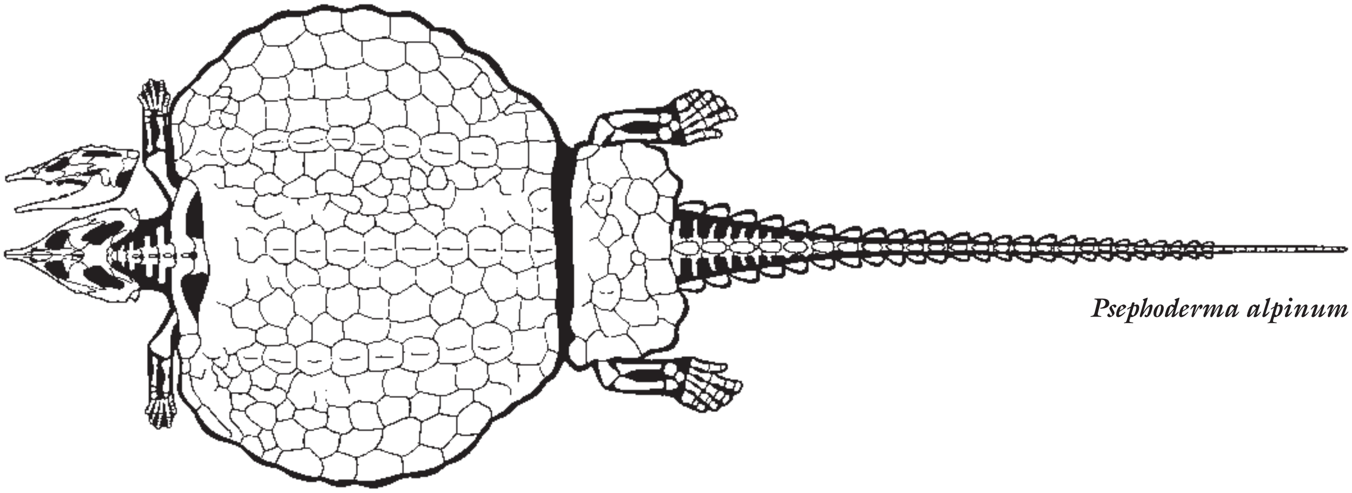
### *Psephoderma alpinum*

**2.4 m (8 ft) TL, 95 kg (200 lb)**

FOSSIL REMAINS Skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head moderately broad, nostrils very small, aft rim of temporal region bears a hornlet, lower jaw rather shallow, 3 pairs of upper and lower teeth. Main trunk and distinct pelvic carapaces present, main carapace profile fairly rounded in top view, pelvic carapace subrectangular in top view, platelets of both modest in size, those of first fairly regular in pattern, three subtle fore-and-aft ridges present along midline, neither carapace lined by hornlets. Tail moderately long, adorned by dorsal and lateral rows of hornlet armor, tail tip bare. Arms and hands smaller than legs and feet.
AGE Late Triassic; middle and/or late Norian.
DISTRIBUTION AND FORMATIONS Italy; Zorzino Limestone.
HABITAT Island nearshore.



**Unnamed genus? *orientalis***



*Psephoderma alpinum*

### *Placochelys placodonta*

**0.8 m (2.6 ft) TL**

**FOSSIL REMAINS** Complete and partial skulls and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head very broad aft because temporal region is very expanded, adorned with numerous hornlets, lower jaw rather deep, 4 pairs of upper teeth. Only one united carapace present, profile subrectangular in top view, pavement consists of small irregular platelets surrounding larger, subconical osteoderms. Tail short, unarmored. Appendages are similar size fore and aft.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Hungary; Physiocardia.
**HABITAT** Island nearshore.
**NOTES** Lack of adequate modern description precludes accurate skeletal restoration or mass estimate at this time, whether limbs were paddles or more flipper-like is not clear.

## HENODONTIDS

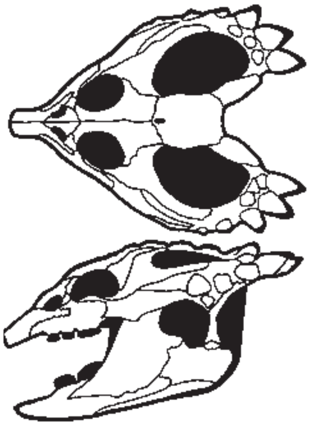
**SMALL TO MEDIUM-SIZED CYAMODONTOIDS FROM THE LATE TRIASSIC OF EUROPE**

**ANATOMICAL CHARACTERISTICS** Upper temporal openings very reduced or closed, teeth very reduced, main surfaces concave, may have had baleen-like soft tissues lining lower jaw. One united carapace, armored both dorsally and ventrally.
**HABITS** Filter feeders on small invertebrates and/or algae.

### *Parahenodus atancensis*

**1 m (3.3 ft) TL, 15 kg (35 lb)**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Head subtriangular in top view, upper temporal opening small.



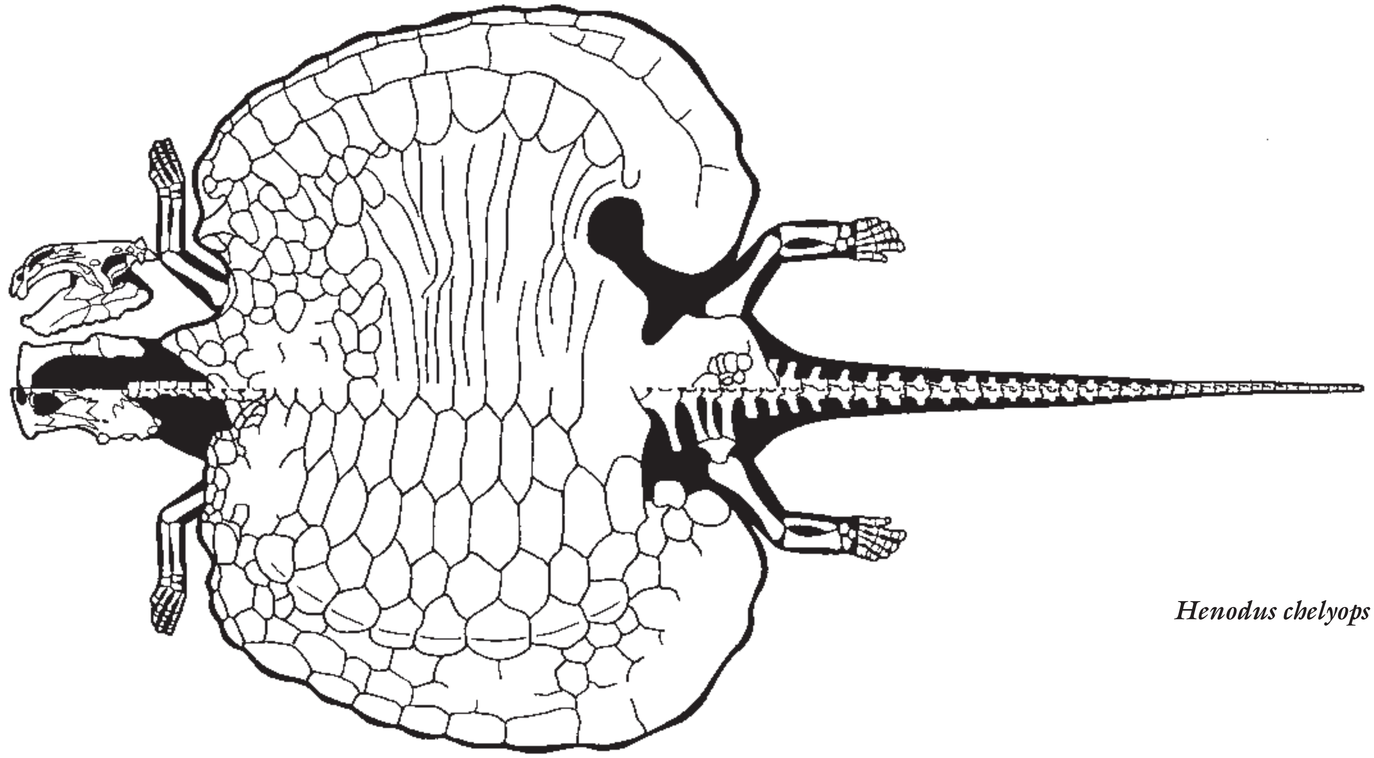
*Placochelys placodonta*

**AGE** Late Triassic; Carnian or Norian.
**DISTRIBUTION AND FORMATIONS** Spain; unnamed.
**HABITAT** Island nearshore.

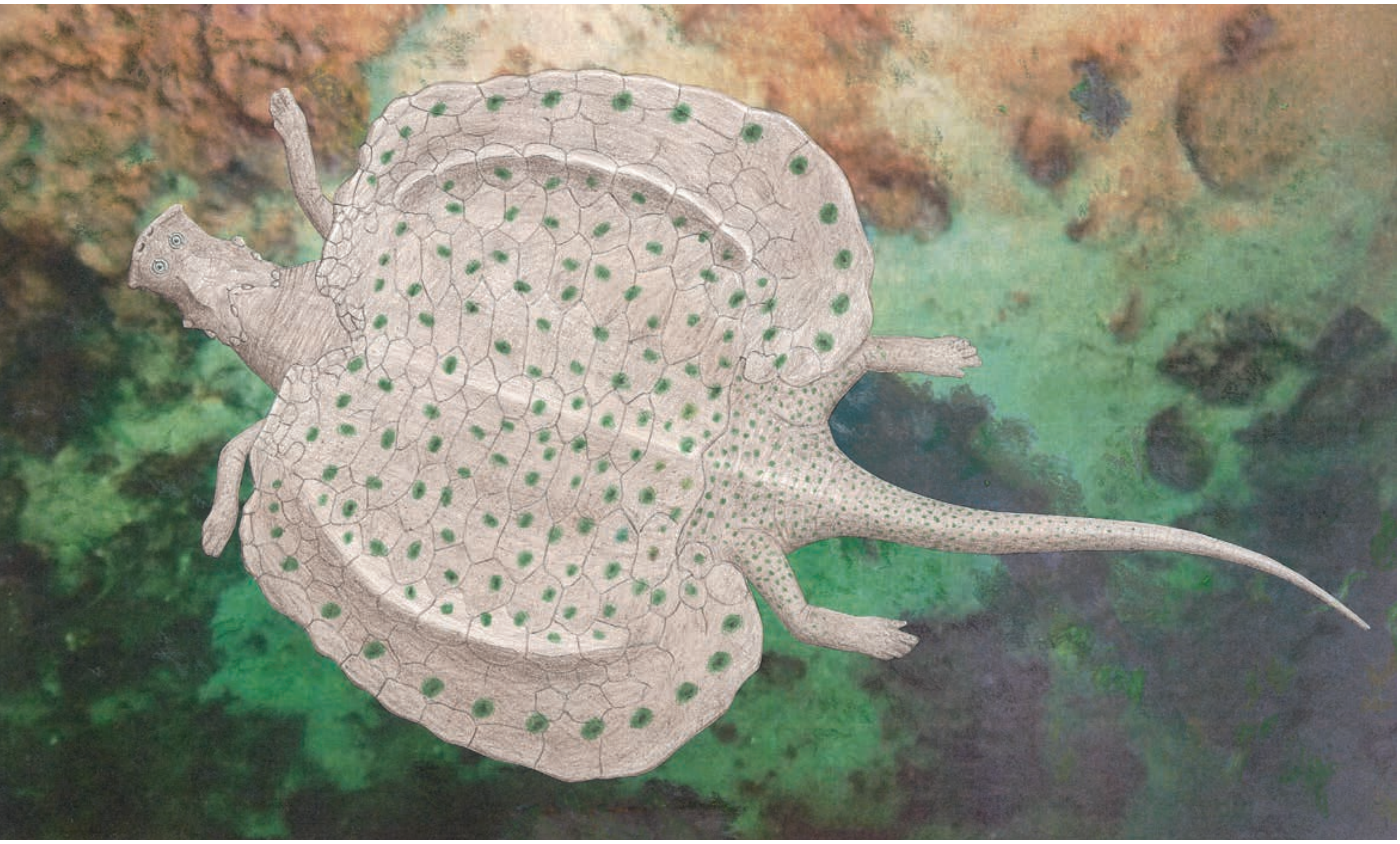
### *Henodus chelyops*

**1.4 m (4.5 ft) TL, 40 kg (90 lb)**

**FOSSIL REMAINS** Several skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head rather small, subrectangular in side and top views, moderately deep, snout broad and square ended, nostrils very near snout tip, orbits at front end of head face strongly upward, upper temporal opening closed, lower jaw deep, one pair of small teeth at front of upper jaw. Carapace extremely broad in dorsal view, side rims rounded in top view, platelets fairly well organized, form a pair of subtle fore-and-aft ridges, forward projection of carapace partly shields neck, no hornlets rimming carapace. Arm and leg very reduced, arm a little smaller than leg.
**AGE** Late Triassic; early Carnian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; lower Keuper.
**HABITAT** Coastal nearshore.



*Henodus chelyops*



## SAUROSPHARGIDS

**SMALL TO MEDIUM-SIZED SAUROPTERYGIANS FROM THE MIDDLE TO LATE TRIASSIC OF ASIA**

**ANATOMICAL CHARACTERISTICS** Heads moderate in size, subtriangular, not deep, nostrils set well back, lower jaw somewhat shorter than upper, teeth stout, subconical. Necks rather short. Trunks broad, ribcages and gastralia heavily built.
**NOTES** Relationships to other basal neodiapsids uncertain, may be related to thalattosaurs and converged with placodontiformes. Major differences in their anatomy may warrant placement of the known genera in different families.

### *Largocephalosaurus polycarpon*
**2 m (6.5 ft) TL, 40 kg (90 lb)**

**FOSSIL REMAINS** Several skulls and partial skeletons.
**ANATOMICAL CHARACTERISTICS** Head moderately broad, nostrils immediately in front of orbits. Trunk moderately broad. Tail moderate in length. Arm and leg moderately large. Lightly armored.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; upper Guanling.
**HABITAT** Coastal nearshore.
**NOTES** May include *L. qianensis.* Shared its habitat with *Panzhousaurus*, *Wumengosaurus*, *Nothosaurus yangjuanensis*, *Xinminosaurus*, *Barracudasauroides*, *Sinosaurosphargis.*

*Largocephalosaurus polycarpon*

### *Sinosaurosphargis yunguiensis*
**1 m (3.3 ft) TL, 10 kg (22 lb)**

**FOSSIL REMAINS** Skull and partial skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head very broad aft. Turtle-like trunk with flattened and very broad carapace, profile rounded in top view, pavement consists of very large number of small ossicles, no hornlets along rim.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; upper Guanling.
**HABITAT** Coastal nearshore.

### *Saurosphargis volzi*
**0.6 m (2 ft) TL**

**FOSSIL REMAINS** Partial skeleton.
**ANATOMICAL CHARACTERISTICS** Turtle-like trunk with flattened and very broad carapace.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Poland; lower Muschelkalk.
**HABITAT** Island nearshore.
**NOTES** Specimen destroyed in World War II. Shared its habitat with *Dactylosaurus*, *Germanosaurus.*

# EOSAUROPTERYGIANS

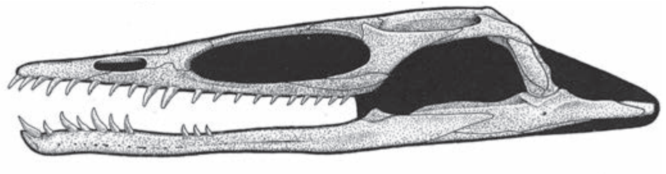
**SMALL TO GIGANTIC SAUROPTERYGIANS FROM THE EARLY TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Fairly variable. Heads very small to very large, generally subtriangular, not very broad, somewhat flattened with orbits facing partly upward, nostrils not near tip of snout, lower jaw not deep, full set of teeth always present, conical, not present on mouth roof, intermeshed if long. Neck, trunk, and front tail vertebrae fairly uniform in structure within a species. Neck not short, sometimes extremely long. Trunks not very broad, gastralia well developed. Tails not long, straight and not expanded aft. Scapula well forward on elongated, broad shoulder girdle complex, blade does not strongly overlap chest ribs. Moderately hydrodynamically streamlined, propulsion provided by limbs modified into hydrofoils, with aft limb sometimes somewhat less powerful than fore, tail primarily for stability and maneuvering.
**HABITAT** Freshwaters to deep oceans.
**HABITS** Swimming performance mediocre to good. Predaceous, most ambush and/or pursuit fishers and hunters of small to big game, some crushers, some filter feeders. Basal examples may have bred and nested on beaches, those with full flippers reproduced aquatically.

## PACHYPLEUROSAURS

**SMALL TO MEDIUM-SIZED EOSAUROPTERYGIANS FROM THE EARLY TO MIDDLE TRIASSIC OF EURASIA**

**ANATOMICAL CHARACTERISTICS** Temporal region and upper temporal opening not enlarged, constricted in top view. Tail base broad.
**HABITS** Swimming performance modest. Ambush and pursuit predators of small to medium-sized game.
**NOTES** Appear to include smallest known sea reptiles.



*Keichousaurus* **(Pachypleurosaurs)**

### *Majiashanosaurus discocoracoidis*
**1 m (3 ft) TL, 2.5 kg (5.5 lb)**

**FOSSIL REMAINS** Majority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Hand as large as foot.
**AGE** Early Triassic; Olenekian.
**DISTRIBUTION AND FORMATIONS** Eastern China; upper Nanlinghu.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with *Sclerocormus*, *Chaohusaurus geishanensis.*

### *Hanosaurus hupehensis*
**0.7 m (2 ft) TL, 1 kg (2 lb)**

**FOSSIL REMAINS** Partial skull and skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Upper temporal opening small, slender teeth moderately long.
**AGE** Middle Triassic; Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; lower Jialingjiang.
**HABITAT** Continental nearshore.

### *Panzhousaurus rotundirostris*
**0.7 m (2 ft) TL, 1 kg (2 lb)**

**FOSSIL REMAINS** Skull and majority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head small, snout fairly broad and rounded, orbits set well forward, upper temporal opening small, teeth large, limited to front half of jaws, strongly curved, procumbent. Neck moderately long. Trunk moderately broad. Hand as large as foot.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; upper Guanling.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with *Largocephalosaurus*, *Sinosaurosphargis*, *Wumengosaurus*, *Nothosaurus yangjuanensis*, *Xinminosaurus*, *Barracudasauroides.*

### *Dianopachysaurus dingi*
**0.2 m (0.7 ft) TL, 0.02 kg (0.05 lb)**

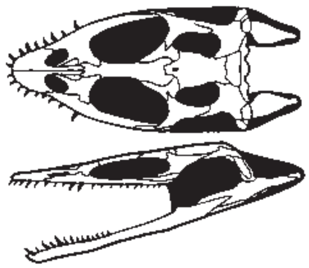
**FOSSIL REMAINS** Skull and majority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Skull fairly broad, orbits set well forward, upper temporal opening small, teeth small. Arm smaller than foot.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; middle Guanling.
**HABITAT** Continental nearshore.
**NOTES**. Shared its habitat with *Atopodentatus*, *Dinocephalosaurus.* Despite very small size appears to be an adult, in which case is the smallest known sea reptile along with *Dactylosaurus.*

### *Dactylosaurus gracilis*
**0.2 m (0.7 ft) TL, 0.02 kg (0.05 lb)**

**FOSSIL REMAINS** Numerous skulls and skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Upper temporal fenestra small.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Poland; lower Muschelkalk.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Saurosphargis*, *Germanosaurus.*

### *Keichousaurus hui*
**2.7 m (9 ft) TL, 50 kg (110 lb)**

**FOSSIL REMAINS** Very large number of skulls and skeletons, adult and juvenile, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head fairly small, moderately broad, upper temporal opening medium sized, front teeth long, procumbent, irregularly intermeshing, slender, gently curved spikes. Hand smaller than foot, ulna in lower arm greatly expanded.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; lower Falang.

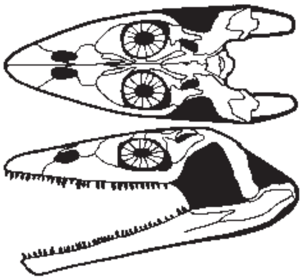


*Keichousaurus hui*

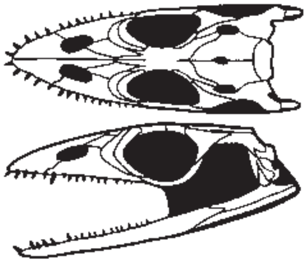
**HABITAT** Continental nearshore.
**HABITS** Modest degree of sexual dimorphism appears to be present. May have given live birth.
**NOTES** The Mesozoic marine reptile perhaps known from the largest number of specimens. Shared its habitat with *Nothosaurus youngi*, *Lariosaurus*, *Qianxisaurus*, *Wangosaurus*, *Qianichthyosaurus.*

### *Anarosaurus heterodontus*
**0.5 m (1.6 ft) TL, 0.35 kg (0.75 lb)**

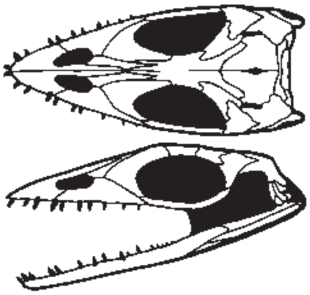
**FOSSIL REMAINS** Skulls and skeletons, most severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head fairly broad, upper temporal opening very small, teeth numerous, small, blunt. Hand smaller than foot.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Central Germany; middle Muschelkalk.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Serpianosaurus germanicus*, *Nothosaurus juvenilis.*



*Anarosaurus heterodontus*



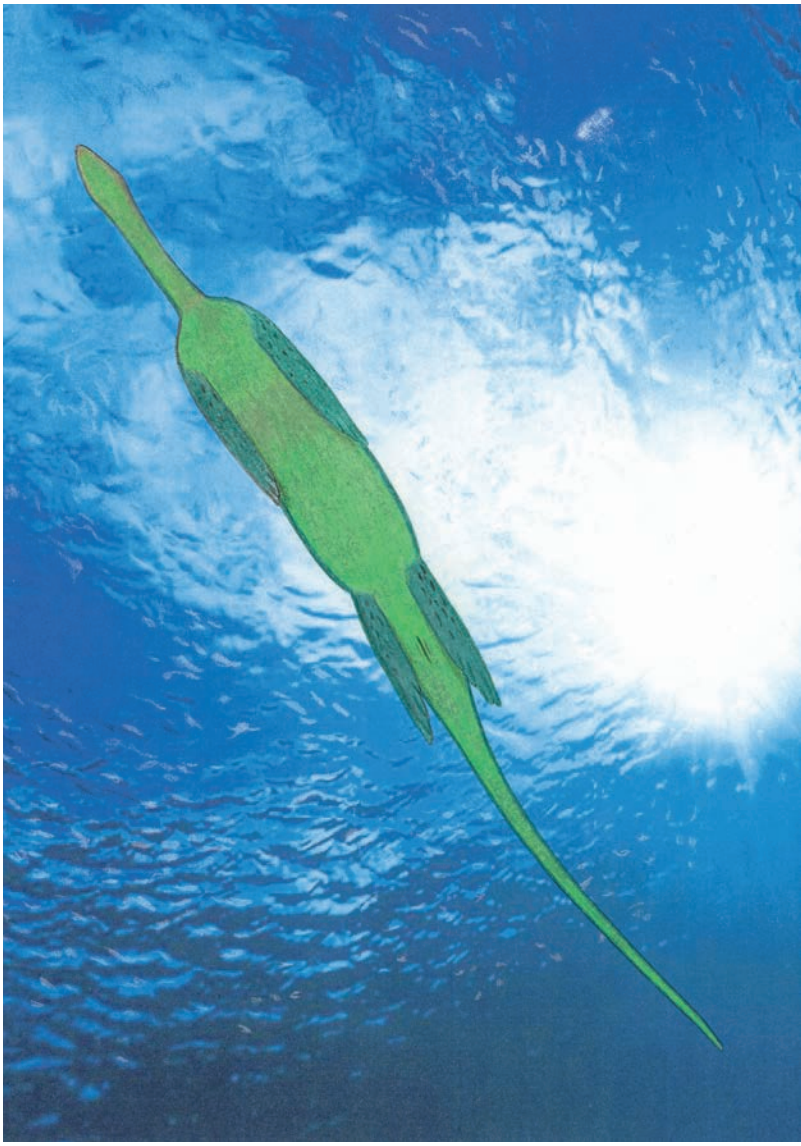
*Neusticosaurus pusillus*



*Neusticosaurus peyeri*

### *Neusticosaurus pusillus*
**0.5 m (1.6 ft) TL, 0.35 kg (0.75 lb)**

**FOSSIL REMAINS** Numerous skulls and skeletons, most severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head small, fairly broad, upper temporal opening extremely small, teeth moderate in number, medium sized, stout. Hand smaller than foot.
**AGE** Middle Triassic; early Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; lower Meride Limestone.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Ceresiosaurus calcagnii.* May be the direct ancestor of *N. peyeri.*



*Neusticosaurus* (or *Pachypleurosaurus*) *edwardsi*

### *Neusticosaurus peyeri*

**0.5 m (1.6 ft) TL, 0.35 kg (0.75 lb)**

**FOSSIL REMAINS** Numerous skulls and skeletons, most severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head small, fairly broad, upper temporal opening nearly closed, teeth moderate in number, medium sized, stout. Hand smaller than foot.
**AGE** Middle Triassic; early Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; lower Meride Limestone.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Ceresiosaurus lanzi*. May be the direct ancestor of *N. toeplitschi*.

### *Neusticosaurus toeplitschi*

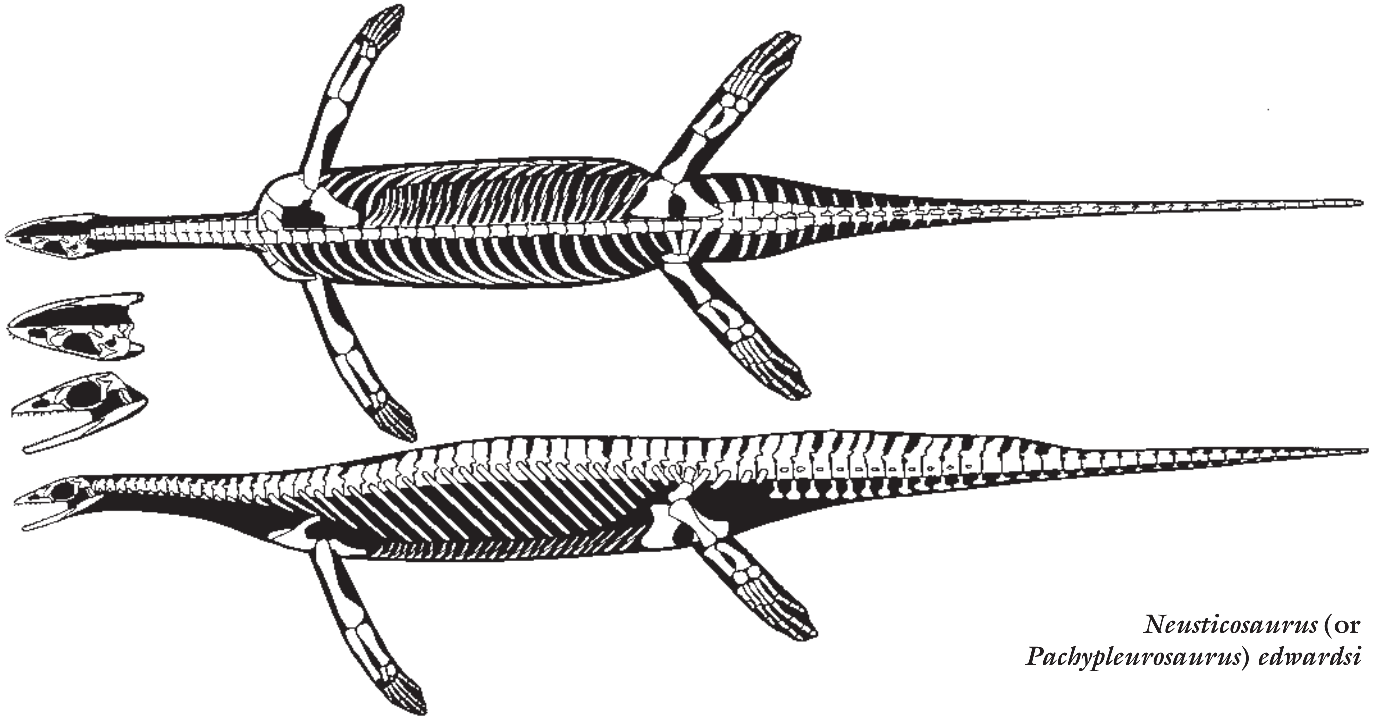
**0.4 m (1.3 ft) TL, 0.18 kg (4 lb)**

**FOSSIL REMAINS** Numerous skulls and skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head small, fairly broad, teeth moderate in number, medium sized, stout.
**AGE** Middle Triassic; late Ladinian and/or early Carnian.
**DISTRIBUTION AND FORMATIONS** Switzerland; Partnach.
**HABITAT** Island nearshore.

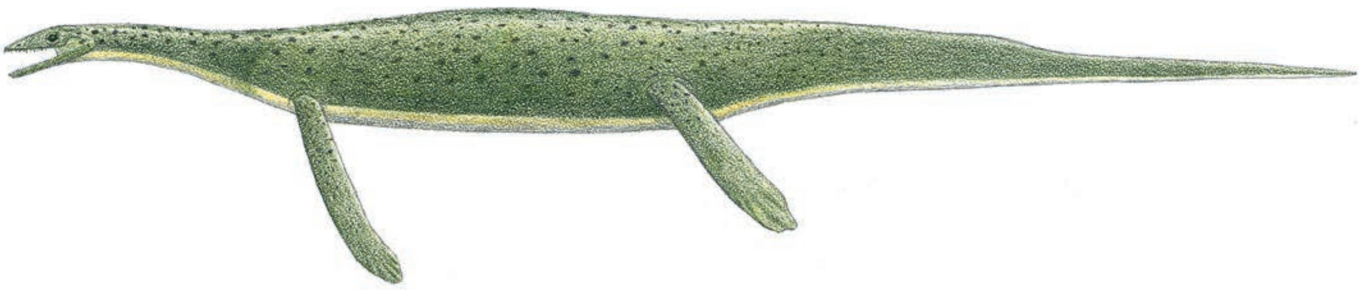
### *Neusticosaurus* (or *Pachypleurosaurus*) *edwardsi*

**1.25 m (4 ft) TL, 5.5 kg (12 lb)**

**FOSSIL REMAINS** Numerous skulls and skeletons, most severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head small, fairly broad, upper temporal opening very small, teeth moderate in number, medium sized, stout. Arm longer and more slender than leg, hand smaller than foot.
**AGE** Middle Triassic; middle Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; middle Meride Limestone.
**HABITAT** Island nearshore.



*Neusticosaurus* (or *Pachypleurosaurus*) *edwardsi*



### *Serpianosaurus germanicus*

**2 m (6 ft) TL, 20 kg (45 lb)**

**FOSSIL REMAINS** Partial skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Central Germany; middle Muschelkalk.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Anarosaurus*, *Nothosaurus juvenilis*. May be direct ancestor of *S. mirigiolensis*.

### *Serpianosaurus mirigiolensis*

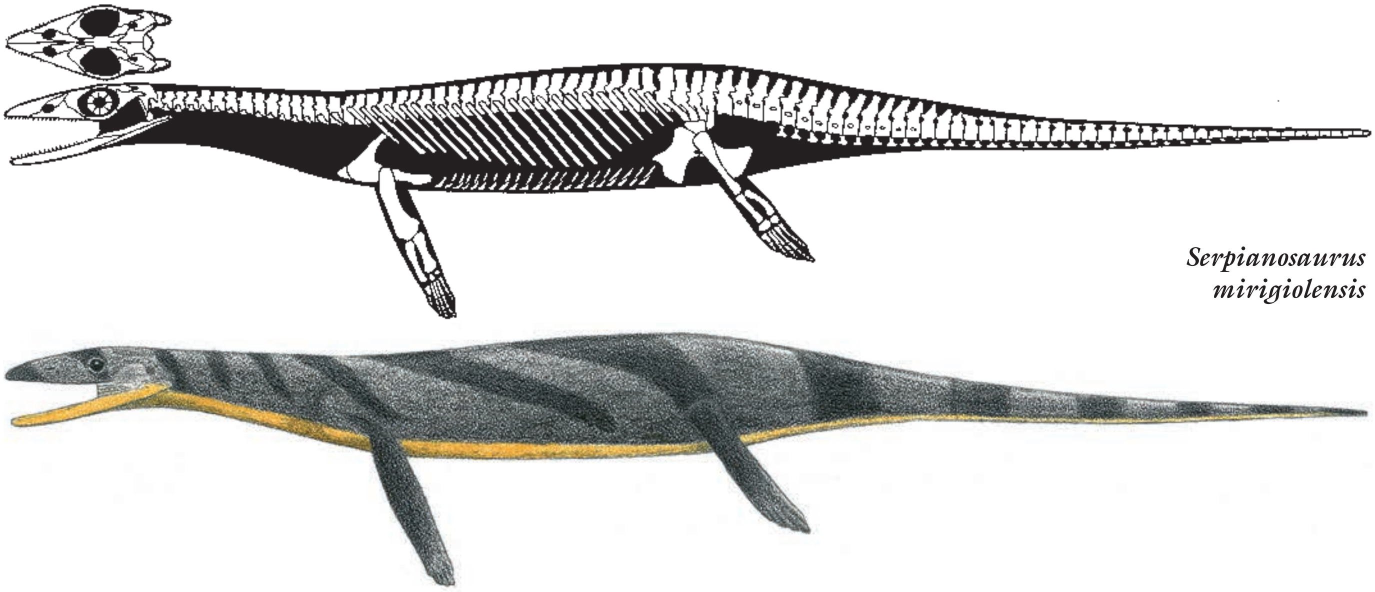
**0.85 m (2.8 ft) TL, 1.7 kg (3.5 lb)**

**FOSSIL REMAINS** Numerous skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head fairly large, orbits large, upper temporal fenestra extremely small, teeth numerous and small. Hand almost as large as foot.
**AGE** Middle Triassic; latest Anisian and earliest Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; Besano.
**HABITAT** Island nearshore.
**NOTES** Shared its habitat with *Askeptosaurus*, *Helveticosaurus*, *Paraplacodus*, *Wimanius*, *Besanosaurus*, unnamed genus *buchseri*, *Mixosaurus cornalianus*, *M.? kuhnschnyderi*.

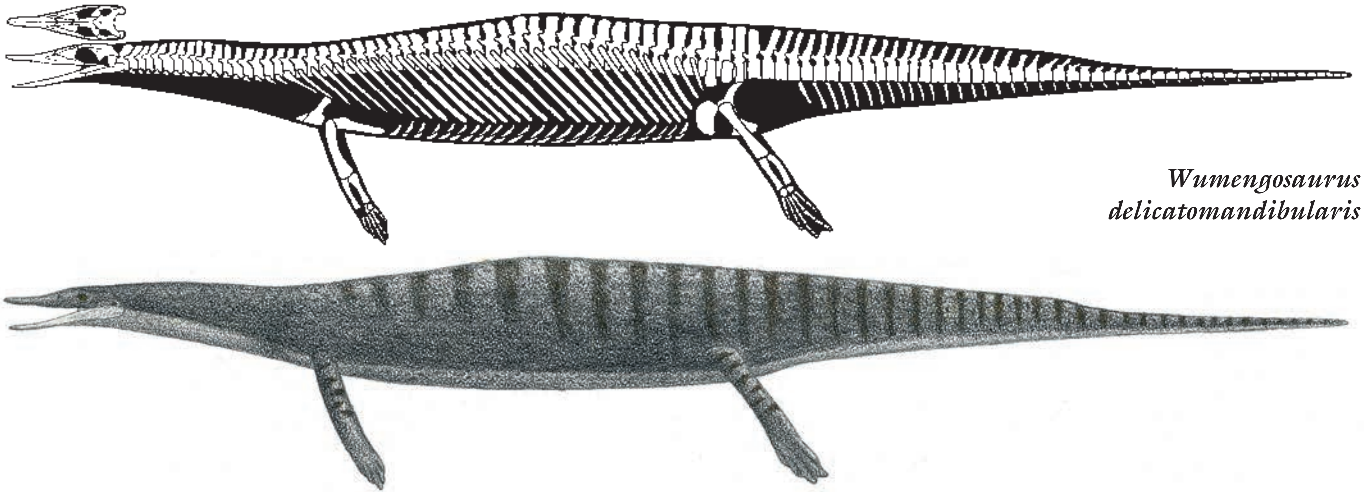
### *Wumengosaurus delicatomandibularis*

**1.3 m (4 ft) TL, 6 kg (12 lb)**

**FOSSIL REMAINS** Skull and two skeletons.
**ANATOMICAL CHARACTERISTICS** Head small, narrow, snout long, nostrils very small, teeth numerous, small, vertical. Arm and leg rather small, hand smaller than foot.



*Serpianosaurus mirigiolensis*



*Wumengosaurus delicatomandibularis*

**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; upper Guanling.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with *Largocephalosaurus*, *Sinosaurosphargis*, *Panzhousaurus*, *Nothosaurus yangjuanensis*, *Xinminosaurus*, *Barracudasauroides.*

## NOTHOSAURS

**SMALL TO LARGE EOSAUROPTERYGIANS FROM THE MIDDLE TRIASSIC OF EURASIA**

**ANATOMICAL CHARACTERISTICS** Heads medium sized, orbits placed well forward because temporal region elongated, sometimes extremely so, nostrils not severely reduced, fairly close to orbits, lower jaws shallow. Neck moderately long. Trunk moderately long, fairly narrow. Tail moderately long. Pelvis attached to vertebral column, ventral elements not highly expanded, arms and legs not full flippers.
**HABITATS** Coastal and brackish shorelines, lagoons, reefs, estuaries, freshwaters.
**HABITS** Swimming performance modest. Most ambush and pursuit predators of small to medium-sized game, some crushers. At least some examples probably gave live birth.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

## SIMOSAURIDS

**MEDIUM-SIZED NOTHOSAURS FROM THE MIDDLE TRIASSIC OF EUROPE**

**ANATOMICAL CHARACTERISTICS** Heads fairly broad, numerous teeth short, blunt.
**HABITS** Small shellfish crushers.

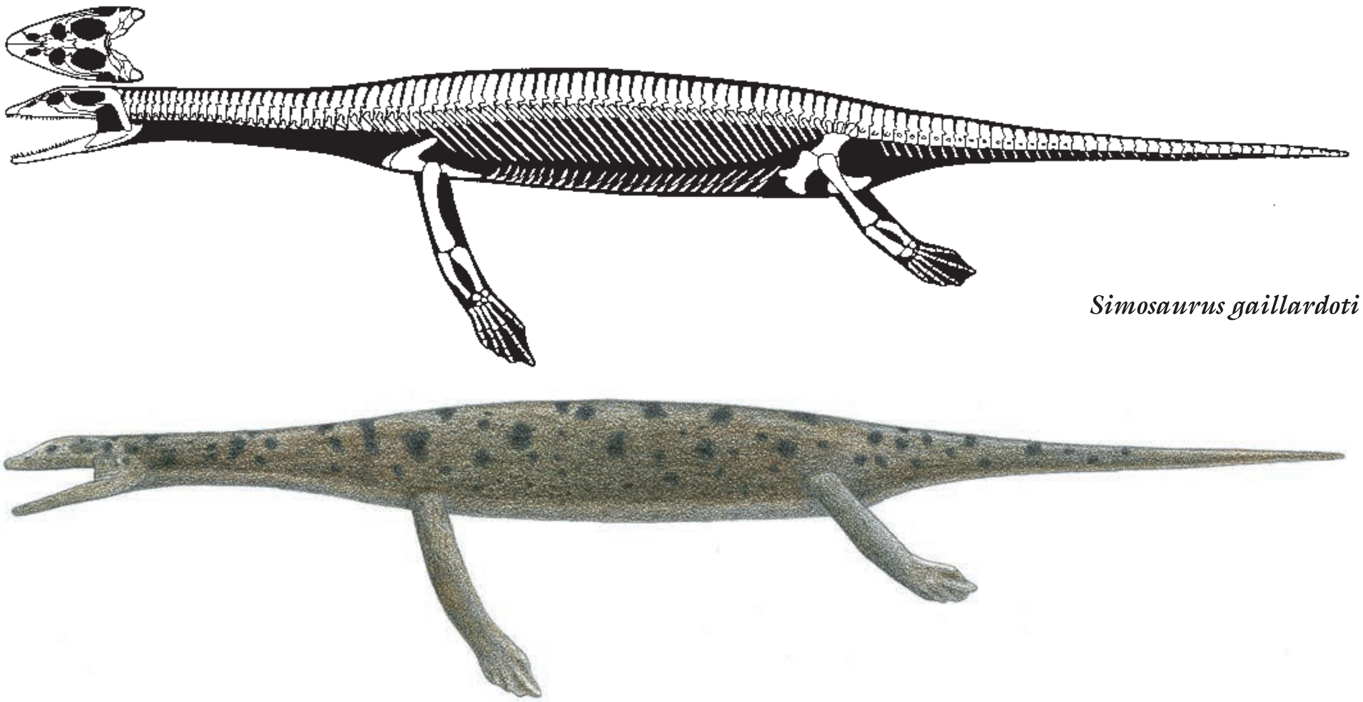
### ***Simosaurus gaillardoti***
**4.2 m (14 ft), 200 kg (440 lb)**

**FOSSIL REMAINS** Skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head medium sized.
**AGE** Middle Triassic; middle Ladinian.
**DISTRIBUTION AND FORMATIONS** France, southern Germany; upper Muschelkalk.
**HABITAT** Island archipelago shallows.

## NOTHOSAURIDS

**SMALL TO LARGE NOTHOSAURS FROM THE MIDDLE TRIASSIC OF EURASIA**

**ANATOMICAL CHARACTERISTICS** Heads narrow, temporal region and openings very to extremely elongated and constricted in top view, modest number of teeth, front set long, procumbent, irregularly intermeshing, slender, gently curved spikes, back teeth small spikelets.
**HABITS** Ambush and pursuit predators of small to medium-sized game.



*Simosaurus gaillardoti*

**NOTES** Not able to estimate masses because of insufficient description of skeletal material.

### *Germanosaurus? schafferi*

**3 m (10 ft) TL**

**FOSSIL REMAINS** Partial skulls, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Temporal region very elongated.
**AGE** Middle Triassic; early Anisian.
**DISTRIBUTION AND FORMATIONS** Poland; lower Muschelkalk.
**HABITAT** Island archipelago shallows.
**NOTES** The validity of the generic title is problematic. Shared its habitat with *Saurosphargis*, *Dactylosaurus*.

### *Nothosaurus marchicus*

**1.2 m (4 ft) TL**

**FOSSIL REMAINS** Several skulls and partial skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Temporal region extremely elongated.
**AGE** Middle Triassic; early and middle Anisian.
**DISTRIBUTION AND FORMATIONS** Central Germany, Netherlands; lower Muschelkalk.
**HABITAT** Island archipelago shallows.
**NOTES** Probably includes *N. winterswijkensis*. Shared its habitat with *Pararcus*, *Lariosaurus vosseveldensis*. May have been direct ancestor of *N. juvenilis*.

### *Nothosaurus juvenilis*

**2 m (6.5 ft) TL**

**FOSSIL REMAINS** Majority of skull.
**ANATOMICAL CHARACTERISTICS** Temporal region extremely elongated.
**AGE** Middle Triassic; middle and late Anisian.
**DISTRIBUTION AND FORMATIONS** Central Germany; middle Muschelkalk.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Anarosaurus*, *Serpianosaurus germanicus*. May have been direct ancestor of *N. mirabilis* and/or *N. giganteus*.

### *Nothosaurus mirabilis*

**3 m (10 ft) TL**

**FOSSIL REMAINS** Several skulls and partial skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Temporal region extremely elongated.
**AGE** Middle Triassic; late Anisian.
**DISTRIBUTION AND FORMATIONS** Central Germany; upper Muschelkalk.
**HABITAT** Island archipelago shallows.
**NOTES** Inadequate descriptions of remains of this well-known genus preclude accurate skeletal restorations at this time. Shared its habitat with *Placodus*, *Pistosaurus*, *Phantomosaurus*, *N. giganteus.*

### *Nothosaurus giganteus*

**7 m (23 ft) TL**

**FOSSIL REMAINS** Several skulls and partial skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Temporal region extremely elongated.
**AGE** Middle Triassic; late Anisian.
**DISTRIBUTION AND FORMATIONS** Central Germany; upper Muschelkalk.
**HABITAT** Island archipelago shallows.

### *Nothosaurus haasi*

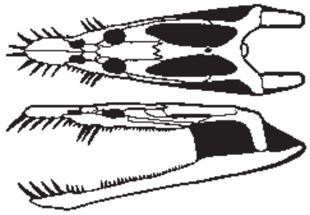
**1.3 m (4 ft) TL**

**FOSSIL REMAINS** Several skulls and partial skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Temporal region extremely elongated.
**AGE** Middle Triassic; late Anisian and/or early Ladinian.
**DISTRIBUTION AND FORMATIONS** Israel; lower Saharonium.
**HABITAT** Continental shallows.
**NOTES** May include *N. tchernovi*. May be same species as one of the European *Nothosaurus* of the same age.

### *Nothosaurus cymatosauroides*

**2.5 m (8 ft) TL**

**FOSSIL REMAINS** Skull, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Temporal region extremely elongated.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Northeastern Spain; upper Muschelkalk.
**HABITAT** Island archipelago shallows.



*Nothosaurus mirabilis*

### *Nothosaurus yangjuanensis*
**3.5 m (12 ft) TL**

**FOSSIL REMAINS** A few skulls and skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; upper Guanling.
**HABITAT** Continental shallows.
**NOTES** May include *N. rostellatus* and *N. zhangi*. May be same species as one of the European *Nothosaurus* of the same age.
**NOTES** Shared its habitat with *Largocephalosaurus*, *Sinosaurosphargis*, *Panzhousaurus*, *Wumengosaurus*, *Xinminosaurus*, *Barracudasauroides*.

### *Nothosaurus youngi*
**2 m (6.5 ft) TL**

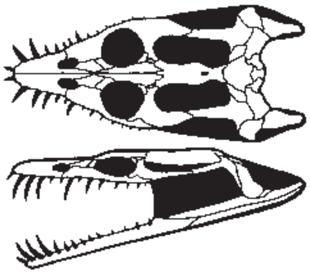
**FOSSIL REMAINS** Majority of two skulls and skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Standard for genus.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; lower Falang.
**HABITAT** Continental nearshore.
**NOTES** May be same species as one of the western *Nothosaurus* of the same age. Shared its habitat with *Keichousaurus*, *Qianxisaurus*, *Wangosaurus*, *Qianichthyosaurus*, *Lariosaurus*.

### *Lariosaurus vosseveldensis*
**5 m (1.5 ft) TL**

**FOSSIL REMAINS** Skull, severely flattened top to bottom, possibly juvenile.
**ANATOMICAL CHARACTERISTICS** Temporal region very elongated.
**AGE** Middle Triassic; early Anisian.
**DISTRIBUTION AND FORMATIONS** Netherlands; lower Muschelkalk.
**HABITAT** Island archipelago shallows.
**NOTES** May include *L. winkelhorsti*. Shared its habitat with *Pararcus*, *Nothosaurus marchicus*. May be a direct ancestor of *L. balsami*.

### *Lariosaurus balsami*
**1.5 m (5 ft) TL**

**FOSSIL REMAINS** Skulls and skeletons, most severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Temporal region very elongated.
**AGE** Middle Triassic; middle to late Ladinian.
**DISTRIBUTION AND FORMATIONS** Northern Italy; Perledo-Varenna.
**HABITAT** Island archipelago shallows.
**NOTES** May include *L. curionii* and *L. valcersii*.


*Lariosaurus balsami*

### *Lariosaurus xingyiensis*
**2.5 m (8 ft) TL**

**FOSSIL REMAINS** Skull and majority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Temporal region very elongated.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; lower Falang.
**HABITAT** Continental nearshore.

### *Ceresiosaurus calcagnii*
**3 m (10 ft) TL**

**FOSSIL REMAINS** Skulls and skeletons, severely flattened.
**ANATOMICAL CHARACTERISTICS** Head rather small. Appendages more flipper shaped.
**AGE** Middle Triassic; early Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; lower Meride Limestone.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Neusticosaurus pusillus*.

### *Ceresiosaurus lanzi*
**3 m (10 ft) TL**

**FOSSIL REMAINS** Skulls and skeletons, flattened.
**ANATOMICAL CHARACTERISTICS** Head fairly large. Appendages more flipper shaped.
**AGE** Middle Triassic; early Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; lower Meride Limestone.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Neusticosaurus peyeri*.

## PAXPLESIOSAURS

**SMALL TO GIGANTIC EOSAUROPTERYGIANS FROM THE MIDDLE TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**HABITATS** Freshwaters to deep oceans.
**HABITS** Swimming performance mediocre to good. Most ambush and/or pursuit fishers and hunters of small to big game, some crushers, some filter feeders.
**NOTES** Eosauropterygians including corosaurs and plesiosauriformes and their common ancestor.

## PAXPLESIOSAUR MISCELLANEA

### *Qianxisaurus chajiangensis*
**1 m (10 ft) TL, 3 kg (6 lb)**

**FOSSIL REMAINS** Skull and majority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head fairly large and broad, snout fairly long, upper temporal fenestra nearly closed, teeth numerous, short and stout. Hand smaller than foot.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Southwestern China; lower Falang.
**HABITAT** Continental nearshore.
**HABITS** Small shellfish crusher.
**NOTES** Shared its habitat with *Keichousaurus*, *Nothosaurus youngi*, *Lariosaurus*, *Qianichthyosaurus*, *Wangosaurus*.

### *Wangosaurus brevirostris*
**3 m (10 ft) TL**

**FOSSIL REMAINS** Majority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head fairly large, narrow, snout very short because temporal region extremely elongated. Neck fairly long. Hand smaller than foot.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; lower Falang.
**HABITAT** Continental nearshore.
**HABITS** Small game fisher.
**NOTES** Not able to estimate masses because of inadequate skeletal material.

### *Augustasaurus hagdorni*
**3 m (10 ft) TL**

**FOSSIL REMAINS** Skull and minority of a skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Snout long, upper temporal opening long, front teeth medium-sized spikes.
**AGE** Middle Triassic; late Anisian.
**DISTRIBUTION AND FORMATIONS** Nevada; upper Favret.
**HABITAT** Continental shallows.
**HABITS** Fisher of small game.
**NOTES** Not able to estimate mass because of inadequate skeletal material. Shared its habitat with unnamed genus and species, unnamed genus *duelferi*, unnamed genus *youngorum*, *Phalarodon*, *Thalattoarchon*.

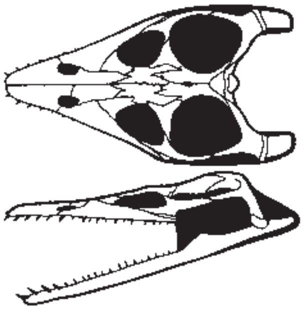
## COROSAURIDS

**SMALL PAXPLESIOSAURS FROM THE EARLY TRIASSIC OF NORTH AMERICA**

**ANATOMICAL CHARACTERISTICS** Head medium sized, broad, flattened, upper temporal opening large, teeth short, procumbent spikes. Tail base very broad.
**HABITATS** Primarily coastal shallows.
**HABITS** Swimming performance modest. Ambush and pursuit predators of small game.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

### *Corosaurus alcovensis*
**1.5 m (5 ft) TL, 7 kg (15 lb)**

**FOSSIL REMAINS** Skull and partial skeletons.
**ANATOMICAL CHARACTERISTICS** Hand smaller than foot.
**AGE** Early Triassic; late Olenekian.
**DISTRIBUTION AND FORMATIONS** Wyoming; lower Chugwater.
**HABITAT** Interior seaway near shore.


*Corosaurus alcovensis*

## CYMATOSAURIDS

**SMALL PAXPLESIOSAURS FROM THE MIDDLE TRIASSIC OF EUROPE**

**HABITS** Swimming performance modest. Ambush and pursuit predators of small game.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

***Cymatosaurus friedericianus***
**2 m (6 ft) TL**

FOSSIL REMAINS Numerous skulls and skeletons, adult and juvenile, partial and/or severely flattened top to bottom.
ANATOMICAL CHARACTERISTICS Temporal region very elongated.
AGE Middle Triassic; lower Anisian.
DISTRIBUTION AND FORMATIONS Eastern Germany, western Poland; lower Muschelkalk.
HABITAT Island archipelago shallows.
NOTES May include *C. latifrons*, *C. multidentatus*, *C. minor*, *C. erikae.*

## PLESIOSAURIFORMES

**SMALL TO GIGANTIC PAXPLESIOSAURS FROM THE MIDDLE TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL**

ANATOMICAL CHARACTERISTICS Limbs are clawless full flippers with increased number of distal elements.
HABITATS Freshwaters to deep oceans.
HABITS Swimming performance mediocre to good. Most ambush and/or pursuit fishers and hunters of small to big game, some filter feeders. Little or no ability to come onto land, so reproduced aquatically in most if not all cases.

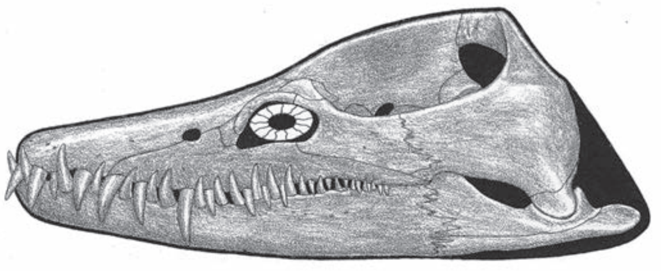
## PISTOSAURIDS

**SMALL TO MEDIUM-SIZED PLESIOSAURIFORMES FROM THE MIDDLE TO LATE TRIASSIC OF EURASIA**

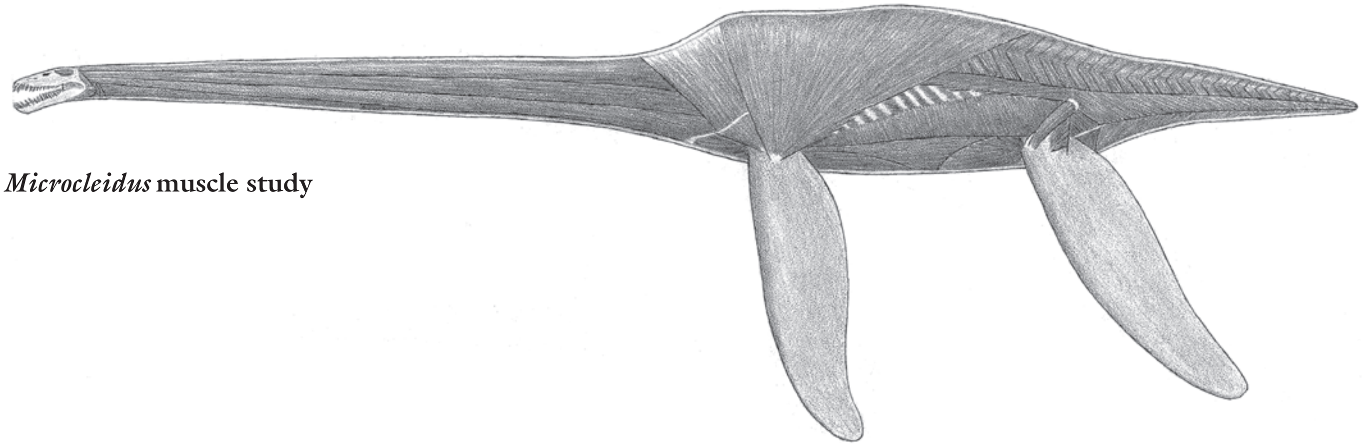
ANATOMICAL CHARACTERISTICS Heads not broad, snout fairly long, nostrils very small, upper temporal opening long, number of teeth modest, procumbent.
NOTES Absence from at least some other seas may reflect lack of sufficient sampling.
HABITAT Coastal shallows and continental shelves.
HABITS Swimming performance modest. Able to dive to deeper waters. Ambush and pursuit fishers of small to medium-sized game. May have given live birth.

***Pistosaurus longaevus***
**3 m (10 ft) TL, 100 kg (220 lb)**

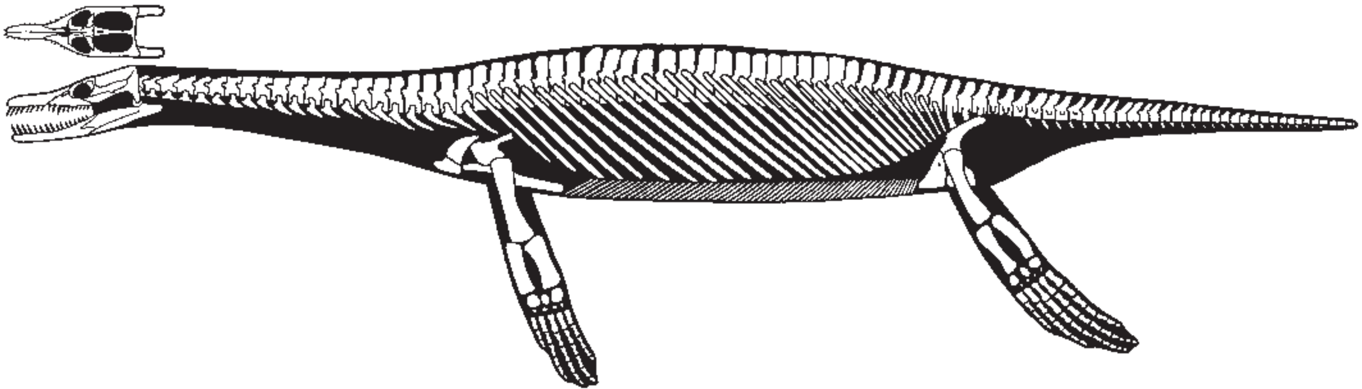
FOSSIL REMAINS Skulls and a skeleton.
ANATOMICAL CHARACTERISTICS Head fairly narrow, all teeth fairly long and strongly built. Neck medium length. Tail medium length. Foreflipper a little smaller than aft.
AGE Middle Triassic; late Anisian.
DISTRIBUTION AND FORMATIONS Southern Germany; upper Muschelkalk.
HABITAT Island archipelago shallows.



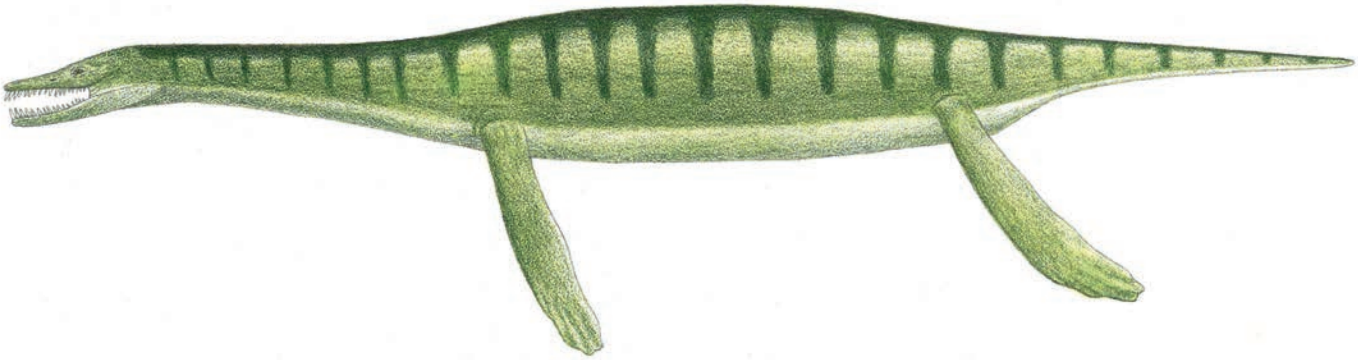
***Thalassiodracon* (Plesiosauriformes)**

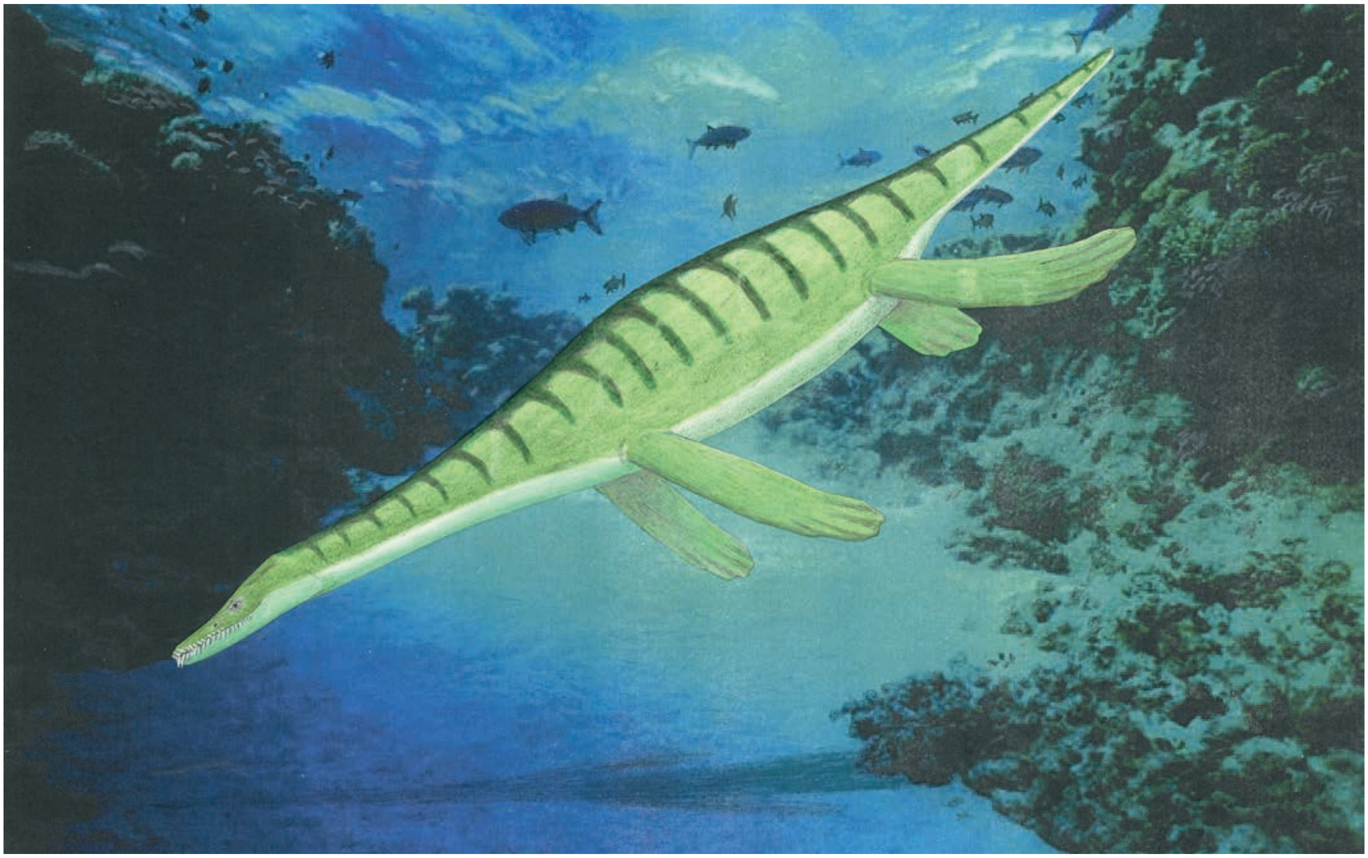


***Microcleidus* muscle study**



*Pistosaurus longaevus*





*Pistosaurus longaevus*

**NOTES** The one skeleton has no skull, so whether it belongs to this species is not certain. Shared its habitat with *Placodus*, *Nothosaurus mirabilis*, *N. giganteus*, *Phantomosaurus*.

### *Yunguisaurus liae*

**1.7 m (5.5 ft) TL, 20 kg (45 lb)**

**FOSSIL REMAINS** Skull and majority of adult skeleton, severely flattened top to bottom, juvenile skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head small, modest number of teeth, front set long, procumbent, irregularly intermeshing, slender, gently curved spikes. Neck and tail fairly long.
**AGE** Late Triassic; early Carnian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; upper Falang.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with *Anshunsaurus huangguoshuensis*, *Miodentosaurus*, *Qianichthyosaurus zhoui*, *Guanlingsaurus*, *Guizhouichthyosaurus*, unnamed genus *orientalis*.

## PLESIOSAURS

**SMALL TO GIGANTIC PLESIOSAURIFORMES FROM THE EARLY JURASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Fairly variable. Heads very small to very large, nostrils small and immediately before orbits. Necks very short to extremely long. Trunk compact, gastralia reduced in number and increased in complexity, robust, central shafts straight, lateral tips swept back. Tail never very long, tip bearing small, either vertical or horizontal flukes in at least some examples. Lower pelvic elements enlarged into large, flat plates. Flippers better developed, with shortened lower arm and increased distal complexes, about as long as trunk, foreflipper at least about as large as aft.
**HABITATS** Freshwaters to deep oceans. Probably all gave live birth.
**HABITS** Swimming performance mediocre to good. Most ambush and/or pursuit fishers and hunters of small to big game, some filter feeders.

## PLESIOSAUR MISCELLANEA

### *Eoplesiosaurus antiquior*

**3 m (10 ft) TL, 150 kg (300 lb)**

**FOSSIL REMAINS** Nearly complete skeleton.
**ANATOMICAL CHARACTERISTICS** Neck long. Fore and aft flippers similar in size.
**AGE** Early Jurassic; earliest Hettangian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Blue Lias.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Stratesaurus*, *Avalonnectes*, *Eurycleidus*, *Atychodracon*, *Thalassiodracon*, *Protoichthyosaurus*.

## PLIOSAUROIDS

**SMALL TO GIGANTIC PLESIOSAURS FROM THE EARLY JURASSIC TO THE EARLY LATE CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Significantly variable. Necks never extremely long.
**HABITATS** Coastal shallows to deep oceans.
**HABITS** Swimming performance modest to good. Ambush and/or pursuit fishers and hunters of small to big game.

## RHOMALEOSAURIDS

**SMALL TO LARGE PLIOSAUROIDS FROM THE EARLY TO MIDDLE JURASSIC OF THE NORTHERN AND SOUTHERN HEMISPHERES**

**ANATOMICAL CHARACTERISTICS** Uniform. Heads medium sized, temporal region expanded. Necks moderately long.
**HABITATS** Coastal shallows and continental shelves.
**HABITS** Swimming performance modest. Ambush and pursuit fishers of small to medium-sized game.

### *Anningasaura lymense*

**Adult size uncertain**

**FOSSIL REMAINS** Skull and partial skeleton, juvenile.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Jurassic.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Lias group.
**HABITAT** Island archipelago shallows.
**NOTES** Exact stratigraphic level unknown. May not be within this family.

### *Lindwurmia thiuda*

**2.5 m (8 ft) TL, 90 kg (200 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Snout short and broad, teeth large.
**AGE** Early Jurassic; early Hettangian.

**DISTRIBUTION AND FORMATIONS** Northwestern Germany; unnamed.
**HABITAT** Island archipelago shallows.
**NOTES** May not be within this family.

### *Stratesaurus taylori*
**1.2 m (4 ft) TL, 10 kg (20 lb)**

**FOSSIL REMAINS** Two skulls, partial skeleton.
**ANATOMICAL CHARACTERISTICS** Head short, fairly deep, teeth large.
**AGE** Early Jurassic; earliest Hettangian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Blue Lias.
**HABITAT** Island archipelago shallows.
**HABITS** Fishers of small to medium-sized game.
**NOTES** Placement in family uncertain. Shared its habitat with *Eoplesiosaurus*, *Avalonnectes*, *Eurycleidus*, *Atychodracon*, *Thalassiodracon*, *Protoichthyosaurus.*

### *Avalonnectes arturi*
**2 m (4 ft) TL, 50 kg (100 lb)**

**FOSSIL REMAINS** Partial skull and majority of skeleton, partial skeleton.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Early Jurassic; earliest Hettangian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Blue Lias.
**HABITAT** Island archipelago shallows.

### *Eurycleidus arcuatus*
**2.5 m (8 ft) TL, 90 kg (200 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Jurassic; earliest Hettangian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Blue Lias.
**HABITAT** Island archipelago shallows.

### *Atychodracon megacephalus*
**4.9 m (16 ft) TL, 650 kg (1,400 lb)**

**FOSSIL REMAINS** Skull and partial skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Jurassic; earliest Hettangian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Blue Lias.
**HABITAT** Island archipelago shallows.

### *Macroplata tenuiceps*
**4.5 m (15 ft) TL, 550 kg (1,200 lb)**

**FOSSIL REMAINS** Partial skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Neck fairly short. Shoulder girdle well developed. Fore and aft flippers similar in size.
**AGE** Early Jurassic; Hettangian.
**DISTRIBUTION AND FORMATIONS** Southern England; Blue Lias.
**HABITAT** Island archipelago shallows.
**HABITS** Powerful swimmer.

### *Meyerasaurus victor*
**3.4 m (11 ft) TL, 275 kg (600 lb)**

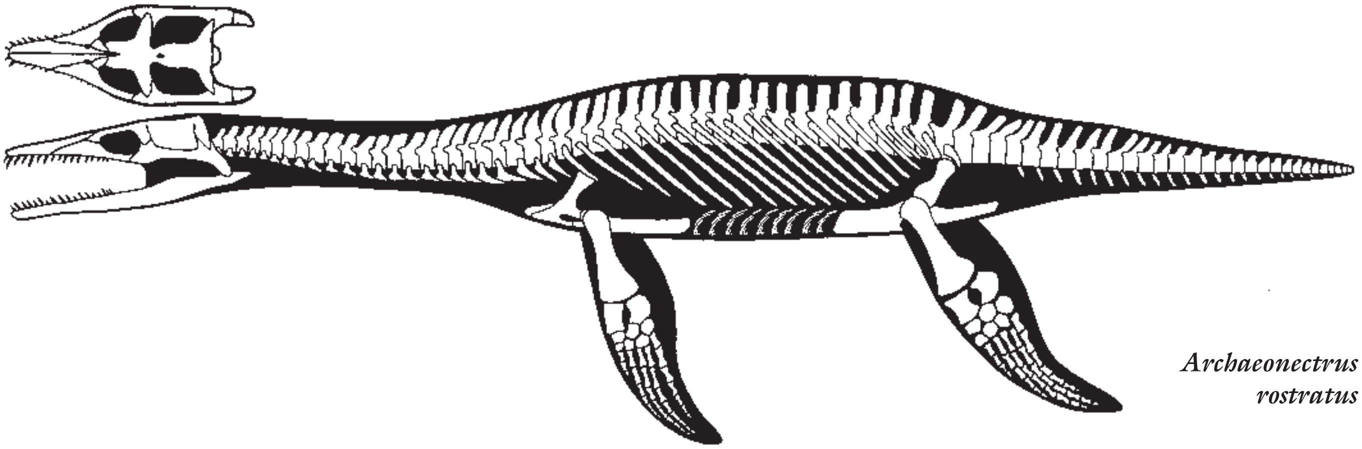
**FOSSIL REMAINS** Complete skull and skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Front teeth large and procumbent. Neck fairly short. Fore and aft flippers similar in size.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Posidonienschiefer.
**HABITAT** Island archipelago shallows.
**HABITS** Hunter of small and medium-sized game.
**NOTES** Has the best-preserved plesiosaur gastralia series. Shared its habitat with *Hauffiosaurus*, *Seeleyosaurus*, *Hydrorion*, *Hauffiopteryx*, unnamed genus *trigonodon*, *Suevoleviathan*, *Eurhinosaurus*, *Stenopterygius*, *Mystriosaurus*, *Platysuchus*, *Macrospondylus.*

### *Maresaurus coccai*
**6 m (20 ft) TL, 1.3 tonnes**

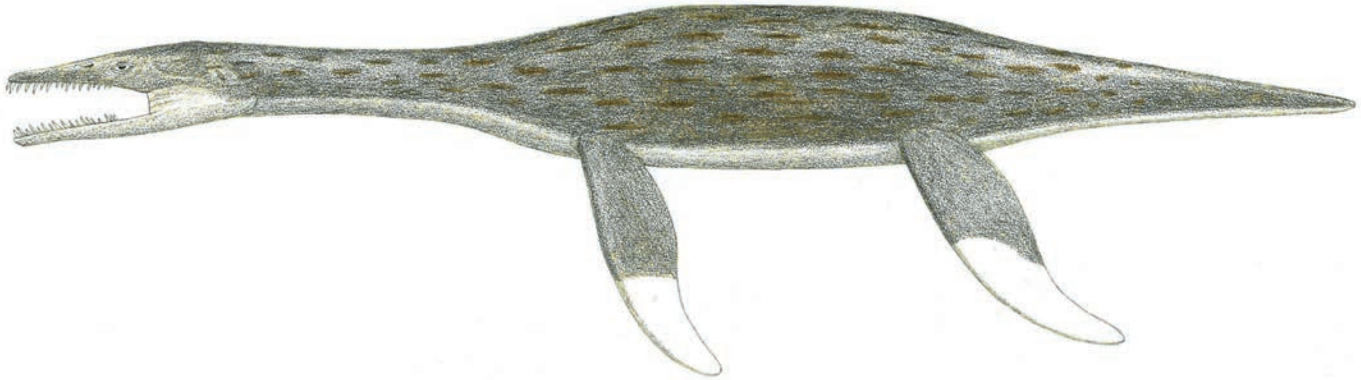
**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Middle Jurassic; early Bajocian.
**DISTRIBUTION AND FORMATIONS** Central Argentina; upper Los Molles.
**HABITAT** Continental shallows.
**NOTES** Shared its habitat with *Chacaicosaurus* and *Mollesaurus.*

### *Archaeonectrus rostratus*
**3.1 m (10 ft) TL, 190 kg (400 lb)**

**FOSSIL REMAINS** Two skulls and skeletons, complete and partial.
**ANATOMICAL CHARACTERISTICS** Head somewhat large, temporal region subrectangular in top view, teeth medium sized and procumbent. Foreflipper a little smaller than aft flipper.



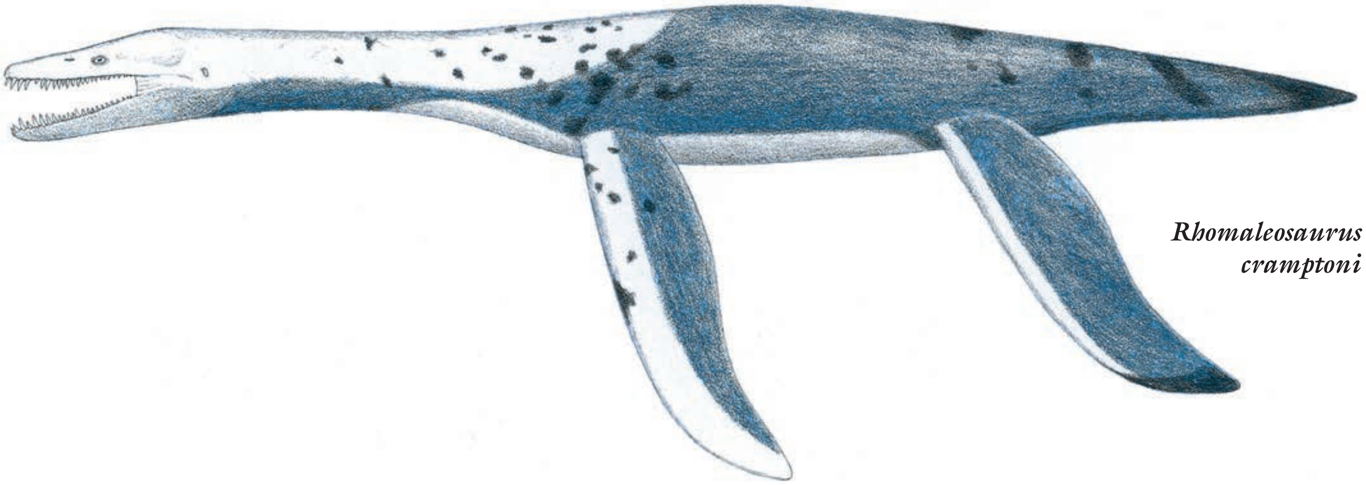
*Archaeonectrus rostratus*



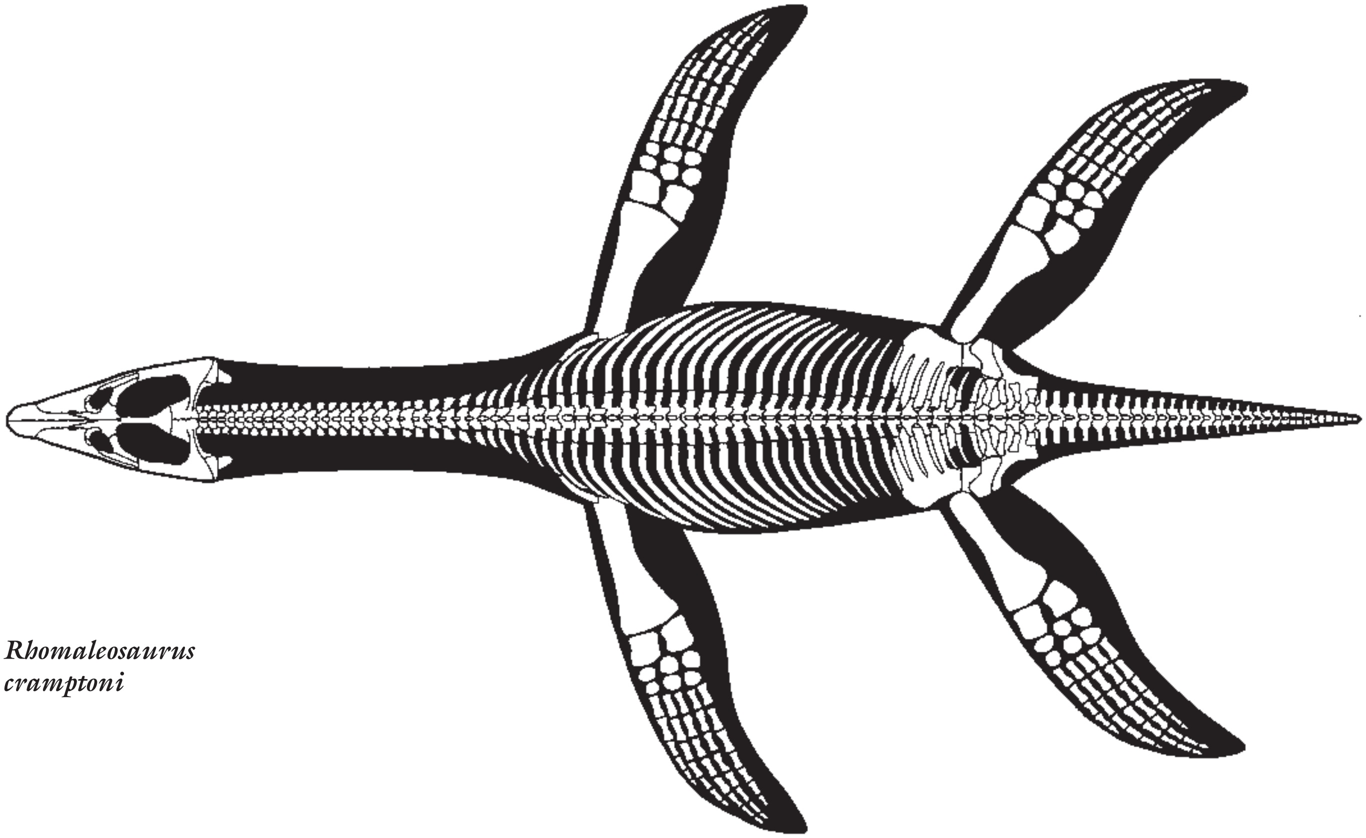
**AGE** Early Jurassic; middle or late Sinemurian.
**DISTRIBUTION AND FORMATIONS** Southeastern England; lower or middle Charmouth Mudstone.
**HABITAT** Island archipelago shallows.

### *Rhomaleosaurus cramptoni*
**6.7 m (22 ft) TL, 2.1 tonnes**

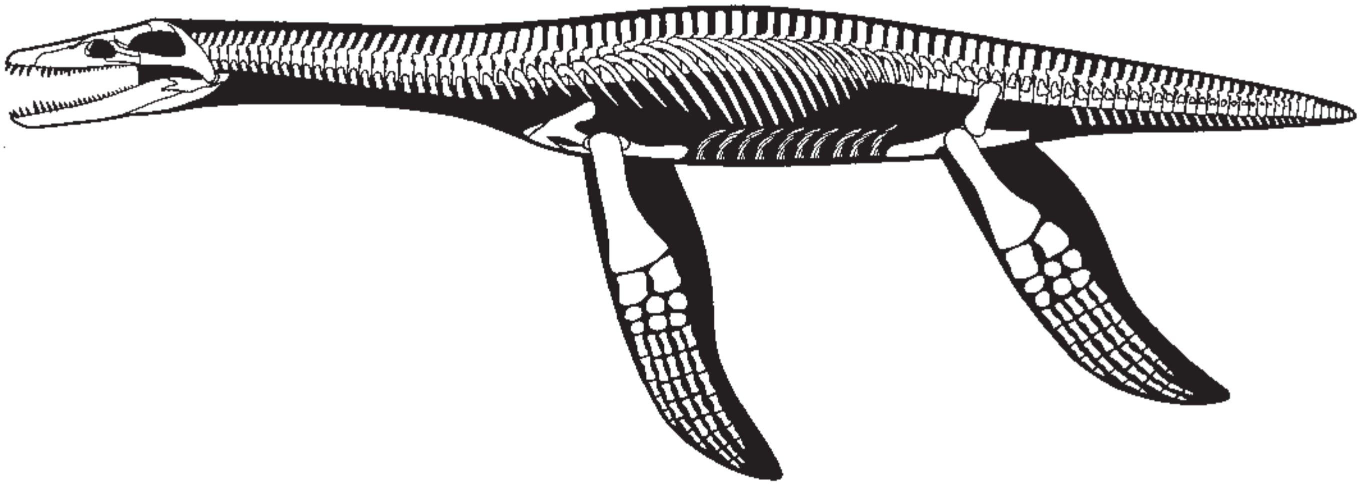
**FOSSIL REMAINS** Skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head somewhat large, strongly triangular in top view, teeth medium sized. Neck medium length. Flippers very large, similar in size.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Northeastern England; lower Whitby Mudstone.
**HABITAT** Island archipelago shallows.
**HABITS** Powerful swimmer.
**NOTES** May include *R. zetlandicus*, *R. propinquus*, and *R. thorntoni*. Shared its habitat with *Hauffiosaurus*, *Eurhinosaurus*, *Plagiophthalmosuchus*, *Mystriosaurus*, *Macrospondylus*.



*Rhomaleosaurus cramptoni*



*Rhomaleosaurus cramptoni*



***Borealonectes russelli***
**3 m (10 ft) TL, 190 kg (400 lb)**

**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Middle Jurassic; late Callovian.
**DISTRIBUTION AND FORMATIONS** Northwest Territories; upper Hiccles Cove.
**HABITAT** Continental shallows, polar.

## PLIOSAURIDS

### SMALL TO GIGANTIC PLIOSAUROIDS FROM THE EARLY JURASSIC TO EARLY CRETACEOUS, GLOBAL

**ANATOMICAL CHARACTERISTICS** Significantly variable. Heads never very small. Necks never very long.
**HABITATS** Coastal shallows to deep oceans.
**HABITS** Swimming performance modest to good. Ambush and/or pursuit fishers and hunters of small to big game.

## ATTENBOROSAURS

**SMALL TO GIGANTIC PLIOSAURIDS FROM THE EARLY TO LATE JURASSIC OF EUROPE**

**ANATOMICAL CHARACTERISTICS** Uniform. Heads not large, necks moderately long.
**HABITATS** Coastal shallows to deep oceans.
**HABITS** Swimming performance modest. Ambush and pursuit fishers of small to medium-sized game.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

### *Thalassiodracon hawkinsii*

**2 m (6.5 ft) TL, 40 kg (90 lb)**

**FOSSIL REMAINS** Half a dozen skulls with at least partial skeletons, latter severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head short, deep aft, moderately broad, teeth medium sized. Fore and aft flippers similar in size.
**AGE** Early Jurassic; earliest Hettangian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Blue Lias.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Eoplesiosaurus*, *Stratesaurus*, *Avalonnectes*, *Eurycleidus*, *Atychodracon*, *Protoichthyosaurus.*

### *Cryonectes neustriacus*

**5 m (16 ft) TL, 450 kg (1,000 lb)**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Teeth large.
**AGE** Early Jurassic; late Pliensbachian.
**DISTRIBUTION AND FORMATIONS** Northern France; Calcaire à Bélemnites.
**HABITAT** Island archipelago shallows.
**HABITS** Fishers of medium-sized game.

### *Hauffiosaurus longirostris*

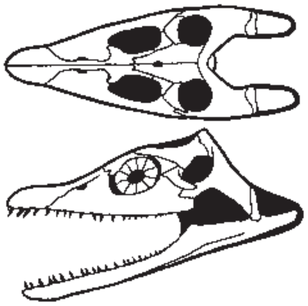
**4.5 m (15 ft) TL, 400 kg (900 lb)**

**FOSSIL REMAINS** Three skulls and skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head fairly long, narrow, snout long and narrow.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany, northern England; Posidonienschiefer, lower Whitby Mudstone.
**HABITAT** Island archipelago shallows.
**NOTES** May include *H. zanoni* and *H. tomistomimus.* Shared its habitat with *Meyerasaurus*, *Rhomaleosaurus*, *Seeleyosaurus*, *Hydrorion*, *Hauffiopteryx*, unnamed genus *trigonodon*, *Suevoleviathan*, *Eurhinosaurus*, *Stenopterygius*, *Plagiophthalmosuchus*, *Mystriosaurus*, *Platysuchus*, *Macrospondylus.*

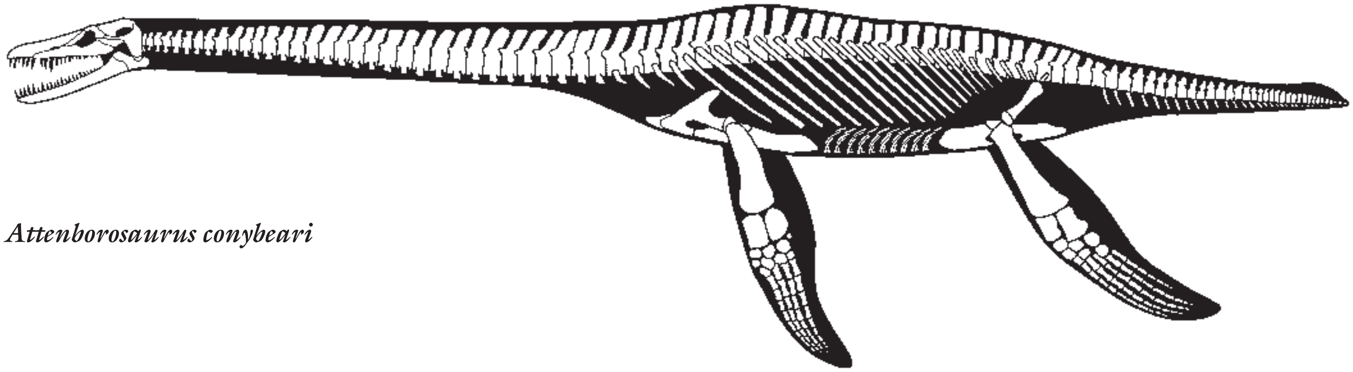
### *Attenborosaurus conybeari*

**7.2 m (24 ft) TL, 1.7 tonnes**

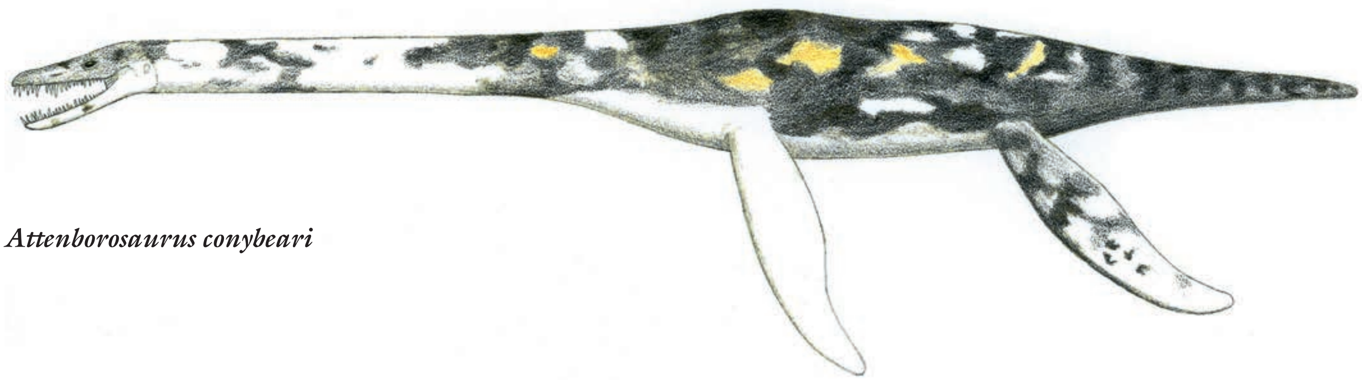
**FOSSIL REMAINS** Skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head moderately elongated, snout long and fairly robust, teeth large. Flippers large, fore a little smaller than aft.
**AGE** Early Jurassic; middle Sinemurian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Charmouth Mudstone.



***Thalassiodracon hawkinsii***



***Attenborosaurus conybeari***



*Attenborosaurus conybeari*

**HABITAT** Island archipelago shallows.
**HABITS** Fisher of medium-sized game.
**NOTES** Original specimen destroyed by Axis bombing in World War II.

### *Marmornectes candrewi*
**10 m (30 ft) TL, 5 tonnes**

**FOSSIL REMAINS** Partial skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Snout narrow.
**AGE** Middle Jurassic; early Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Oxford Clay.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Peloneustes*, *Pachycostasaurus*, *Simolestes*, *Liopleurodon*, *Cryptoclidus*, *Muraenosaurus*, *Tricleidus*, *Ophthalmosaurus*, *Tyrannoneustes*, *Suchodus*, *Gracilineustes.*

### *Anguanax zignoi*
**3.5 m (12 ft) TL, 200 kg (450 lb)**

**FOSSIL REMAINS** Partial skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; middle Oxfordian.
**DISTRIBUTION AND FORMATIONS** Northern Italy; middle Rosso Ammonitico Veronese.
**HABITAT** Island archipelago shallows.

## THALASSOPHONEANS

**MEDIUM-SIZED TO GIGANTIC PLIOSAURIDS FROM THE MIDDLE JURASSIC TO EARLY CRETACEOUS, GLOBAL**

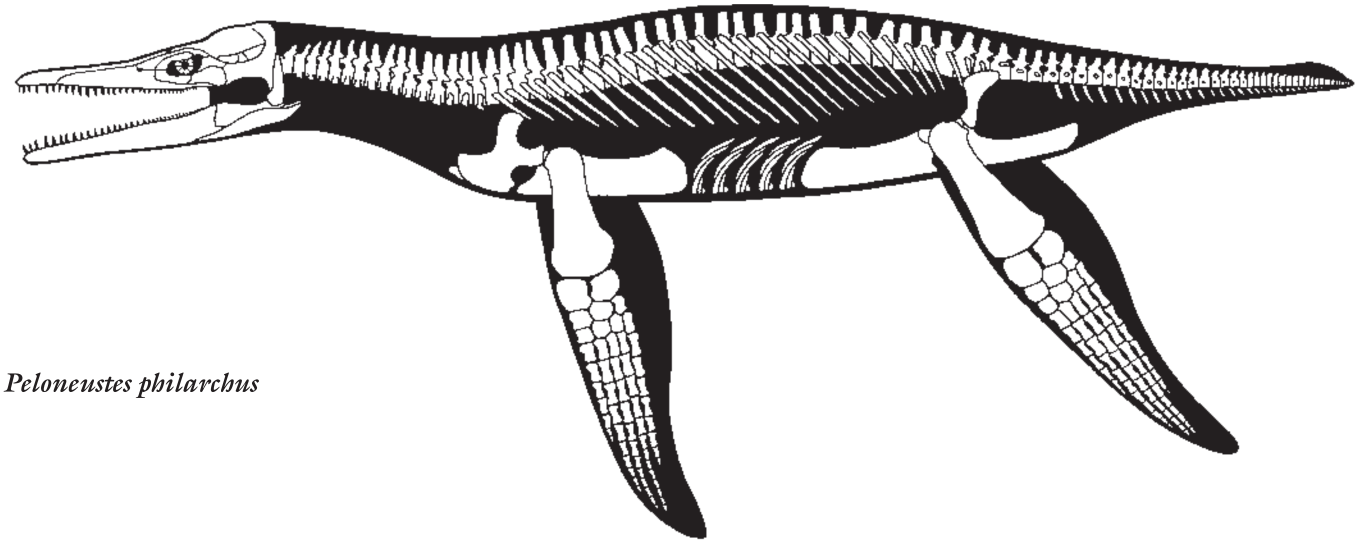
**ANATOMICAL CHARACTERISTICS** Uniform. Heads very large, elongated, snouts half or more head length, temporal regions greatly expanded. Necks short. Flippers medium sized to large.
**HABITAT** Coastal shallows to deep oceans.
**HABITS** Swimming performance mediocre to good. Pursuit fishers and hunters of medium-sized and especially big game.
**NOTES** Some partial remains indicate largest known examples exceeded 12 m (40 ft) in length and approached 20 tonnes, probably the most massive known sea reptiles.

### *Peloneustes philarchus*
**3.8 m (8.4 ft) TL, 600 kg (1,300 lb)**

**FOSSIL REMAINS** Skull and skeleton(s).
**ANATOMICAL CHARACTERISTICS** Snout long, teeth medium sized, stout. Flippers very large, similar in size.
**AGE** Middle Jurassic; early Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Oxford Clay.
**HABITAT** Island archipelago shallows.
**HABITS** Powerful swimmer. Prey included shelled ammonoids.
**NOTES** Shared its habitat with *Simolestes*, *Liopleurodon*, *Cryptoclidus*, *Muraenosaurus*, *Tricleidus*, *Ophthalmosaurus*, *Tyrannoneustes*, *Suchodus*, *Gracilineustes*, *Pachycostasaurus.*

### *Pachycostasaurus dawni*
**3 m (10 ft) TL, 300 kg (600 lb)**

**FOSSIL REMAINS** Nearly complete skull and skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Flippers medium sized.
**AGE** Middle Jurassic; early Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Oxford Clay.
**HABITAT** Island archipelago shallows.
**HABITS** Mediocre swimmer.



*Peloneustes philarchus*

### *Gallardosaurus iturraldei*

**Adult size uncertain**

**FOSSIL REMAINS** Partial skull and minority of skeleton, immature.

**ANATOMICAL CHARACTERISTICS** Insufficient information.

**AGE** Middle Jurassic; middle and/or late Oxfordian.

**DISTRIBUTION AND FORMATIONS** Cuba; Jagua.

**HABITAT** Continental shallows.

**NOTES** At that time Cuba was attached to South America. Shared its habitat with *Vinialesaurus.*

### *Simolestes? keileni*

**6 m (20 ft) TL, 2 tonnes**

**FOSSIL REMAINS** Partial remains.

**ANATOMICAL CHARACTERISTICS** Insufficient information.

**AGE** Middle Jurassic; late Bajocian.

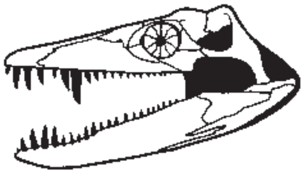
**DISTRIBUTION AND FORMATIONS** Northeastern France; La Gravclotte Marls.

**HABITAT** Island archipelago shallows.

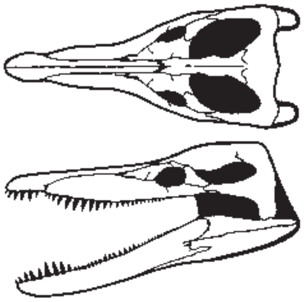
**NOTES** Whether this species belongs in the much later genus *Simolestes* is problematic.

*Peloneustes philarchus*

*Simolestes vorax*



*Acostasaurus pavachoquensis*



*Pliosaurus brachydeirus*

## *Simolestes vorax*

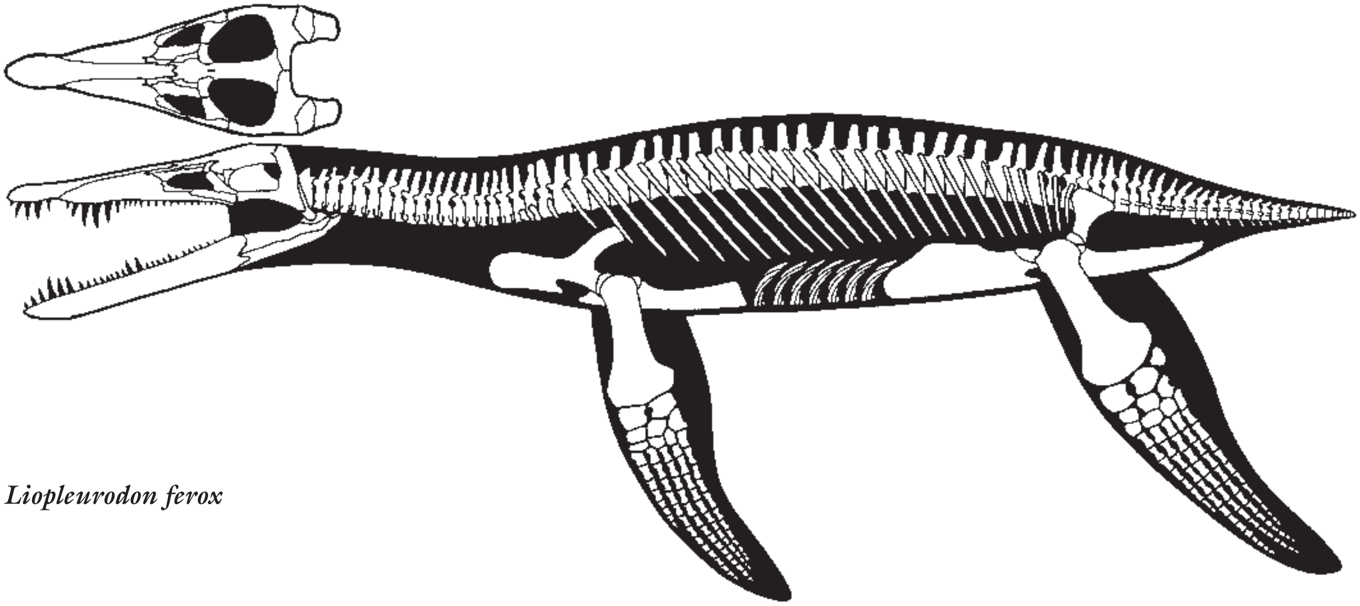
**4.5 m (15 ft) TL, 1 tonne**

FOSSIL REMAINS Skulls and skeletons, complete to partial, severely flattened top to bottom.
ANATOMICAL CHARACTERISTICS Head moderately broad, snout about half head length, front teeth large and robust. Flippers large.
AGE Middle Jurassic; early Callovian.
DISTRIBUTION AND FORMATIONS Southern England; lower Oxford Clay.
HABITAT Island archipelago shallows.
HABITS Powerful swimmer. Prey included shelled ammonoids.
NOTES Shared its habitat with *Peloneustes*, *Pachycostasaurus*, *Cryptoclidus*, *Muraenosaurus*, *Tricleidus*, *Ophthalmosaurus*, *Tyrannoneustes*, *Suchodus*, *Gracilineustes*, *Liopleurodon*.

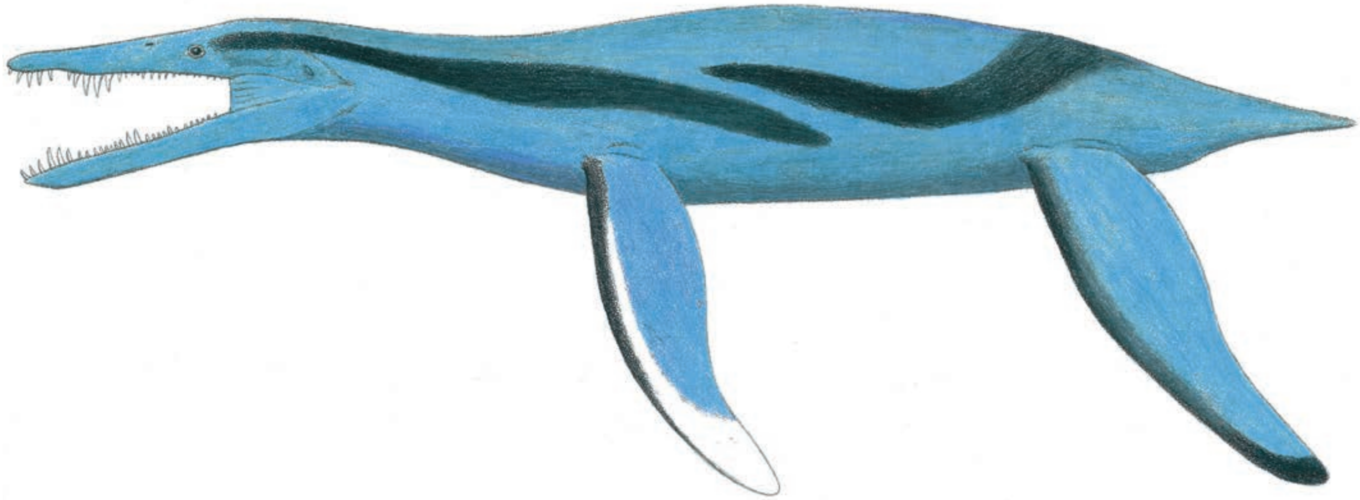
## *Acostasaurus pavachoquensis*

**4 m (14 ft) TL, 1 tonne**

FOSSIL REMAINS Skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Snout stout, about half of head length, front teeth, especially upper, large and robust, lower jaw robust.
AGE Early Cretaceous; early Barremian.
DISTRIBUTION AND FORMATIONS Colombia; lower Paja.
HABITAT Continental shallows.



*Liopleurodon ferox*



## *Liopleurodon ferox*

**6.6 m (22 ft) TL, 3.3 tonnes**

**FOSSIL REMAINS** Skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Snout long, front teeth very large. Tail quite short. Flippers large, aft set a little larger.
**AGE** Middle Jurassic; early Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Oxford Clay.
**HABITAT** Island archipelago shallows.
**HABITS** Powerful swimmer.
**NOTES** Claims of this being 25 m (80 ft) long are greatly exaggerated.

## *Pliosaurus brachydeirus*

**8 m (26 ft) TL, 5 tonnes**

**FOSSIL REMAINS** Skulls complete and partial, partial skeletons.
**ANATOMICAL CHARACTERISTICS** Snout long, teeth medium sized.
**AGE** Late Jurassic; early Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Kimmeridge Clay.
**HABITAT** Island archipelago shallows.
**NOTES** May include *P. kevani*. Shared its habitat with *Colymbosaurus megadeirus*, *Bathysuchus*, *Torvoneustes*, *Plesiosuchus*. May be the direct ancestor of *Pliosaurus westburyensis*.

### *Pliosaurus westburyensis*

**8 m (26 ft) TL, 5 tonnes**

**FOSSIL REMAINS** Crushed skulls and partial skeletal remains.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; middle Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern England; middle Kimmeridge Clay.
**HABITAT** Island archipelago shallows.
**NOTES** May include *P. carpenteri*. Shared its habitat with *Nannopterygius enthekiodon*, *Grendelius mordax*. May be the direct ancestor of *P. macromerus.*

### *Pliosaurus macromerus*

**8 m (26 ft) TL, 5 tonnes**

**FOSSIL REMAINS** Partial skull and other remains.
**ANATOMICAL CHARACTERISTICS** Snout long, robustly built.
**AGE** Late Jurassic; late Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern England; upper Kimmeridge Clay.
**HABITAT** Island archipelago shallows.

### *Pliosaurus? funkei*

**10–12+ m (33–40+ ft) TL**

**FOSSIL REMAINS** Minority of two skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; middle Tithonian.
**DISTRIBUTION AND FORMATIONS** Svalbard; upper Agardhfjellet.
**HABITAT** Open continental shelf, polar.
**NOTES** Placement in earlier *Pliosaurus* problematic. Claims of this being 15 m (50 ft) long are exaggerated. Shared its habitat with *Colymbosaurus? svalbardensis*, *Spitrasaurus*, *Keilhauia*, *Palvennia*, *Janusaurus*, *Cryopterygius.*

### *Pliosaurus? patagonicus*

**Adult size uncertain**

**FOSSIL REMAINS** Partial skull, badly damaged, possibly juvenile.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; middle Tithonian.
**DISTRIBUTION AND FORMATIONS** Western Argentina; lower Vaca Muerta.
**HABITAT** Continental shallows.
**NOTES** Placement in earlier *Pliosaurus* problematic. Shared its habitat with *Caypullisaurus*, *Cricosaurus araucanensis.*

### *Pliosaurus? rossicus*

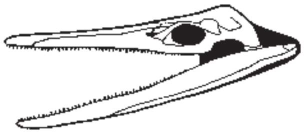
**10 m (33 ft) TL, 11 tonnes**

**FOSSIL REMAINS** A few partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; early and/or middle Tithonian.
**DISTRIBUTION AND FORMATIONS** Southwestern Russia, Kazakhstan; unnamed.
**HABITAT** Continental shallows.
**NOTES** May not be within *Pliosaurus.*

### *Stenorhynchosaurus munozi*

**5.3 m (17 ft) TL, 1.7 tonnes**

**FOSSIL REMAINS** Skull and minority of skeleton of adult, majority of skull and skeleton of immature.
**ANATOMICAL CHARACTERISTICS** Snout very long, teeth very numerous and small. Flippers long, aft set a little larger.
**AGE** Early Cretaceous; middle Barremian.
**DISTRIBUTION AND FORMATIONS** Colombia; lower Paja.
**HABITAT** Continental shallows.
**HABITS** Powerful swimmer. Fisher of medium-sized game.



*Stenorhynchosaurus munozi*

### *Sachicasaurus vitae*

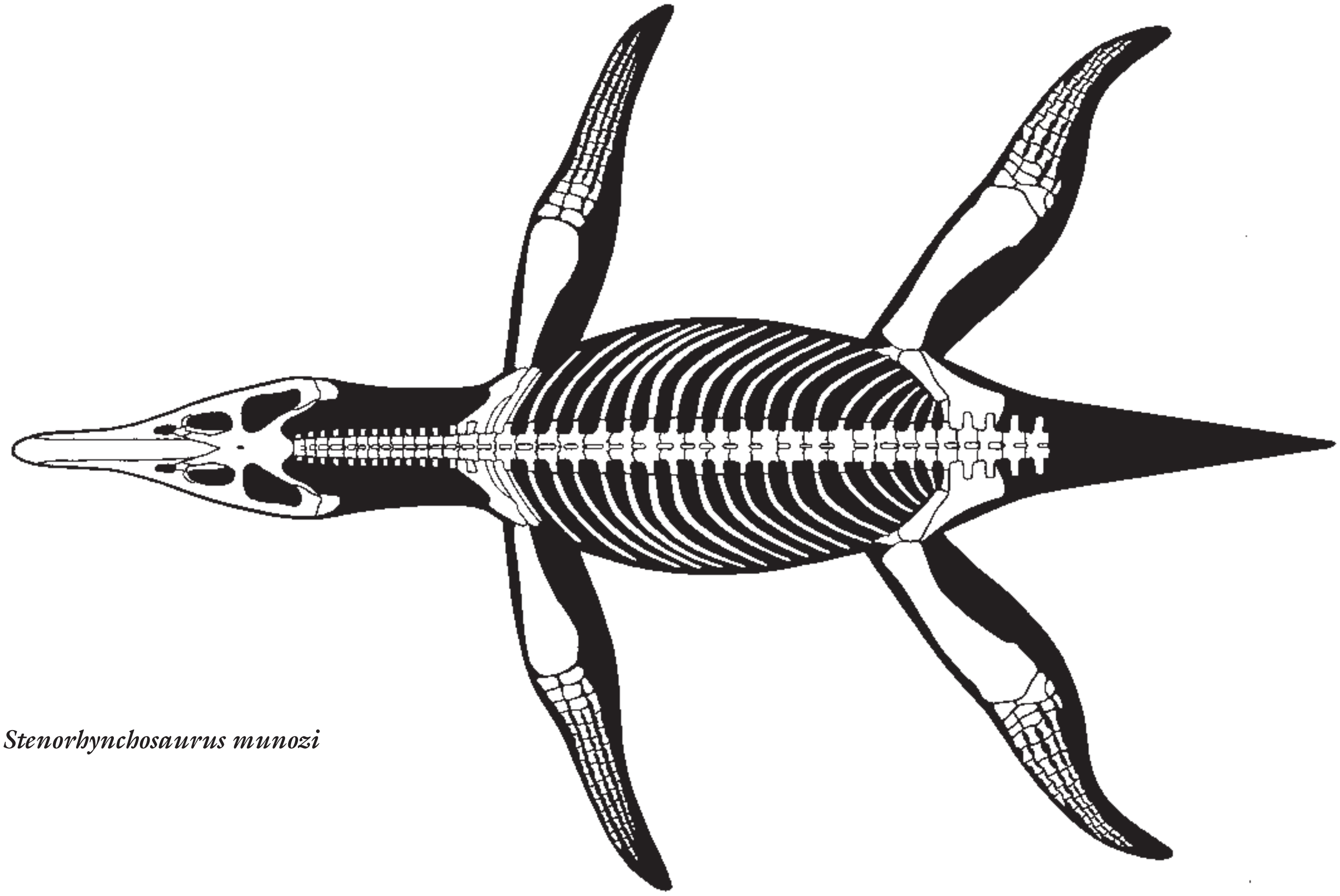
**10.8 (35 ft) TL, 13.5 tonnes**

**FOSSIL REMAINS** Majority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head very large, massive, especially broad aft section, most teeth medium sized except one pair of large teeth on upper and lower jaws. Flippers fairly large.
**AGE** Early Cretaceous; late Barremian.
**DISTRIBUTION AND FORMATIONS** Colombia; middle Paja.
**HABITAT** Continental shallows.
**HABITS** Good swimmer. Prey included shelled ammonoids.
**NOTES** Most massive well-preserved plesiosaur.

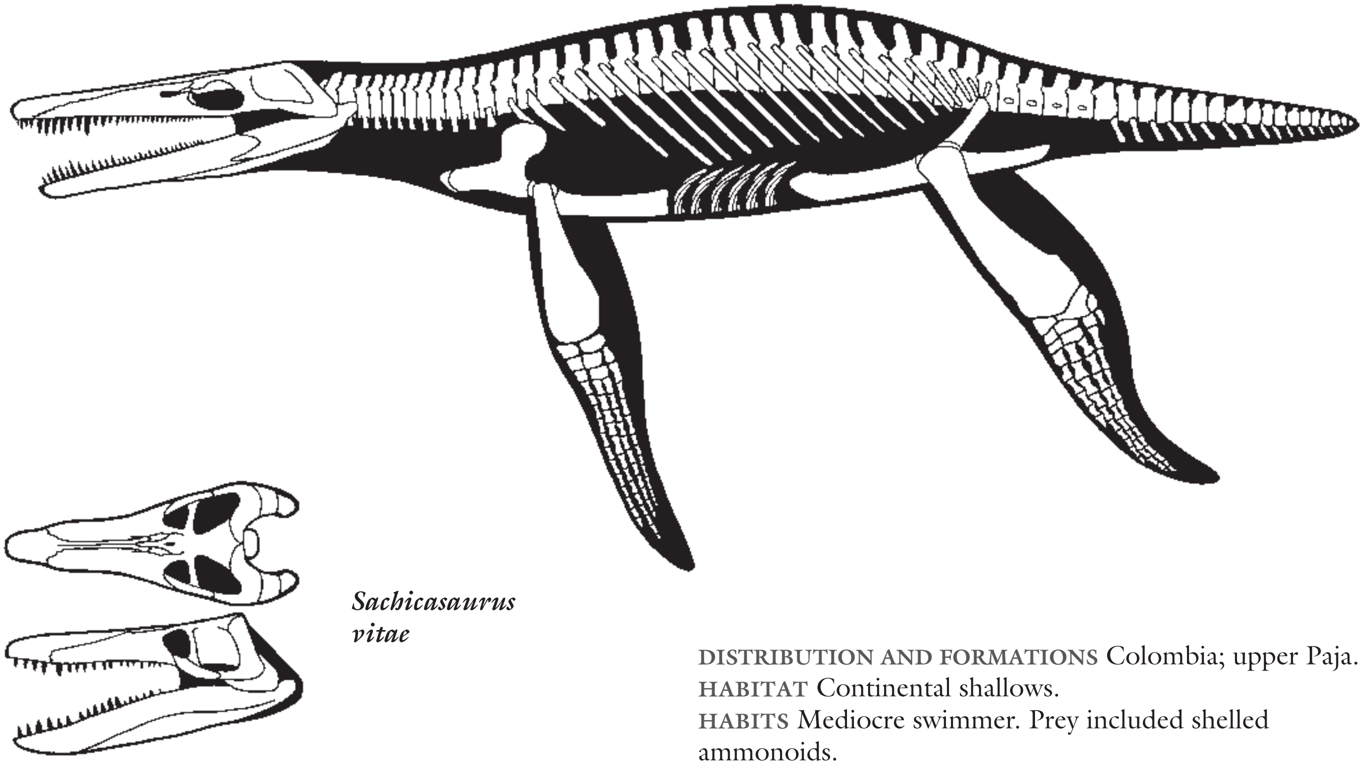
### *Monquirasaurus boyacensis*

**9.4 m (31 ft) TL, 9.1 tonnes**

**FOSSIL REMAINS** Majority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head very large, especially relative to body, particularly massive, especially unusually broad aft section, front teeth large, rest medium sized to small. Flippers not large, aft a little larger.
**AGE** Early Cretaceous; late Aptian.

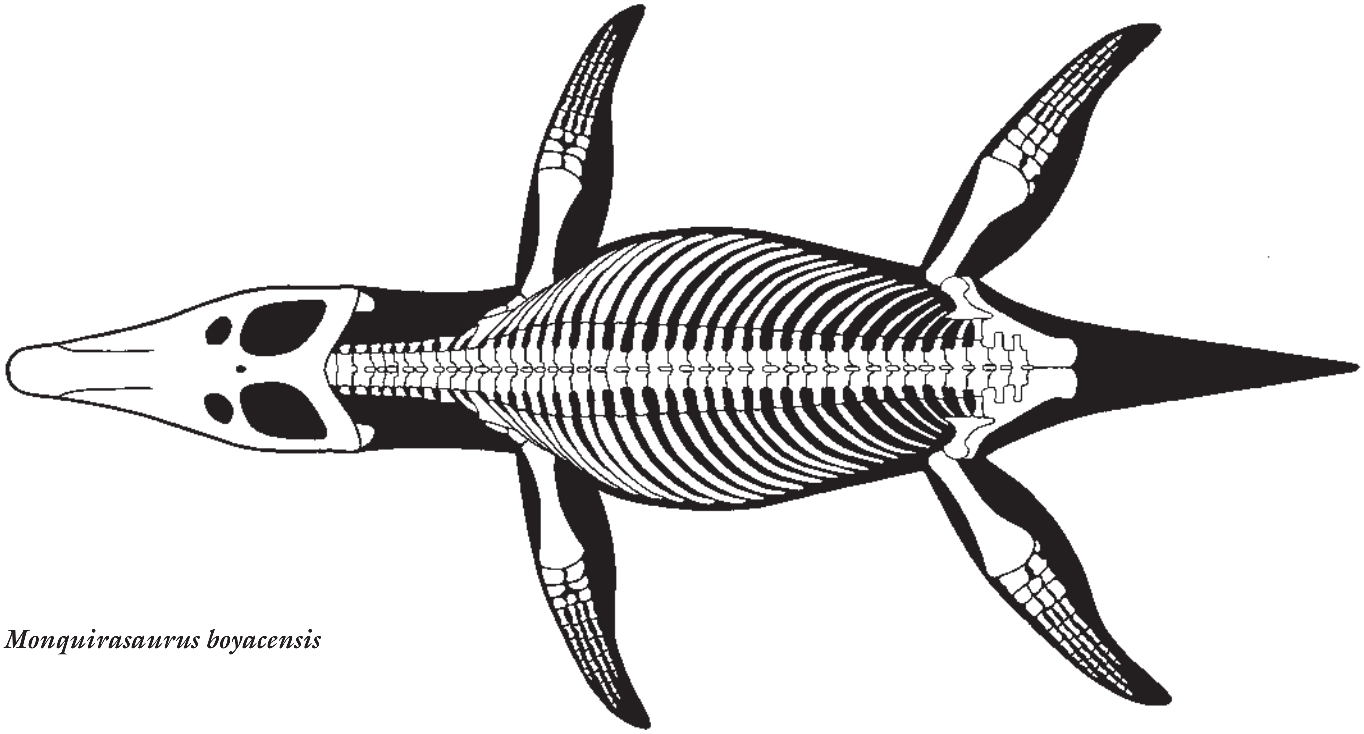


*Stenorhynchosaurus munozi*

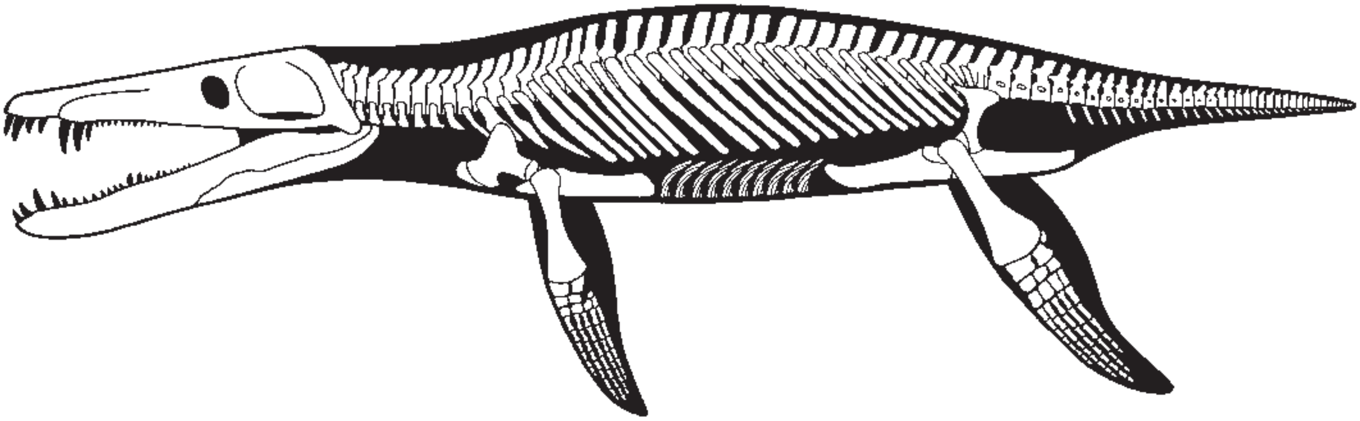


*Sachicasaurus vitae*

**DISTRIBUTION AND FORMATIONS** Colombia; upper Paja.
**HABITAT** Continental shallows.
**HABITS** Mediocre swimmer. Prey included shelled ammonoids.



*Monquirasaurus boyacensis*



**NOTES** Originally placed in *Kronosaurus*. Shared its habitat with *Callawayasaurus*, *Kyhytysuka*. The biggest-headed and most strongly built known plesiosaur, with the most powerful bite force.

### *Eiectus longmani*

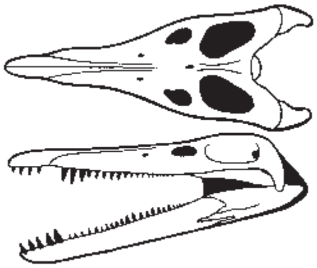
**10 m (33 ft) TL, 11 tonnes**

**FOSSIL REMAINS** A few partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head long, somewhat shallow, moderately broad aft, snout long and rather narrow, some front teeth large, others medium sized to small. Flippers fairly large.
**AGE** Early Cretaceous; late Aptian.
**DISTRIBUTION AND FORMATIONS** Northeastern Australia; Wallumbilla.
**HABITAT** Interior seaway.
**HABITS** Good swimmer. Prey included shelled ammonoids.
**NOTES** Originally placed in later and more fragmentary *Kronosaurus queenslandicus*, the remains constitute an iconic large-headed plesiosaur, albeit now with a new name that may be challenged in the future. Remains are not well preserved or described, and claims of this being 13 m (42 ft) long are exaggerated.

### *?Kronosaurus queenslandicus*

**Size uncertain**

FOSSIL REMAINS A few partial skull and skeletal remains.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous; middle Albian.
DISTRIBUTION AND FORMATIONS Northeastern Australia; Toolebuc.
HABITAT Interior seaway.
HABITS Prey included shelled ammonoids.
NOTES An iconic large-headed plesiosaur name, the best remains are currently placed in the new *Eiectus longmani*; the original *K. queenslandicus* specimen is too fragmentary to base a species on, but an attempt to revive the classic name may occur by reapplying it to *Eiectus longmani* fossils. Shared its habitat with *Eromangasaurus*, *Longirostra*, *Cratochelone*, *Notochelone*, *Bouliachelys.*



*Kronosuarus queenslandicus*

### *Brachauchenius lucasi*

**7 m (23 ft) TL, 3.5 tonnes**

FOSSIL REMAINS Four skulls and minority of skeletons.
ANATOMICAL CHARACTERISTICS Snout very long, small crest atop back of skull, teeth medium sized, robust.
AGE Late Cretaceous; early to middle Turonian.
DISTRIBUTION AND FORMATIONS Kansas; lower Carlile Shale.
HABITAT Interior seaway.
HABITS Prey included shelled ammonoids.
NOTES *Megacephalosaurus eulerti* appears to be the adult of this species. Shared its habitat with *Trinacromerum bentonianum.*

*Brachauchenius lucasi*

## PLESIOSAUROIDS

**SMALL TO GIGANTIC PLESIOSAURS FROM THE EARLY JURASSIC TO THE END OF THE MESOZOIC, GLOBAL**

ANATOMICAL CHARACTERISTICS Fairly variable. Heads very small to very large. Necks very short to extremely long.
HABITATS Freshwaters to deep oceans.
HABITS Swimming performance mediocre to good. Most ambush and/or pursuit fishers and hunters of small to big game, some filter feeders.

## PLESIOSAURIDS

**SMALL TO GIGANTIC PLESIOSAUROIDS FROM THE EARLY TO LATE JURASSIC OF EURASIA**

ANATOMICAL CHARACTERISTICS Uniform. Heads not large, necks moderately long.
HABITATS Freshwaters, coastal shallows, continental shelves.
HABITS Swimming performance modest to good. Ambush and pursuit fishers of small to medium-sized game.
NOTES Absence from at least some other seas may reflect lack of sufficient sampling.

### *Bishanopliosaurus youngi*

**4 m (13 ft) TL, 300 kg (650 lb)**

FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Jurassic; Toarcian.
DISTRIBUTION AND FORMATIONS Central China; upper Ziliujing.
HABITAT Lakes, possibly rivers.
HABITS May have occasionally snapped up small swimming land creatures.
NOTES Whether this taxon was a permanent freshwater plesiosaur or a transient is not certain.

### *Bishanopliosaurus? zigongensis*

**4 m (13 ft) TL, 300 kg (650 lb)**

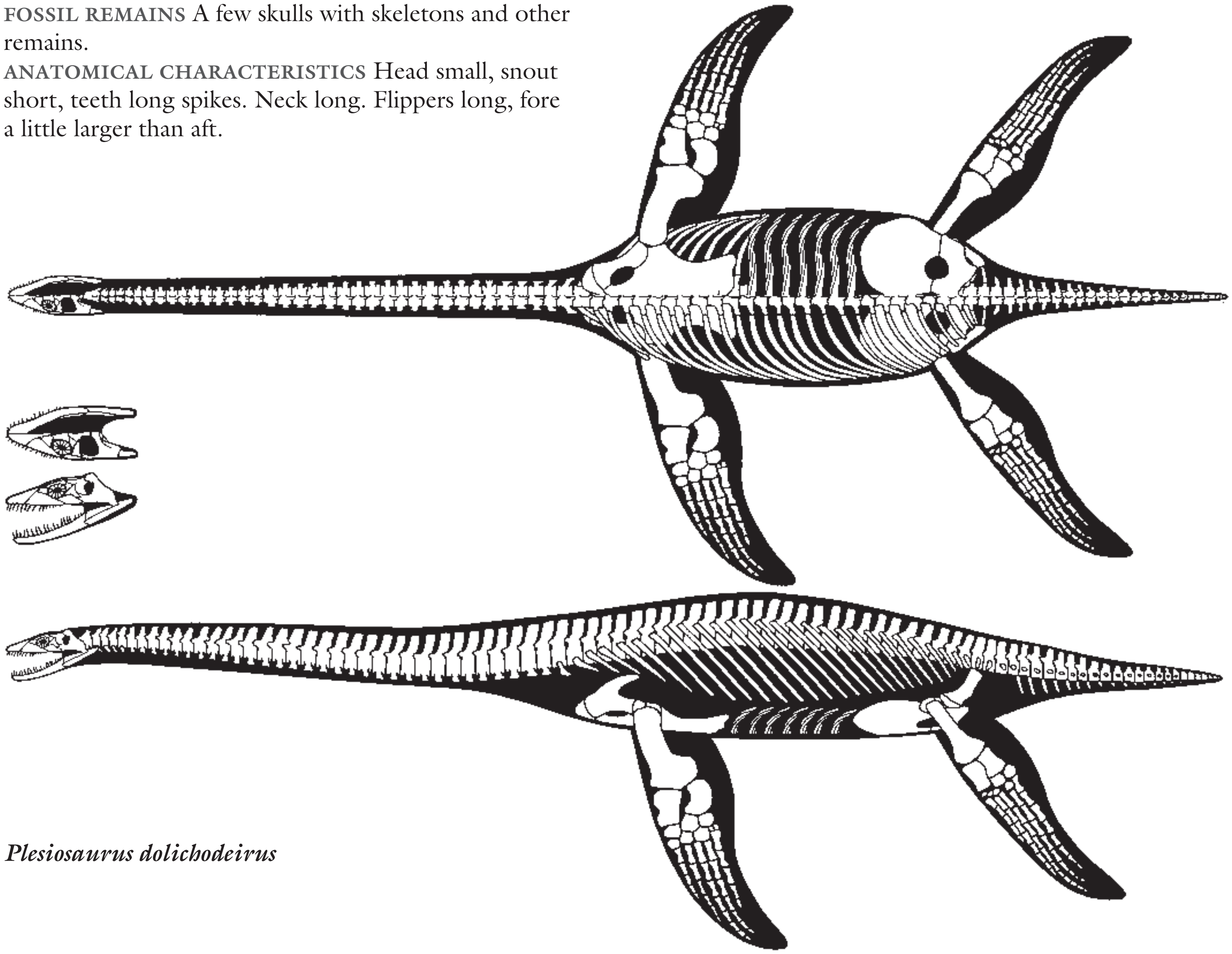
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic.
DISTRIBUTION AND FORMATIONS Central China; lower Shaximiao.
HABITAT Lakes, possibly rivers.
HABITS May have occasionally snapped up small swimming land creatures.

**NOTES** May not be within *Bishanopliosaurus*. Whether this taxon was a permanent freshwater plesiosaur or a transient is not certain.

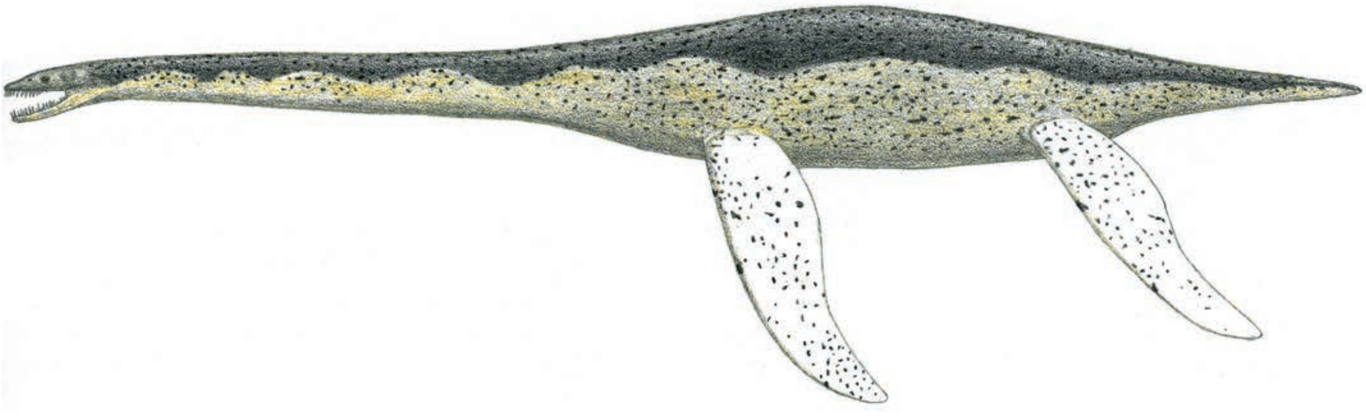
### *Plesiosaurus dolichodeirus*

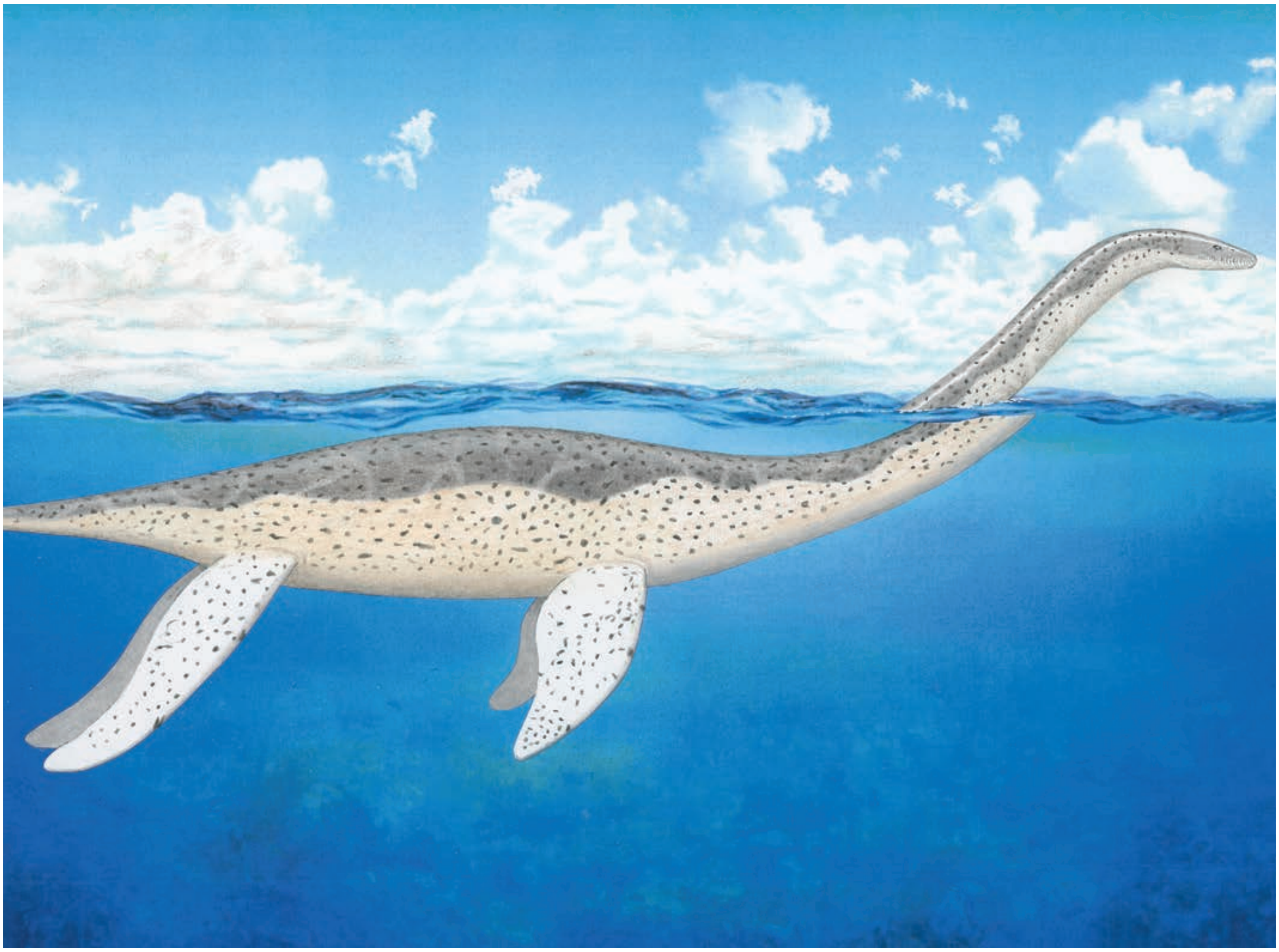
**3.4 m (11 ft) TL, 185 kg (400 lb)**

**FOSSIL REMAINS** A few skulls with skeletons and other remains.
**ANATOMICAL CHARACTERISTICS** Head small, snout short, teeth long spikes. Neck long. Flippers long, fore a little larger than aft.
**AGE** Early Jurassic; early Sinemurian.
**DISTRIBUTION AND FORMATIONS** Southern England; upper Blue Lias.
**HABITAT** Island archipelago shallows.



*Plesiosaurus dolichodeirus*





*Plesiosaurus dolichodeirus*

**HABITS** Swimming performance good.
**NOTES** Shared its habitat with *Excalibosaurus*, *Eretmosaurus*, *Leptonectes tenuirostris*, *Temnodontosaurus*, *Ichthyosaurus communis*, unnamed genus *eurycephalus*.

## MICROCLEIDIDS

### SMALL TO MEDIUM-SIZED PLESIOSAUROIDS FROM THE EARLY TO LATE JURASSIC OF EURASIA

**ANATOMICAL CHARACTERISTICS** Head small, snout short. Neck fairly long.
**HABITAT** Coastal shallows.
**HABITS** Swimming performance good. Ambush and pursuit fishers of small to medium-sized game.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

### *Lusonectes sauvagei*

**2 m (6.5 ft) TL, 35 kg (80 lb)**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Jurassic; Toarcian.
**DISTRIBUTION AND FORMATIONS** Portugal; Sao Giao.
**HABITAT** Island archipelago shallows.

### *Eretmosaurus rugosus*

**3.7 m (12 ft) TL, 225 kg (500 lb)**

**FOSSIL REMAINS** Skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Neck long. Flippers large, similar in size.
**AGE** Early Jurassic; middle Sinemurian.
**DISTRIBUTION AND FORMATIONS** Southern England; upper Blue Lias.
**HABITAT** Island archipelago shallows.

**NOTES** Shared its habitat with *Excalibosaurus*, *Plesiosaurus*, *Leptonectes tenuirostris*, *Temnodontosaurus*, *Ichthyosaurus communis*, unnamed genus *eurycephalus.*

### *Westphaliasaurus simonsensii*

**4.5 m (15 ft) TL, 400 kg (900 lb)**

**FOSSIL REMAINS** Majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Jurassic; Pliensbachian.
**DISTRIBUTION AND FORMATIONS** Northwestern Germany; unnamed.
**HABITAT** Island archipelago shallows.

### *Plesiopharos moelensis*

**Adult size uncertain**

**FOSSIL REMAINS** Partial skeleton, probably juvenile.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Jurassic; late Sinemurian.
**DISTRIBUTION AND FORMATIONS** Portugal; lower Coimbra.
**HABITAT** Island archipelago shallows.

### *Seeleyosaurus guilelmiimperatoris*

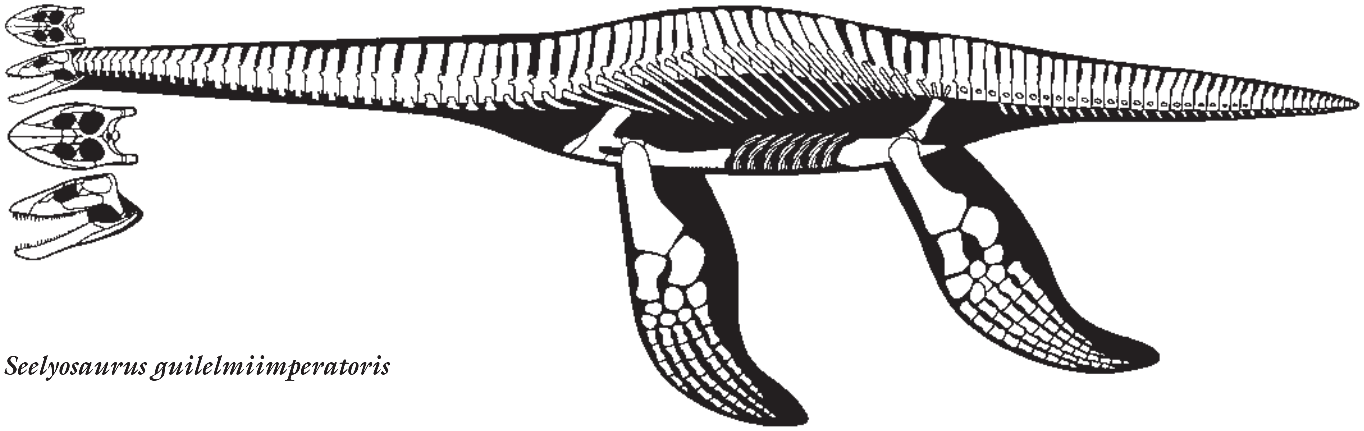
**3.8 m (12.5 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Complete skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head very small, fairly broad and subtriangular in top view, teeth numerous and small. Neck long. Tail moderately long. Flippers very large, similar in size, strongly distally swept back.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Posidonienschiefer.
**HABITAT** Island archipelago shallows. Shared its habitat with *Meyerasaurus*, *Hauffiosaurus*, *Hydrorion*, *Hauffiopteryx*, unnamed genus *trigonodon*, *Suevoleviathan*, *Eurhinosaurus*, *Stenopterygius*, *Mystriosaurus*, *Platysuchus*, *Macrospondylus.*

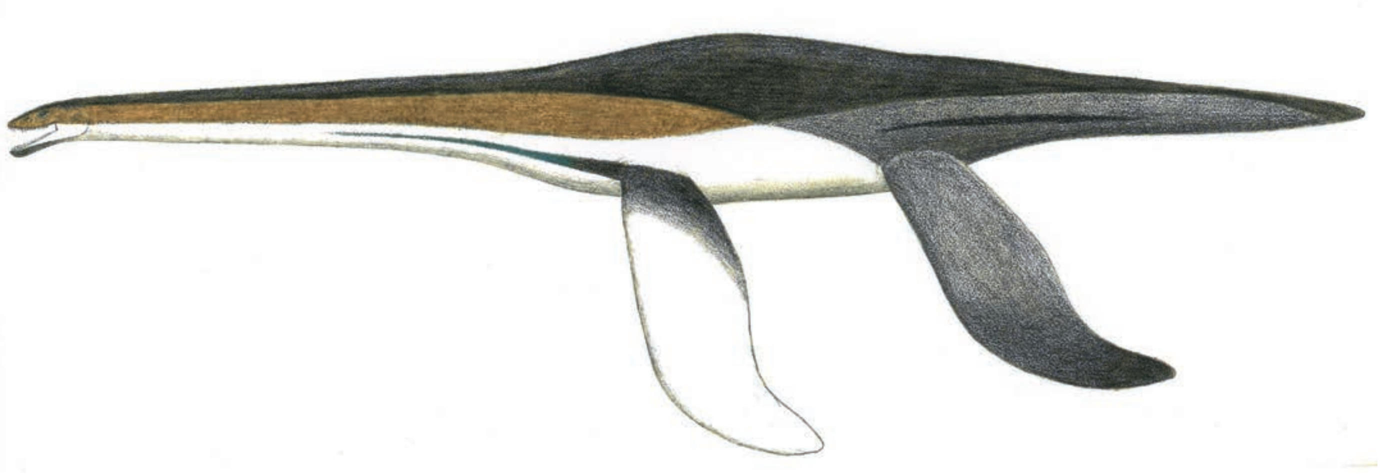
### *Microcleidus melusinae*

**3 m (10 ft) TL, 120 kg (250 lb)**

**FOSSIL REMAINS** Skull and partial skeleton, severely damaged.
**ANATOMICAL CHARACTERISTICS** Head moderately broad, subrectangular at back, front teeth large and procumbent.



*Seelyosaurus guilelmiimperatoris*



**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Luxembourg; unnamed.
**HABITAT** Island archipelago shallows.
**NOTES** May be the direct ancestor of *M. homalospondylus.*

### *Microcleidus homalospondylus*
**5.1 m (17 ft) TL, 650 kg (1,400 lb)**

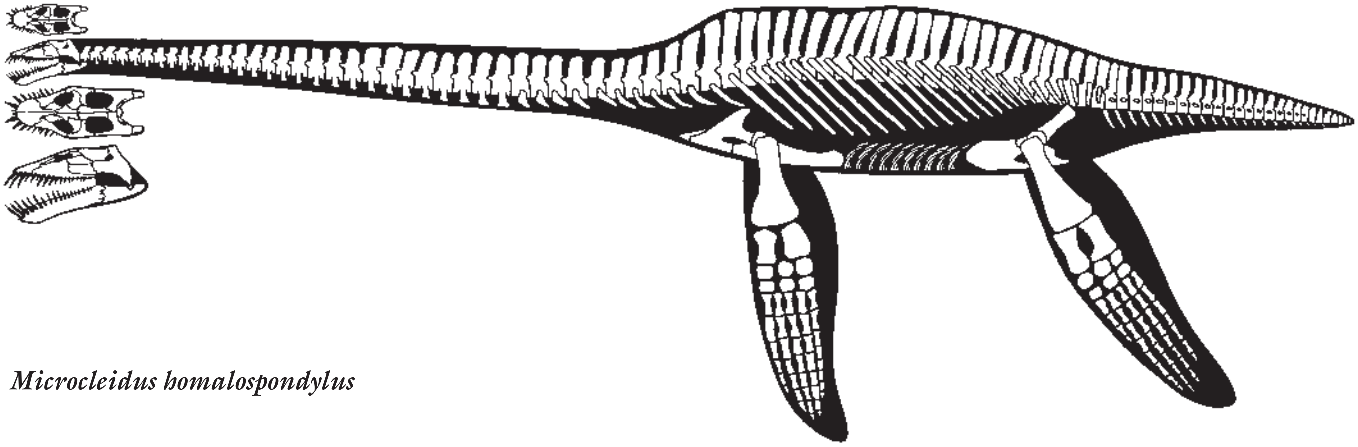
**FOSSIL REMAINS** Three nearly complete skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head very small, narrow, subrectangular at back, front teeth very large and procumbent, intermeshing spikes. Neural spines over trunk very tall. Neck very long. Flippers very large, similar in size.
**AGE** Early Jurassic; late early Toarcian.
**DISTRIBUTION AND FORMATIONS** Northeastern England; upper Whitby Mudstone.
**HABITAT** Island archipelago shallows.
**HABITS** Probably includes *M. macropterus.* Combination of tall spines of trunk vertebrae and large flippers indicates very powerful propulsion.

### *Microcleidus? tournemirensis*
**4 m (13 ft) TL, 300 kg (650 lb)**

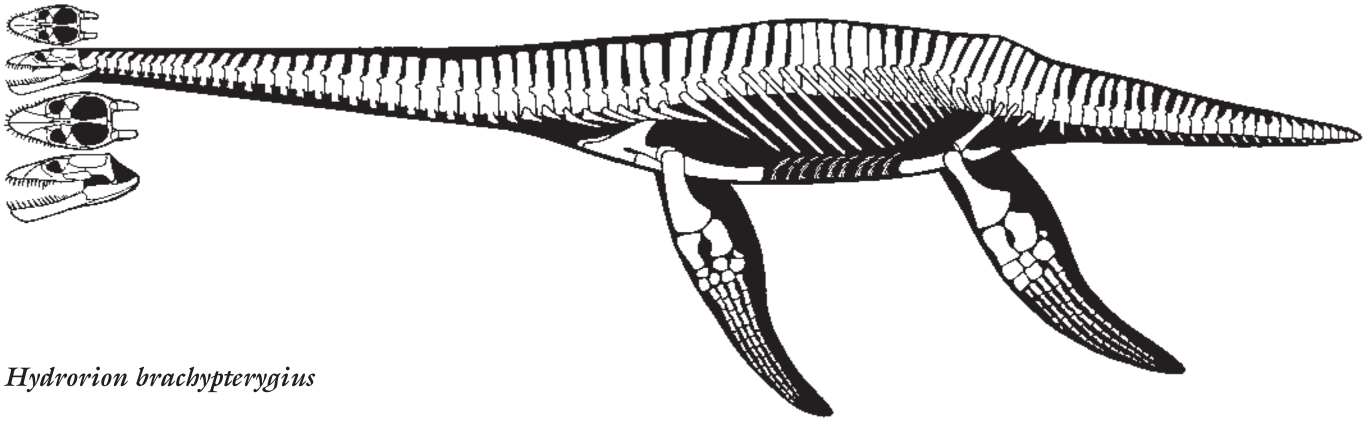
**FOSSIL REMAINS** Skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head moderately broad, widest at midpoint, teeth large and procumbent. Neck long.
**AGE** Early Jurassic; late Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern France; unnamed.
**HABITAT** Island archipelago shallows.

### *Hydrorion brachypterygius*
**3.2 m (10.5 ft) TL, 150 kg (330 lb)**

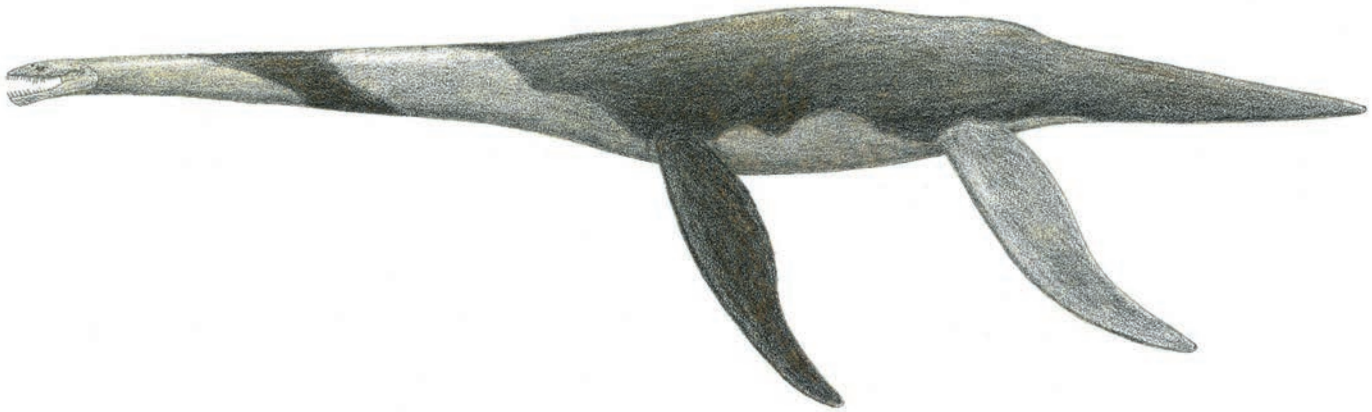
**FOSSIL REMAINS** Complete skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head small, fairly broad, widest at midpoint, teeth fairly long, slender, procumbent intermeshing spikes. Trunk vertebral spines tall. Flippers large, fore a little smaller than aft.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Posidonienschiefer.
**HABITAT** Island archipelago shallows.



*Microcleidus homalospondylus*



*Hydrorion brachypterygius*



**HABITS** Combination of tall spines of trunk vertebrae and large flippers indicates very powerful propulsion.
**NOTES** Shared its habitat with *Meyerasaurus*, *Hauffiosaurus*, *Seeleyosaurus*, *Hauffiopteryx*, unnamed genus *trigonodon*, *Suevoleviathan*, *Eurhinosaurus*, *Stenopterygius*, *Mystriosaurus*, *Platysuchus*, *Macrospondylus*.

## CRYPTOCLIDIANS

**MEDIUM-SIZED TO GIGANTIC PLESIOSAUROIDS FROM THE MIDDLE JURASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Flippers more highly developed, with lower arm and leg elements shorter and more blocklike.
**HABITAT** Freshwaters to deep oceans.
**HABITS** Swimming performance mediocre to good. Most ambush and/or pursuit fishers and hunters of small to big game, some filter feeders.

## CRYPTOCLIDIDS

**MEDIUM-SIZED TO LARGE CRYPTOCLIDIANS FROM THE MIDDLE JURASSIC TO EARLY CRETACEOUS OF THE NORTHERN HEMISPHERE.**

**ANATOMICAL CHARACTERISTICS** Necks moderately long.
**HABITAT** Freshwaters, coastal shallows, continental shelves.
**HABITS** Swimming performance modest. Ambush and pursuit fishers of small to medium-sized game.
**NOTES** Absence from Southern Hemisphere may reflect lack of sufficient sampling.

### *Abyssosaurus nataliae*

**7 m (23 ft) TL, 1.8 tonnes**

**FOSSIL REMAINS** Partial skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; late Hauterivian.
**DISTRIBUTION AND FORMATIONS** Western Russia; unnamed.
**HABITAT** Continental shallows.

### *Colymbosaurus megadeirus*

**5 m (16 ft) TL, 700 kg (1,500 lb)**

**FOSSIL REMAINS** Possible partial skull, partial skeletons.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; middle and/or late Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Kimmeridge Clay, Haddenham.
**HABITAT** Island archipelago shallows.
**NOTES** *Kimmerosaurus langhami* skull may belong to this species. Shared its habitat with *Pliosaurus brachydeirus*, *Bathysuchus*, *Torvoneustes*, *Plesiosuchus*.

### *Colymbosaurus? svalbardensis*

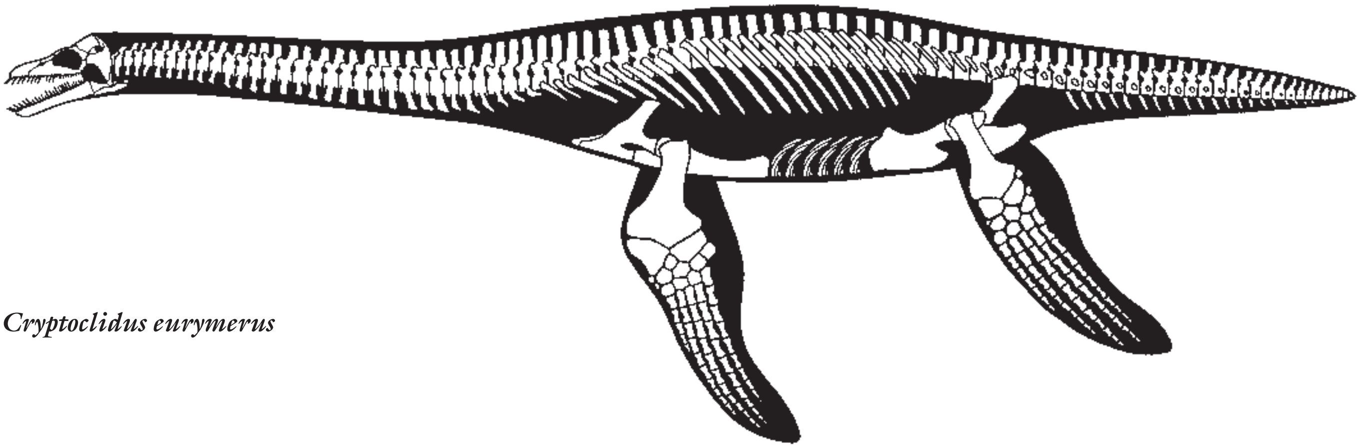
**5 m (16 ft) TL, 700 kg (1,500 lb)**

**FOSSIL REMAINS** Four partial skeletons, one juvenile.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; late Tithonian.
**DISTRIBUTION AND FORMATIONS** Svalbard; upper Agardhfjellet.
**HABITAT** Open continental shelf, polar.
**HABITAT** Open continental shelf, polar.
**NOTES** *Djupedalia engeri* may be the juvenile of this species. Placement in much earlier *Colymbosaurus* is uncertain. Shared its habitat with *Pliosaurus? funkei*, *Spitrasaurus*, *Keilhauia*, *Palvennia*, *Janusaurus*, *Cryopterygius*.

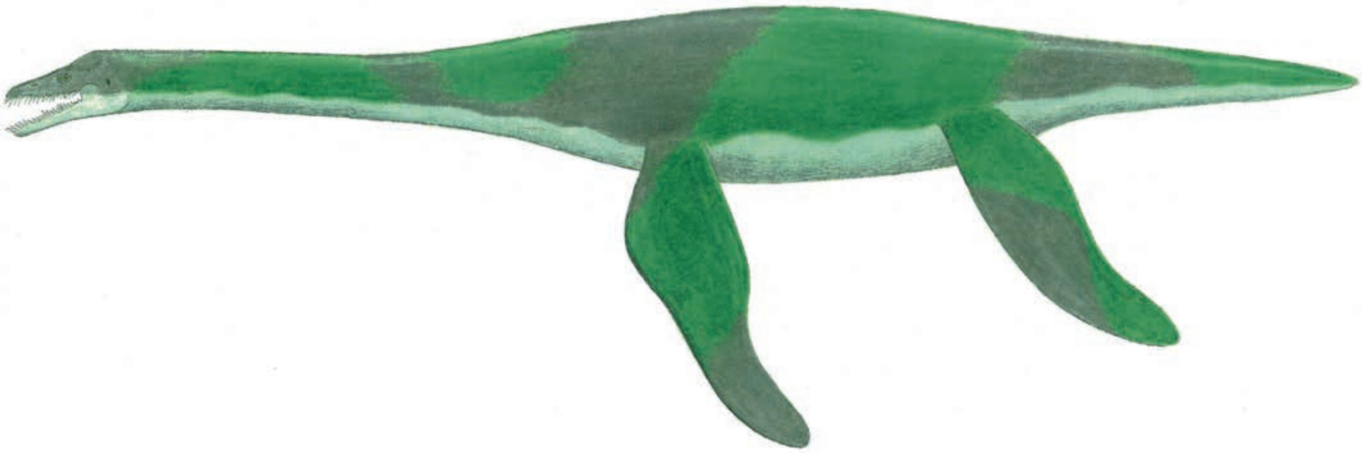
### *Cryptoclidus eurymerus*

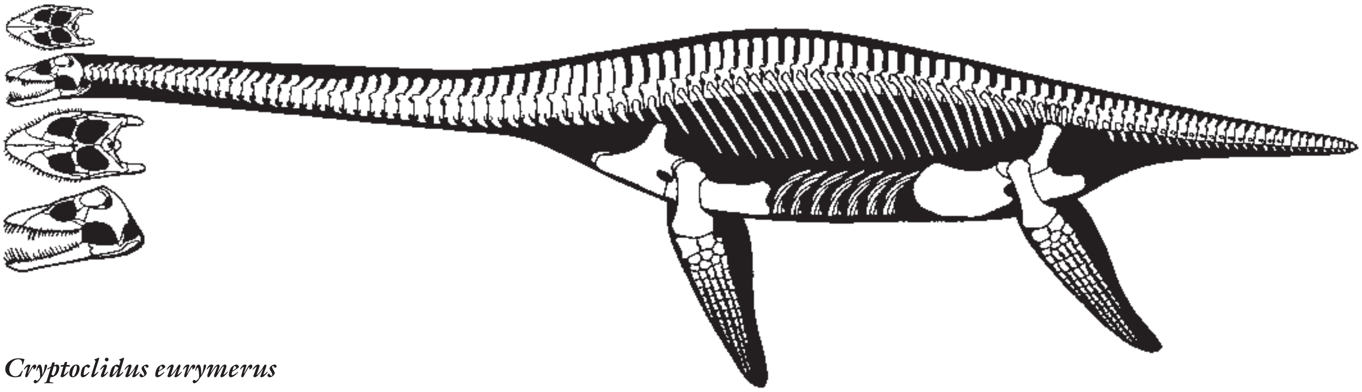
**5.5 m (18 ft) TL, 1 tonne**

**FOSSIL REMAINS** Skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Front teeth large, procumbent, intermeshing slender spikes. Flippers similar in size.
**AGE** Middle Jurassic; early or middle Callovian.
**DISTRIBUTION AND FORMATIONS** Central England; lower Oxford Clay.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Peloneustes*, *Pachycostasaurus*, *Simolestes*, *Liopleurodon*, *Tricleidus*, *Ophthalmosaurus*, *Tyrannoneustes*, *Suchodus*, *Gracilineustes*, *Muraenosaurus*.

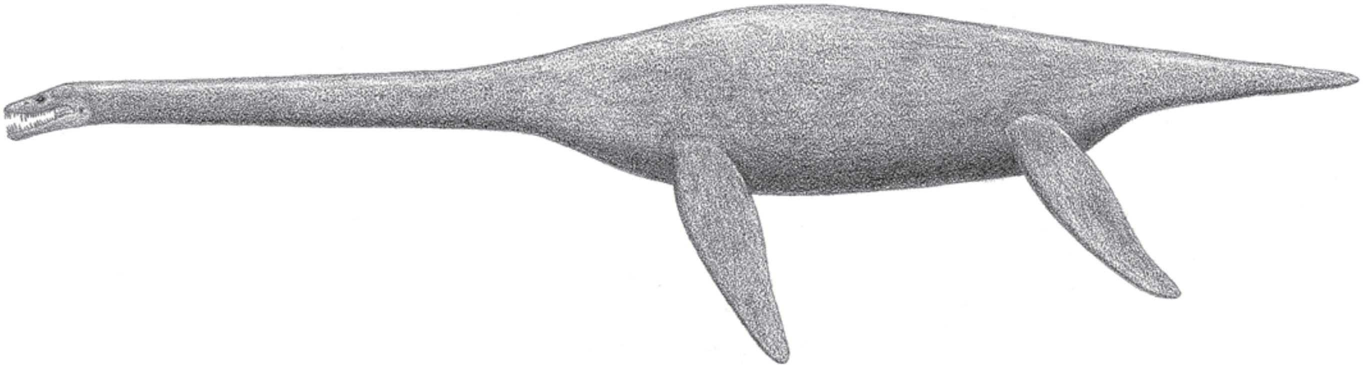


*Cryptoclidus eurymerus*





*Cryptoclidus eurymerus*



### *Muraenosaurus leedsii*

**5.9 m (19 ft) TL, 1 tonne**

**FOSSIL REMAINS** Complete and partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head fairly broad, teeth medium sized. Trunk fairly long, hefty. Flippers moderate and similar in size.
**AGE** Middle Jurassic; middle Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Oxford Clay.
**HABITAT** Island archipelago shallows.
**HABITS** Swimming performance mediocre.

### *Pantosaurus striatus*

**3.5 m (11 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Partial skeletons.
**ANATOMICAL CHARACTERISTICS** Foreflipper distally swept back because radius is much larger than ulna.
**AGE** Late Jurassic; early Oxfordian.
**DISTRIBUTION AND FORMATIONS** Wyoming; upper Sundance.
**HABITAT** Interior seaway.
**NOTES** Shared its habitat with *Tatenectes*, *Baptanodon*.

### *Tatenectes laramiensis*

**3 m (10 ft) TL, 450 kg (1,000 lb)**

**FOSSIL REMAINS** Two partial skeletons.
**ANATOMICAL CHARACTERISTICS** Trunk may be shallower than usual.
**AGE** Late Jurassic; early Oxfordian.
**DISTRIBUTION AND FORMATIONS** Wyoming; upper Sundance.
**HABITAT** Interior seaway.

### *Spitrasaurus wensaasi*

**Adult size uncertain**

**FOSSIL REMAINS** Partial juvenile skeletons.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; late Tithonian.
**DISTRIBUTION AND FORMATIONS** Svalbard; upper Agardhfjellet.
**HABITAT** Open continental shelf, polar.
**NOTES** May include *S. larseni*. Shared its habitat with *Pliosaurus? funkei*, *Colymbosaurus? svalbardensis*, *Keilhauia*, *Palvennia*, *Janusaurus*, *Cryopterygius*.

### *Ophthalmothule cryostea*

**4.5 m (15 ft) TL, 500 kg (1,000 lb)**

FOSSIL REMAINS Skull severely flattened top to bottom, majority of skeleton.
ANATOMICAL CHARACTERISTICS Neck fairly long, foreflipper somewhat larger than aft.
AGE Late Jurassic or Early Cretaceous; latest Tithonian or early Berriasian.
DISTRIBUTION AND FORMATIONS Svalbard; uppermost Agardhfjellet.
HABITAT Open continental shelf, polar.
NOTES May extend group into the Early Cretaceous.

### *Tricleidus seeleyi*

**5 m (16 ft) TL, 700 kg (1,500 lb)**

FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Front teeth large.
AGE Middle Jurassic; middle Callovian.
DISTRIBUTION AND FORMATIONS Southern England; lower Oxford Clay.
HABITAT Island archipelago shallows.
NOTES Shared its habitat with *Peloneustes*, *Pachycostasaurus*, *Simolestes*, *Liopleurodon*, *Cryptoclidus*, *Muraenosaurus*, *Ophthalmosaurus*, *Tyrannoneustes*, *Suchodus*, *Gracilineustes.*

### *Vinialesaurus caroli*

**3.5 m (11 ft) TL, 250 kg (550 lb)**

FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head broad, teeth large spikes.
AGE Late Jurassic; middle and/or late Oxfordian.
DISTRIBUTION AND FORMATIONS Cuba; Jagua.
HABITAT Continental shallows.
NOTES At that time Cuba was attached to South America. Shared its habitat with *Gallardosaurus.*

## ELASMOSAURIDS

**MEDIUM-SIZED TO GIGANTIC CRYPTOCLIDIANS FROM THE EARLY CRETACEOUS TO THE END OF THE MESOZOIC, GLOBAL**

ANATOMICAL CHARACTERISTICS Heads small, ears absent. Necks very to extremely long.
HABITAT Mainly coastal shallows, a few in freshwaters.
HABITS Swimming performance mediocre to modest. Ambush hunters of small and medium-sized game.
NOTES The placement of the very poorly preserved Late Triassic *Alexeyisaurus* in the otherwise entirely Cretaceous group is highly problematic.

## BASOELASMOSAURIDS

**MEDIUM-SIZED TO GIGANTIC ELASMOSAURIDS FROM THE EARLY CRETACEOUS TO THE END OF THE MESOZOIC, GLOBAL**

HABITS Swimming performance modest.

### *Lagenanectes richterae*

**8 m (26 ft) TL, 1.3 tonnes**

FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Front teeth large.
AGE Early Cretaceous; late Hauterivian.
DISTRIBUTION AND FORMATIONS Northern Germany; Stadthagen.
HABITAT Island archipelago shallows.
NOTES Shared its habitat with *Enaliosuchus.*

### *Eromangasaurus australis*

**5 m (17 ft) TL, 350 kg (800 lb)**

FOSSIL REMAINS Nearly complete skull, severely damaged.
ANATOMICAL CHARACTERISTICS Teeth small.
AGE Early Cretaceous; middle Albian.
DISTRIBUTION AND FORMATIONS Northeastern Australia; Toolebuc.
HABITAT Interior seaway.
HABITS Fisher of small game.
NOTES Shared its habitat with ?*Kronosaurus*, *Longirostra*, *Cratochelone*, *Notochelone*, *Bouliachelys.*

### *Callawayasaurus colombiensis*

**8 m (26 ft) TL, 1.3 tonnes**

FOSSIL REMAINS Two nearly complete skulls and skeletons.
ANATOMICAL CHARACTERISTICS Teeth large, robust.
AGE Early Cretaceous; Aptian.
DISTRIBUTION AND FORMATIONS Colombia; upper Paja.
HABITAT Continental coastal.
NOTES Shared its habitat with *Monquirasaurus*, *Kyhytysuka*.

***Callawayasaurus colombiensis***

### *Wapuskanectes betsynichollsae*

**10 m (33 ft) TL, 2 tonnes**

**FOSSIL REMAINS** Partial skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; earliest Albian.
**DISTRIBUTION AND FORMATIONS** Alberta; lower Clearwater.
**HABITAT** Interior seaway, polar.
**NOTES** Shared its habitat with *Athabascasaurus*, *Nichollssaura*.

### *Woolungasaurus glendowerensis*

**9 m (30 ft) TL, 1.8 tonnes**

**FOSSIL REMAINS** Majority of skeleton, three partial skeletons.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; late Aptian.
**DISTRIBUTION AND FORMATIONS** Northeastern Australia; Wallumbilla.
**HABITAT** Interior seaway.

### *Libonectes morgani*

**9 m (30 ft) TL, 1.8 tonnes**

**FOSSIL REMAINS** Partial skull, minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth large, stout, procumbent.
**AGE** Late Cretaceous; late Turonian.
**DISTRIBUTION AND FORMATIONS** Texas; Britton.
**HABITAT** Continental coastal.
**NOTES** Presence of taxon in Morocco is problematic.

### *Futabasaurus suzukii*

**7 m (23 ft) TL, 700 kg (1,500 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth medium sized. Foreflipper larger than aft.
**AGE** Late Cretaceous; early Santonian.
**DISTRIBUTION AND FORMATIONS** Japan; upper Tamayama.
**HABITAT** Continental coastal.
**NOTES** At that time Japan was attached to Asia.

### *Kawanectes lafquenianum*

**3.8 m (12 ft) TL, 140 kg (300 lb)**

**FOSSIL REMAINS** A few partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Campanian and/or early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Southern Argentina; middle Allen, lower La Colonia?
**HABITAT** Continental coastal.

### *Fluvionectes sloanae*

**5 m (16 ft) TL, 500 kg (1,000 lb)**

**FOSSIL REMAINS** Partial skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Campanian.
**DISTRIBUTION AND FORMATIONS** Alberta; lower Dinosaur Park.
**HABITAT** Coastal rivers, possibly brackish waters.
**HABITS** May have occasionally snapped up small swimming land creatures.
**NOTES** With other remains from the region reaching 7 m (23 ft), these are the largest known freshwater plesiosaurs.

### *Nakonanectes bradti*

**5.5 m (18 ft) TL, 600 kg (1,300 lb)**

**FOSSIL REMAINS** Complete skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Head deep at back, most teeth large and stout. Neck moderately long.
**AGE** Late Cretaceous; early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Montana; upper Bearpaw Shale.
**HABITAT** Interior seaway was becoming very narrow.
**NOTES** Shared its habitat with *Terminonatator*, *Tylosaurus saskatchewanensis*, *Plioplatecarpus*? *primaevus*.

*Nakonanectes bradti*

### *Cardiocorax mukulu*

**6 m (20 ft) TL**

**FOSSIL REMAINS** Skull crushed and partial skeleton, two partial skeletons.
**ANATOMICAL CHARACTERISTICS** Some teeth large.
**AGE** Late Cretaceous; early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Angola; Mocuio.
**HABITAT** Continental coastal.

### *Vegasaurus molyi*

**7 m (23 ft) TL, 700 kg (1,500 lb)**

**FOSSIL REMAINS** Majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Neck very long.
**AGE** Late Cretaceous; early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Antarctic Peninsula; Snow Hill Island.
**HABITAT** Continental coastal, polar.

### *Morenosaurus stocki*

**6 m (20 ft) TL, 450 kg (1,000 lb)**

**FOSSIL REMAINS** Two partial skeletons, one juvenile.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Central California; middle Moreno.
**HABITAT** Continental coastal.
**NOTES** *Fresnosaurus drescheri* may be the juvenile of this species.

### *Aphrosaurus furlongi*

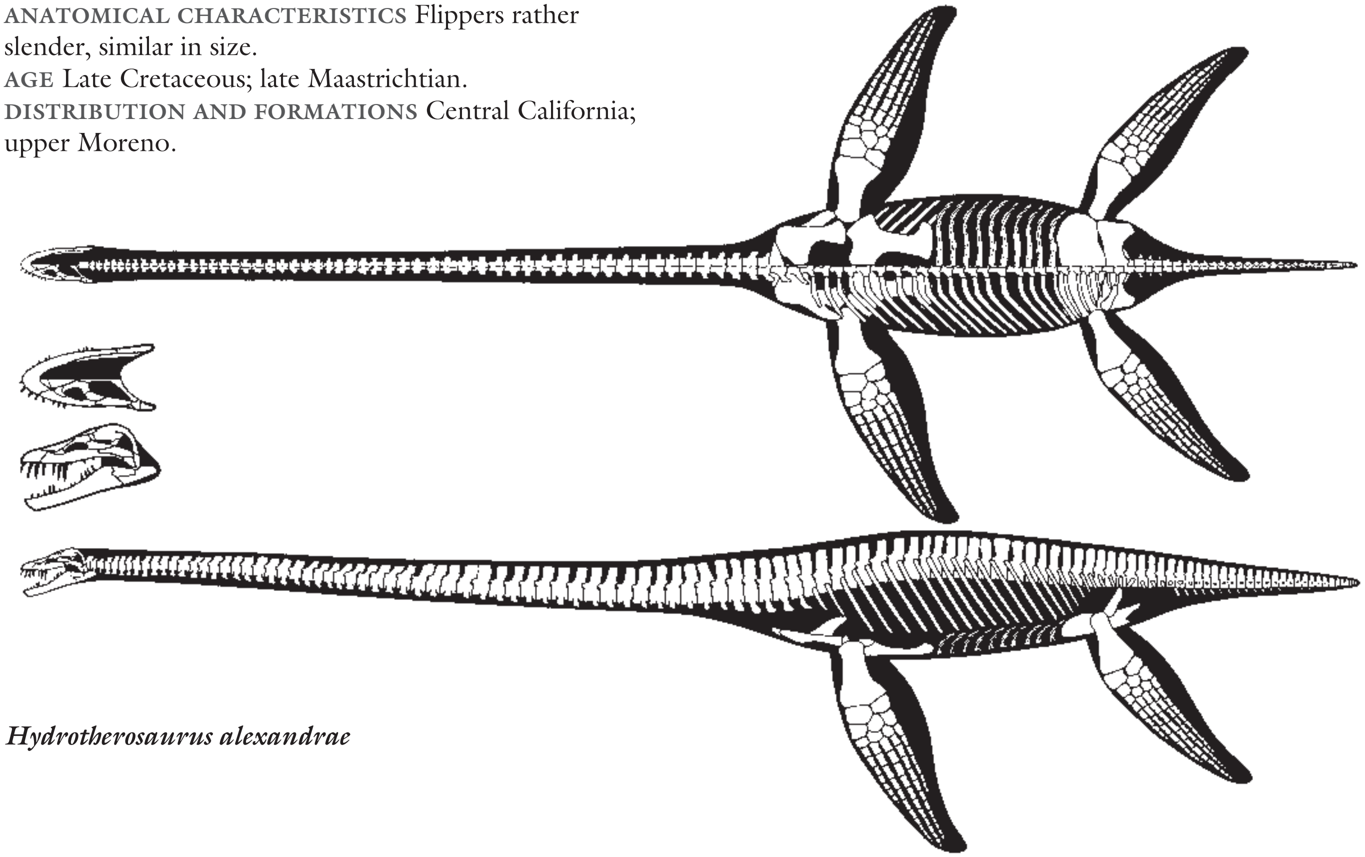
**10 m (33 ft) TL, 1 tonne**

**FOSSIL REMAINS** Minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Flippers rather slender, similar in size.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Central California; upper Moreno.
**HABITAT** Continental coastal.
**NOTES** Shared its habitat with *Hydrotherosaurus alexandrae*.

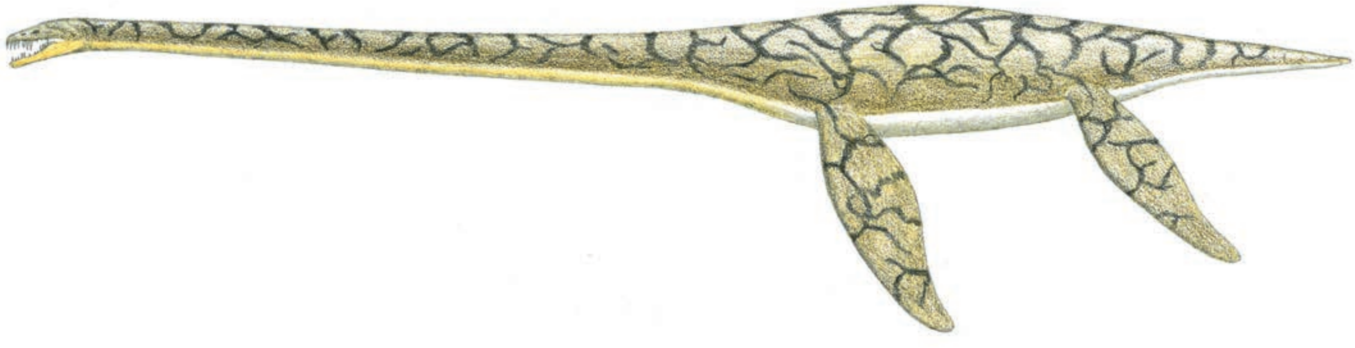
### *Hydrotherosaurus alexandrae*

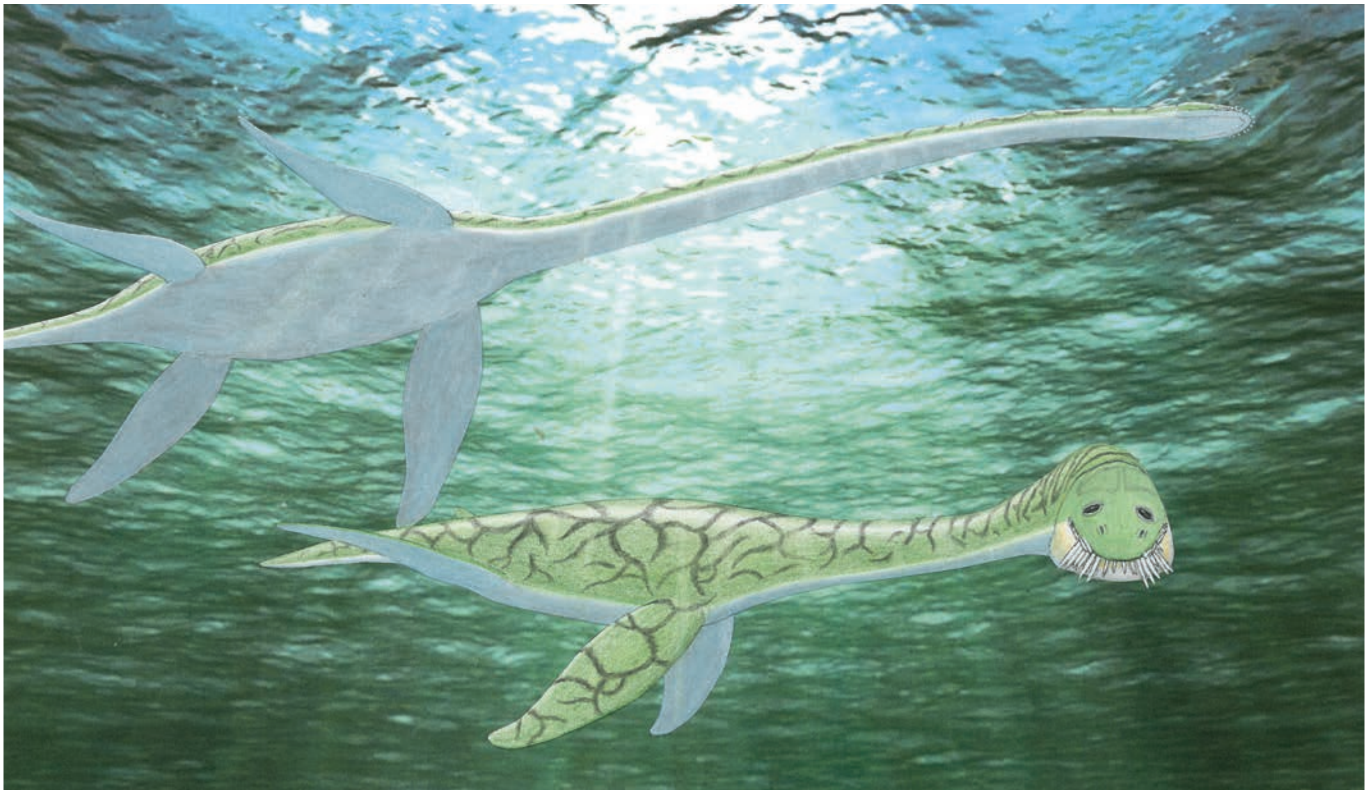
**8 m (26 ft) TL, 1.1 tonnes**

**FOSSIL REMAINS** Complete skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head moderately broad, front upper teeth large, robust. Neck extremely long. Flippers very large, fore a little larger than aft.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Central California; upper Moreno.
**HABITAT** Continental coastal.



*Hydrotherosaurus alexandrae*





*Hydrotherosaurus alexandrae*

### *Cimoliasaurus magnus*

**7.5 m (25 ft) TL, 1 tonne**

**FOSSIL REMAINS** Partial skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** New Jersey; Navesink.
**HABITAT** Continental shelf.
**NOTES** Assignment of other remains from various locations to this taxon is problematic. Shared its habitat with *Mosasaurus*? *conodon*.

### *Zarafasaura oceanis*

**3.5 m (11 ft) TL, 100 kg (220 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth large and stout. Neck moderately long.
**AGE** Late Cretaceous; latest Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Morocco; unnamed.
**HABITAT** Continental coastal.
**NOTES** Shared its habitat with *Ocepechelon*.

### *Tuarangisaurus keyesi*

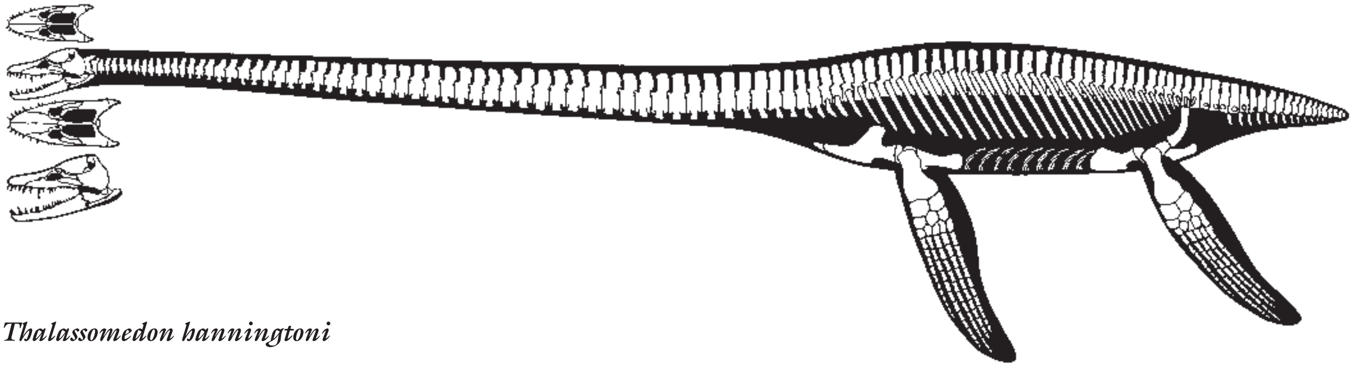
**8 m (26 ft) TL, 1 tonne**

**FOSSIL REMAINS** Nearly complete, badly damaged skull and minority of skeleton, possible juvenile remains.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Campanian and/or early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Southern New Zealand; upper Tahora.
**HABITAT** Island coastal.

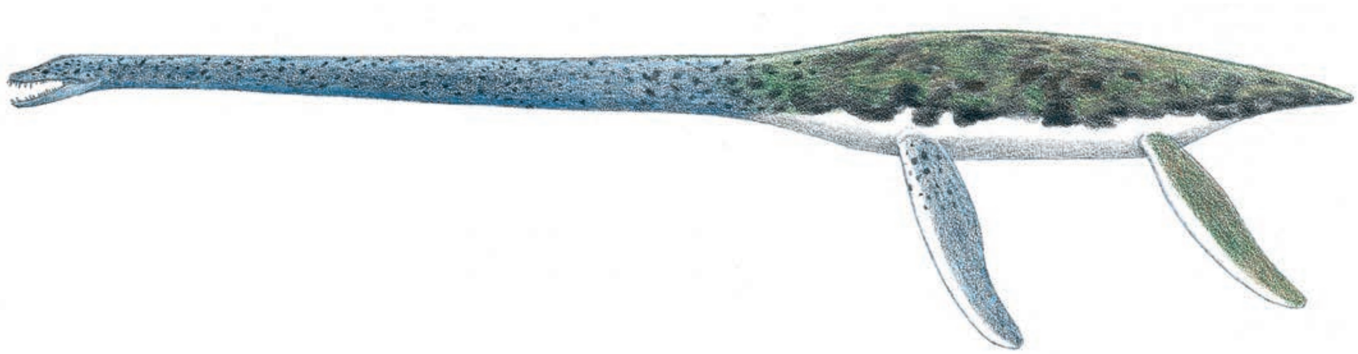
### *Thalassomedon hanningtoni*

**10.1 m (33 ft) TL, 2.5 tonnes**

**FOSSIL REMAINS** Two skulls and several skeletons from nearly complete to partial.
**ANATOMICAL CHARACTERISTICS** Head moderately broad, deep aft, teeth medium sized. Neck extremely long. Tail short. Flippers large, similar in size.
**AGE** Late Cretaceous; early Cenomanian.
**DISTRIBUTION AND FORMATIONS** Colorado, Montana; Graneros Shale, Belle Fourche.
**HABITAT** Interior seaway.
**NOTES** Shared its habitat with *Plesiopleurodon*.



*Thalassomedon hanningtoni*



## ELASMOSAURINES

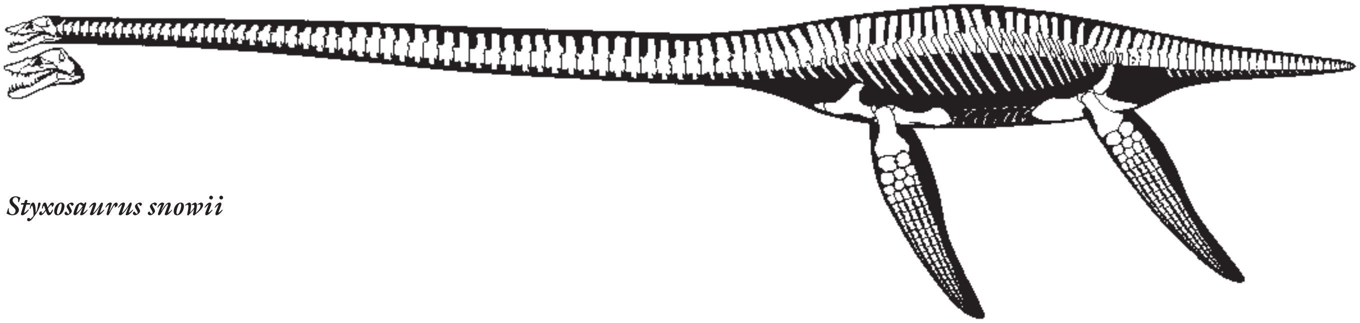
### GIGANTIC ELASMOSAURIDS FROM THE LATE CRETACEOUS OF NORTH AMERICA

**ANATOMICAL CHARACTERISTICS** Long, procumbent spike teeth. Necks very to extremely long.
**HABITAT** Interior seaway.
**HABITS** Swimming performance mediocre. Ambush fishers of small and medium-sized game.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

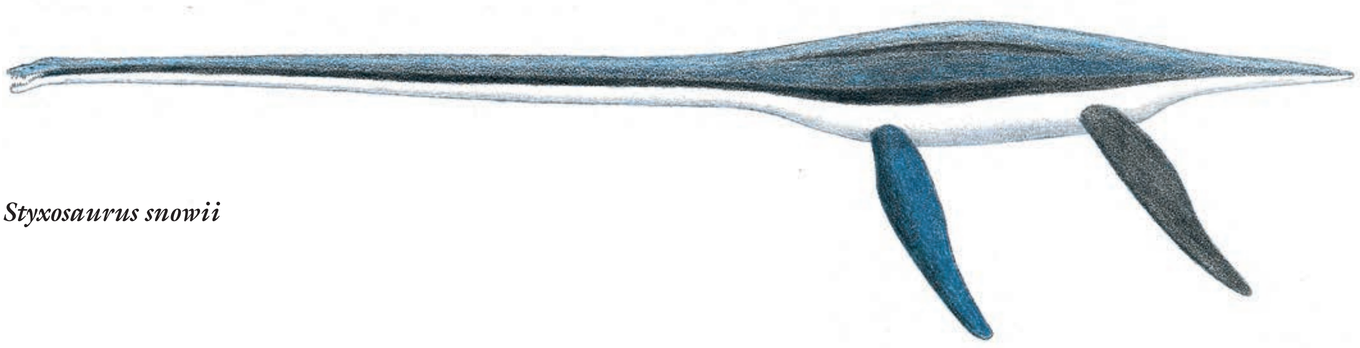
### *Styxosaurus snowii*

**10.5 m (34.5 ft) TL, 2.3 tonnes**

**FOSSIL REMAINS** Two skulls and several skeletons from nearly complete to partial.
**ANATOMICAL CHARACTERISTICS** Small bump atop midline of back of snout, teeth modest in number, fairly stout. Neck extremely long. Flippers long, fairly narrow, similar in size.
**AGE** Late Cretaceous; earliest Campanian.
**DISTRIBUTION AND FORMATIONS** Kansas, South Dakota; uppermost Niobrara.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** Because seaway was so broad and deep, shallow coastal waters that preserved elasmosaurine fossils in marine sediments were are not abundant from this time and region. Shared its habitat with *Polycotylus latipinnis*, *Dolichorhynchops osborni*, *Platecarpus tympanicus*, *Eonatator sternbergii*, *Clidastes propython*, *Ctenochelys stenoporus*, *Protostega gigas.*



*Styxosaurus snowii*



*Styxosaurus snowii*

### *Styxosaurus browni*

**10.5 m (34.5 ft) TL, 2.3 tonnes**

**FOSSIL REMAINS** Complete skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Head not broad, teeth modest in number, medium sized. Neck extremely long. Flippers long, fairly narrow, similar in size.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** Wyoming; lower Pierre Shale.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** May be a little larger than *S. snowii*. Shared its habitat with *Dolichorhynchops bonneri*, *Tylosaurus proriger*, *Latoplatecarpus*, *Globidens*? *dakotensis*, *Toxochelys latiremus*, *Elasmosaurus*.

### *Elasmosaurus platyurus*

**10.3 (34 ft) TL, 2 tonnes**

**FOSSIL REMAINS** Minority of skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Neck extremely long.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** Kansas; lower Pierre Shale.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** Although an iconic plesiosaur, is known from only one incomplete specimen.

### *Albertonectes vanderveldei*

**11 m (24 ft) TL, 2 tonnes**

**FOSSIL REMAINS** Complete skeleton without skull.
**ANATOMICAL CHARACTERISTICS** Neck extremely long, flippers similar in size.
**AGE** Late Cretaceous; late Campanian.
**DISTRIBUTION AND FORMATIONS** Alberta; lower Bearpaw Shale.
**HABITAT** Interior seaway was becoming much narrower.
**HABITS** Extremely long neck combined with modest propulsive power indicates a rather slow ambush fisher.
**NOTES** Shared its habitat with *Dolichorhynchops herschelensis*, *Prognathodon*? *overtoni*. Longest known plesiosaur, and longest known plesiosaur neck both absolute and relative, with 76 vertebrae and 6.5 m (21.3 ft) long.

### *Terminonatator ponteixensis*

**9 m (30 ft) TL, 1.6 tonnes**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth modest in number, large, quite robust, procumbent spikes.
**AGE** Late Cretaceous; latest Campanian.
**DISTRIBUTION AND FORMATIONS** Saskatchewan; upper Bearpaw Shale.
**HABITAT** Interior seaway was becoming very narrow.
**NOTES** Shared its habitat with *Nakonanectes*, *Tylosaurus saskatchewanensis*, *Plioplatecarpus*? *primaevus*.

## ARISTONECTIDS

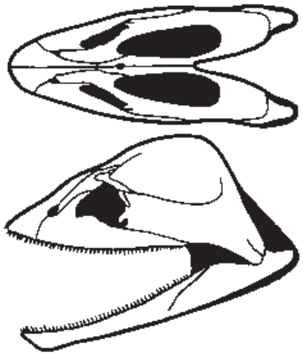
**LARGE TO GIGANTIC CRYPTOCLIDIANS FROM THE LATE CRETACEOUS OF THE SOUTHERN HEMISPHERE**

**ANATOMICAL CHARACTERISTICS** Skull short, broad, tall aft, snout rounded, teeth numerous, small, delicate needle spikes, forming interlocking but nonoccluding dental combs. Necks moderately long.
**HABITS** Swimming performance mediocre. Probably suction filter feeders comparable to baleen whales.
**NOTES** Placement of these highly specialized filter feeders within elasmosaurids not logical. Absence from the Northern Hemisphere may reflect lack wwof sufficient sampling.

### *Kaiwhekea katiki*

**7 m (23 ft) TL, 1.5 tonnes**

**FOSSIL REMAINS** Majority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Skull very deep aft, fairly narrow, small teeth numerous, somewhat procumbent.
**AGE** Late Cretaceous; middle Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Southern New Zealand; lower or middle Katiki.
**HABITAT** Island coastal.



*Kaiwhekea katiki*

***Aristonectes parvidens***
**Adult size not certain**

FOSSIL REMAINS Partial skull and skeleton, possibly immature.
ANATOMICAL CHARACTERISTICS Very numerous, small and slender teeth, upper teeth strongly procumbent, lower teeth directed sideways and a little downward.
AGE Late Cretaceous; Maastrichtian.
DISTRIBUTION AND FORMATIONS Southern Argentina; Paso del Sapo.
HABITAT Continental coastal.
NOTES May be same as, or direct ancestor of, *A. quiriquinensis.*

***Aristonectes quiriquinensis***
**10 m (33 ft) TL, 4 tonnes**

FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Very numerous, small and slender teeth, upper teeth strongly procumbent, lower teeth directed sideways and a little downward. Flippers very large.
AGE Late Cretaceous; late Maastrichtian.
DISTRIBUTION AND FORMATIONS Central Chile; Quiriquina.
HABITAT Continental coastal.

***Morturneria seymourensis***
**Adult size uncertain**

FOSSIL REMAINS Partial skull and minority of skeleton, juvenile.
ANATOMICAL CHARACTERISTICS Very numerous, small and slender teeth, upper teeth strongly procumbent, lower teeth directed sideways and a little downward.
AGE Late Cretaceous; late Maastrichtian.
DISTRIBUTION AND FORMATIONS Antarctic Peninsula; Lopez de Bertodano.
HABITAT Continental coastal, polar.
NOTES Shared its habitat with *Kaikaifilu.*

## LEPTOCLEIDIANS

MEDIUM-SIZED TO LARGE CRYPTOCLIDIANS FROM THE EARLY CRETACEOUS TO THE END OF THE MESOZOIC, GLOBAL

ANATOMICAL CHARACTERISTICS Heads at least moderately long. Necks not long.
HABITAT Freshwaters to continental shelves.
HABITS Swimming performance good. Pursuit fishers and hunters of medium-sized to big game.

## LEPTOCLEIDIDS

MEDIUM-SIZED TO LARGE LEPTOCLEIDIANS FROM THE EARLY CRETACEOUS TO THE END OF THE MESOZOIC, GLOBAL

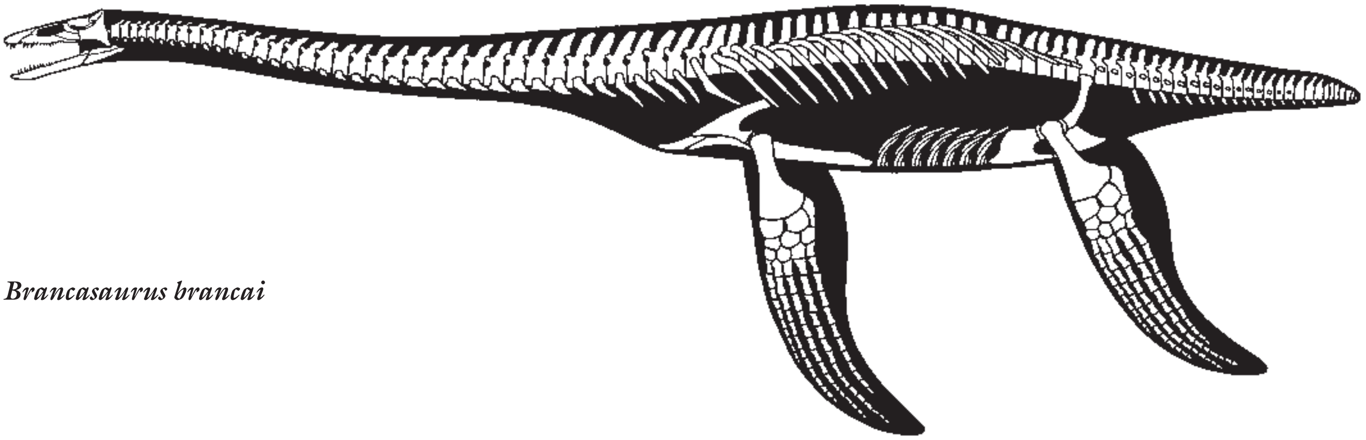
ANATOMICAL CHARACTERISTICS Heads not broad, temporal region somewhat elongated. Necks moderate in length.
HABITAT Freshwaters to continental shelves.
HABITS Fishers of medium-sized game.

***Nichollssaura borealis***
**2.6 m (8.5 ft) TL, 80 kg (170 lb)**

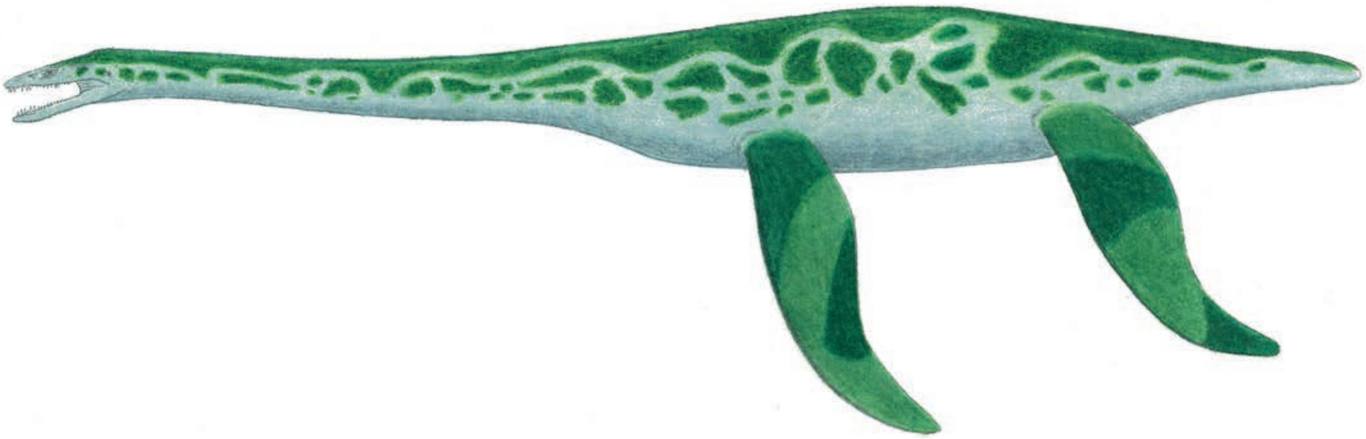
FOSSIL REMAINS Complete skull and skeleton, severely flattened top to bottom.
ANATOMICAL CHARACTERISTICS Teeth medium sized. Flippers medium sized, similar in size.
AGE Early Cretaceous; early Albian.
DISTRIBUTION AND FORMATIONS Alberta; lower Clearwater.
HABITAT Interior seaway, polar.
NOTES Shared its habitat with *Athabascasaurus, Wapuskanectes.*

***Hastanectes valdensis***
**Adult size uncertain**

FOSSIL REMAINS Two partial skeletons, possibly immature.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous; Valanginian.
DISTRIBUTION AND FORMATIONS Southern England; Wadhurst Clay.
HABITAT Island estuary.



*Brancasaurus brancai*



### *Brancasaurus brancai*

**4.1 m (13 ft) TL, 350 kg (750 lb)**

**FOSSIL REMAINS** Majority of skull and skeleton, partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head fairly narrow, teeth medium sized, fairly stout. Tail short. Flippers very large, similar in size, lower arm and leg very short, rest of flippers elongated, strongly swept back.
**AGE** Early Cretaceous; middle to late Berriasian.
**DISTRIBUTION AND FORMATIONS** Northwestern Germany; Bückeberg.
**HABITAT** Lakes, possibly rivers.
**HABITS** Powerful swimmers. May have occasionally snapped up small swimming land creatures.
**NOTES** Whether this taxon was a permanent freshwater plesiosaur or a transient is not certain.

### *Umoonasaurus demoscyllus*

**2.5 m (8 ft) TL, 70 kg (150 lb)**

**FOSSIL REMAINS** Partial skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth long and slender. Neck short. Last five tail vertebrae fused into a pygostyle. Flippers large.
**AGE** Early Cretaceous; Aptian and/or early Albian.
**DISTRIBUTION AND FORMATIONS** South Australia; Bulldog Shale.
**HABITAT** Interior seaway, polar, lacking sharks.
**NOTES** Shared its habitat with *Opallionectes.*

### *Opallionectes andamookaensis*

**5.5 m (19 ft) TL, 750 (1,600 lb)**

**FOSSIL REMAINS** Teeth, partial skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth slender.
**AGE** Early Cretaceous; Aptian and/or early Albian.
**DISTRIBUTION AND FORMATIONS** South Australia; Bulldog Shale.
**HABITAT** Interior seaway, polar, lacking sharks.
**HABITS** Consumed small prey.
**NOTES** Phylogenetic position is not certain.

### *Leptocleidus capensis*

**4.5 m (15 ft) TL, 400 kg (1,300 lb)**

**FOSSIL REMAINS** Majority of skull, severely flattened top to bottom, and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; Valanginian.

**DISTRIBUTION AND FORMATIONS** South Africa; Sundays River.
**HABITAT** Continental coastline.

### *Leptocleidus superstes*
**4 m (13 ft) TL, 300 kg (650 lb)**

**FOSSIL REMAINS** Majority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head fairly broad, snout rather short, teeth moderate in number, fairly large.
**AGE** Early Cretaceous; Barremian.
**DISTRIBUTION AND FORMATIONS** Southern England; upper Weald Clay.
**HABITAT** Island archipelago shallows.

### *Vectocleidus pastorum*
**1.5 m (5 ft) TL, 15 kg (30 lb)**

**FOSSIL REMAINS** Partial skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; latest Barremian.
**DISTRIBUTION AND FORMATIONS** Southern England; upper Vectis.
**HABITAT** Island archipelago shallows.

## POLYCOTYLIDS

**MEDIUM-SIZED TO LARGE LEPTOCLEIDIANS FROM THE EARLY CRETACEOUS TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Necks fairly short.
**HABITAT** Coastal nearshore to deep oceans.
**HABITS** Swimming performance modest to good. Fishers and hunters of medium-sized to big game.

### *Mauriciosaurus fernandezi*
**Adult size uncertain**

**FOSSIL REMAINS** Skull and skeleton, juvenile, severely flattened top to bottom, soft tissues.
**ANATOMICAL CHARACTERISTICS** Head large, elongated, snout long and narrow, teeth medium sized, procumbent. Flippers large, similar in size.
**AGE** Late Cretaceous; early Turonian.
**DISTRIBUTION AND FORMATIONS** Northeastern Mexico; lower Agua Nueva.
**HABITAT** Continental shelf.

### *Pahasapasaurus haasi*
**Adult size uncertain**

**FOSSIL REMAINS** Skull and skeleton, juvenile.
**ANATOMICAL CHARACTERISTICS** Head elongated, snout long and narrow.
**AGE** Late Cretaceous; middle Cenomanian.
**DISTRIBUTION AND FORMATIONS** South Dakota; lower Greenhorn Limestone.
**HABITAT** Interior seaway rather narrow and shallow.

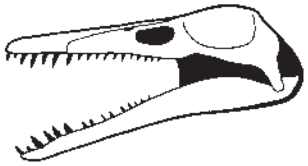
### *Edgarosaurus muddi*
**3.5 m (11 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head elongated, snout long and narrow but robust, teeth large. Neck moderately long.
**AGE** Early Cretaceous; middle Albian.
**DISTRIBUTION AND FORMATIONS** Montana; middle Thermopolis Shale.
**HABITAT** Interior seaway narrow and shallow.

***Edgarosaurus muddi***

### *Plesiopleurodon wellesi*
**7 m (23 ft) TL, 2 tonnes**

**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth moderate in size.
**AGE** Late Cretaceous; early Cenomanian.
**DISTRIBUTION AND FORMATIONS** Wyoming; Belle Fourche Shale.
**HABITAT** Interior seaway.



***Plesiopleurodon wellesi***

### *Eopolycotylus rankini*
**4 m (13 ft) TL, 350 kg (700 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; early Turonian.
**DISTRIBUTION AND FORMATIONS** Utah; middle Tropic Shale.
**HABITAT** Interior seaway.
**NOTES** Shared its habitat with *Dolichorhynchops? tropicensis.*

### *Polycotylus latipinnis*

**5 m (16 ft) TL, 700 kg (1,500 lb)**

**FOSSIL REMAINS** Partial skeletons, including a probable fetus.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; earliest Campanian.
**DISTRIBUTION AND FORMATIONS** Kansas, Alabama; uppermost Niobrara, lower Mooreville Chalk.
**HABITAT** Interior seaway was continuing to become less broad and deep, continental shelf.
**NOTES** The presence of a young skeleton within an adult skeleton indicates live birth in the group, the calves being large in at least some plesiosaurs. Shared its habitat with *Styxosaurus snowii*, *Dolichorhynchops osborni*, *Selmasaurus russelli*, *Platecarpus tympanicus*, *Eonatator sternbergii*, *Clidastes propython*, *Ctenochelys stenoporus*, *Protostega gigas.*

### *Polycotylus? sopozkoi*

**4 m (13 ft) TL, 350 kg (700 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Fore and aft flippers similar in size.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** Central Russia; unnamed.
**HABITAT** Continental coastline.
**NOTES** Placement in *Polycotylus* not certain.

### *Georgiasaurus penzensis*

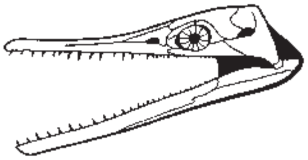
**4 m (13 ft) TL, 450 kg (1,000 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; Santonian.
**DISTRIBUTION AND FORMATIONS** Western Russia; unnamed.
**HABITAT** Continental coastline.

### *Trinacromerum bentonianum*

**3 m (10 ft) TL, 150 kg (300 lb)**

**FOSSIL REMAINS** Three skulls.
**ANATOMICAL CHARACTERISTICS** Head elongated, snout long and narrow, teeth rather small.
**AGE** Late Cretaceous; middle Turonian.
**DISTRIBUTION AND FORMATIONS** Kansas; upper Greenhorn Limestone, lower Carlile Shale.
**HABITAT** Interior seaway shifting from its greatest maximum to less broad and deep.
**NOTES** Shared its habitat with *Brachauchenius*. May have been directly ancestral to *Trinacromerum kirki*.



*Trinacromerum bentonianum*

### *Trinacromerum kirki*

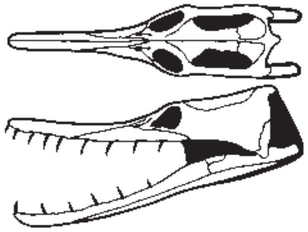
**4.5 m (15 ft) TL, 500 kg (1,100 lb)**

**FOSSIL REMAINS** Minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; middle Turonian.
**DISTRIBUTION AND FORMATIONS** Manitoba; upper Favel.
**HABITAT** Interior seaway.

### *Manemergus anguirostris*

**2 m (6 ft) TL, 30 kg (60 lb)**

**FOSSIL REMAINS** Skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head elongated, narrow, snout long, quite narrow and shallow, temporal region elongated and robustly constructed, teeth few, slender, and long.
**AGE** Late Cretaceous; late Turonian.
**DISTRIBUTION AND FORMATIONS** Morocco; Akrabou.
**HABITAT** Continental coastal.
**NOTES** Shared its habitat with *Thililua*.



*Manemergus anguirostris*

### *Thililua longicollis*

**6 m (20 ft) TL, 1.3 tonnes**

**FOSSIL REMAINS** Skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head elongated, low along entire length, robustly constructed, teeth moderate in number and medium sized, fairly robust. Neck length moderate.
**AGE** Late Cretaceous; late Turonian.

*Thililua longicollis*

**DISTRIBUTION AND FORMATIONS** Morocco; Akrabou.
**HABITAT** Continental coastal.

### *Dolichorhynchops? tropicensis*

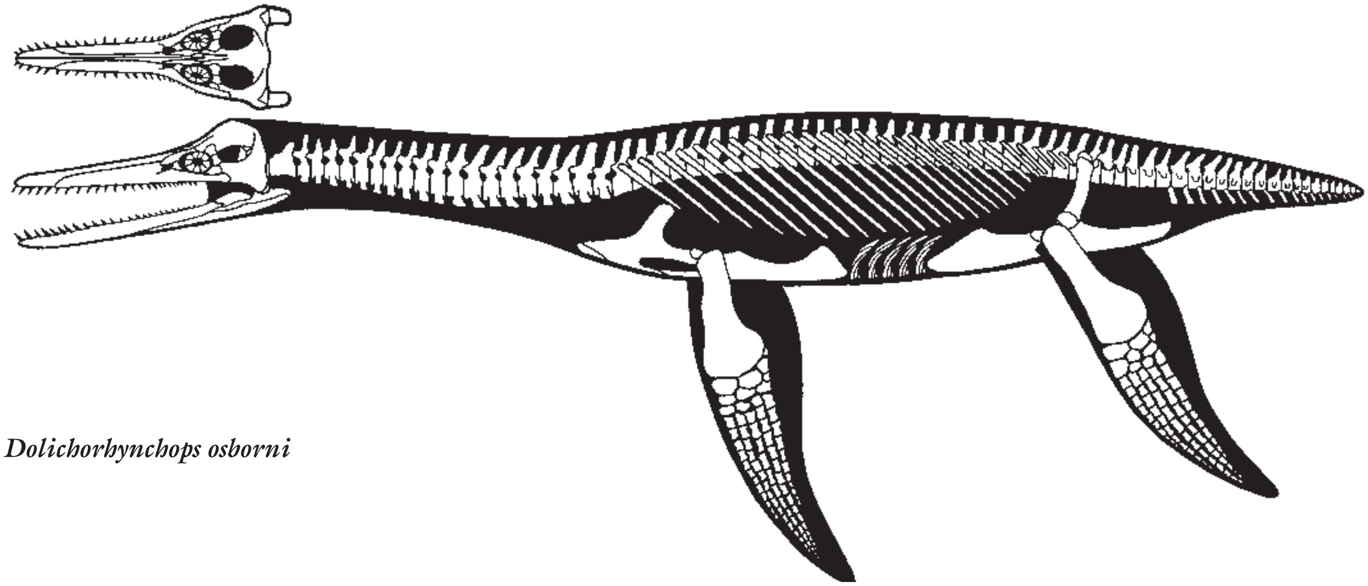
**3 m (10 ft) TL, 200 kg (450 lb)**

**FOSSIL REMAINS** Majority of skull and skeleton, minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; early Turonian.
**DISTRIBUTION AND FORMATIONS** Utah; middle Tropic Shale.
**HABITAT** Interior seaway.
**NOTES** Whether this species belongs to the same genus as the much later *D. osborni* is problematic. Shared its habitat with *Eopolycotylus.*

### *Dolichorhynchops osborni*

**5.2 m (17 ft) TL, 1 tonne**

**FOSSIL REMAINS** Three skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head elongated and narrow, snout very long, modest crest along midline of temporal region, teeth fairly numerous, rather small, not slender, procumbent, intermeshing. Neck moderately long. Trunk somewhat elongated. Tail short. Flippers long, rather narrow, similar in size.
**AGE** Late Cretaceous; earliest Campanian.
**DISTRIBUTION AND FORMATIONS** Kansas; uppermost Niobrara.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** Shared its habitat with *Styxosaurus snowii*, *Polycotylus latipinnis*, *Platecarpus tympanicus*, *Eonatator*



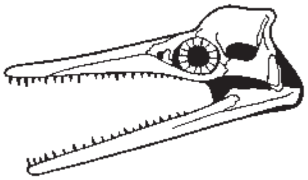
*Dolichorhynchops osborni*

*sternbergii*, *Clidastes propython*, *Ctenochelys stenoporus*, *Protostega gigas*. May be directly ancestral to *D. bonneri*.

### *Dolichorhynchops bonneri*

**4.8 m (15.5 ft) TL, 800 kg (1,750 lb)**

**FOSSIL REMAINS** Majority of skull and skeletons.
**ANATOMICAL CHARACTERISTICS** Head elongated and narrow, snout very long, fairly large crest along midline of temporal region, teeth fairly numerous, rather small, fairly robust, intermeshing. Neck moderately long.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** Wyoming; lower Pierre Shale.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** Shared its habitat with *Styxosaurus browni*, *Elasmosaurus*, *Tylosaurus proriger*, *Latoplatecarpus*, *Globidens*? *dakotensis*, *Toxochelys latiremus*.



*Dolichorhynchops bonneri*

### *Dolichorhynchops herschelensis*

**Adult size not certain**

**FOSSIL REMAINS** Majority of skull and partial skeleton, possibly immature.
**ANATOMICAL CHARACTERISTICS** Head elongated and narrow, snout very long, fairly large crest along midline of temporal region, teeth fairly numerous.
**AGE** Late Cretaceous; late Campanian and/or early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Saskatchewan; lower Bearpaw Shale.
**HABITAT** Interior seaway was becoming much narrower.
**NOTES** Shared is habits with *Albertonectes*, *Prognathodon*? *overtoni*.

### *Palmulasaurus quadratus*

**Adult size not certain**

**FOSSIL REMAINS** Partial skull and skeleton, possibly immature.
**ANATOMICAL CHARACTERISTICS** Snout very slender. Foreflipper smaller than aft.
**AGE** Late Cretaceous; earliest Turonian.
**DISTRIBUTION AND FORMATIONS** Utah; lower Tropic Shale.
**HABITAT** Interior seaway.

### *Sulcusuchus erraini*

**Adult size uncertain**

**FOSSIL REMAINS** Two partial skulls, possibly immature.
**ANATOMICAL CHARACTERISTICS** Head elongated, heavily constructed.
**AGE** Late Cretaceous; late Campanian and/or Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Southern Argentina; Los Alamitos.
**HABITAT** Continental coastal.
**HABITS** Fisher and hunter of big game, including hard-shelled ammonoids.

# ICHTHYOSAUROMORPHS

**SMALL TO GIGANTIC NEODIAPSIDS FROM THE EARLY TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Highly variable. Skulls akinetic, nostrils far behind snout tip and immediately in front of orbits, scleral rings often present, lower temporal openings ventrally open, teeth neither very large nor on mouth roof. Necks short. Tails flattened side to side. Limbs modified into stiff-jointed partial hydrofoils. Forelimb at least as long as aft. Primarily axial undulators from anguilliform to thunniform, flippers primarily for stability and maneuvering.
**HABITAT** Coastal nearshore to deep oceans.
**HABITS** Swimming performance mediocre to extremely high. Predaceous, ambush and/or pursuit fishers and hunters of small to big game, some crushers.

## HUPEHSUCHIANS

**SMALL ICHTHYOSAUROMORPHS FROM THE EARLY TRIASSIC OF ASIA**

**ANATOMICAL CHARACTERISTICS** Skeletons very heavy boned. Necks not very short. Trunks long, narrow, not deep, neural spine/hornlet complexes elevated, gastralia massive. Tails long, straight, and unexpanded aft. Arms larger than legs, which are not full flippers, rigidly jointed, presumably webbed. Moderately hydrodynamically streamlined, transitional anguilliform-carangiform swimmers.
**HABITAT** Coastal and brackish shorelines, lagoons, reefs, estuaries.
**HABITS** Swimming performance mediocre to modest. Ambush and/or pursuit fishers of small to medium-sized game.

## NANCHANGOSAURIDS

**SMALL HUPEHSUCHIANS FROM THE EARLY TRIASSIC OF ASIA**

**ANATOMICAL CHARACTERISTICS** Heads elongated, narrow, snout a highly elongated, very shallow, fairly broad, toothless beak, upper beak longer than lower.

### *Nanchangosaurus suni*

**1 m (3 ft) TL, 1.5 kg (3 lb)**

**FOSSIL REMAINS** Two partial skulls and skeletons, severely flattened top to bottom, probable juvenile skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Neural spines/armor hornlets complex, moderately tall.
**AGE** Early Triassic; late Olenekian.
**DISTRIBUTION AND FORMATIONS** Eastern China; upper Jialingjiang.
**HABITAT** Continental nearshore.
**NOTES** *Eohupehsuchus brevicollis* may be the juvenile of this species. Shared its habitat with *Eohupehsuchus*, *Parahupehsuchus*, *Hupehsuchus*, *Eretmorhipis*, *Chaohusaurus zhangjiawanensis*.

## HUPEHSUCHIDS

**SMALL HUPEHSUCHIANS FROM THE EARLY TRIASSIC OF ASIA**

## HUPEHSUCHINES

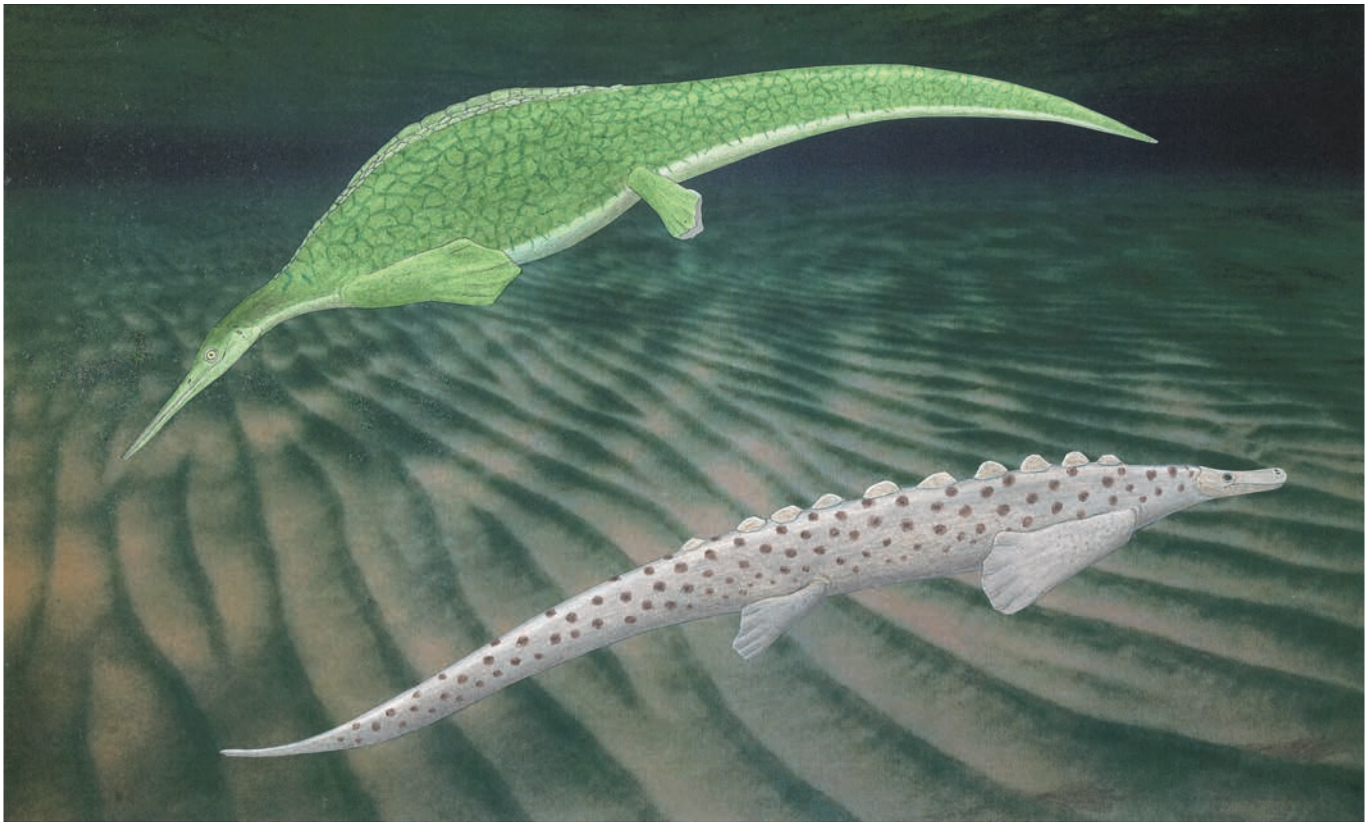
**SMALL HUPEHSUCHIDS FROM THE EARLY TRIASSIC OF ASIA**

**ANATOMICAL CHARACTERISTICS** Upper and lower beaks same length. Neural spines/armor hornlets complex, very tall. Arms large.

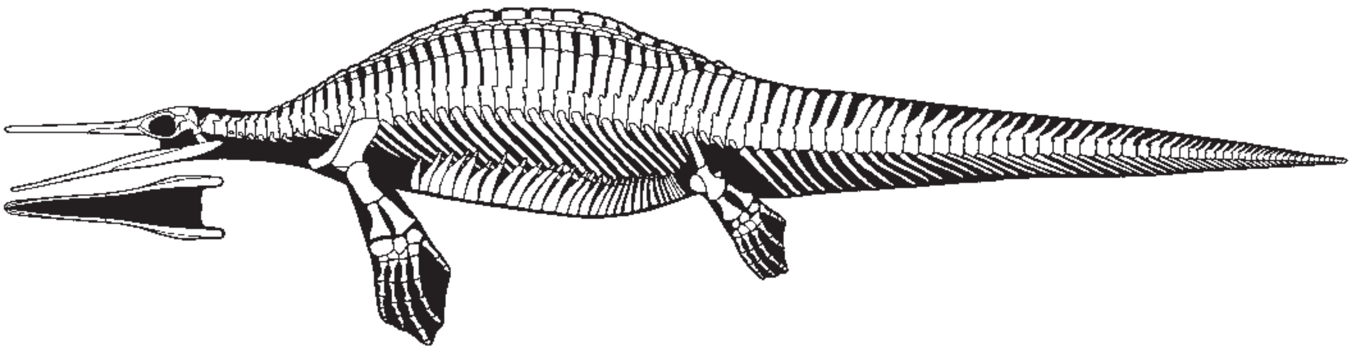
### *Hupehsuchus nanchangensis*

**0.95 m (3.1 ft) TL, 2.5 kg (5.5 lb)**

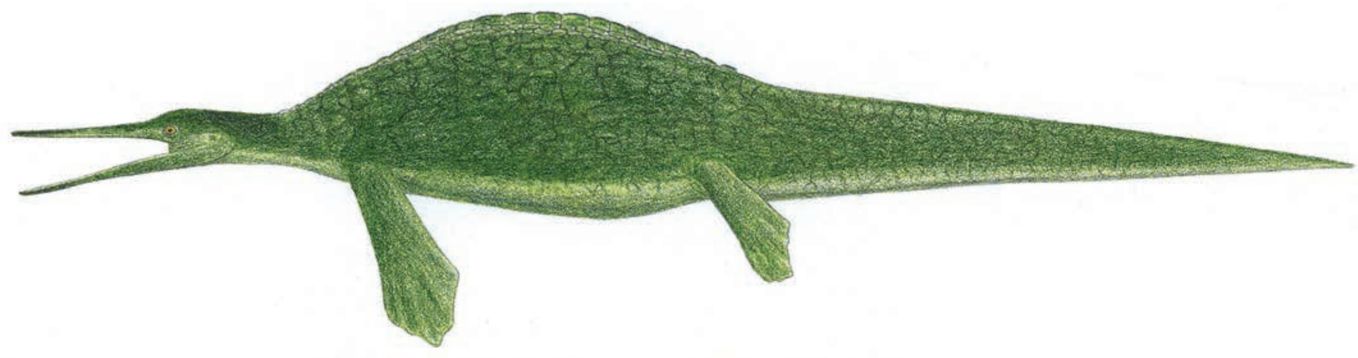
**FOSSIL REMAINS** Two skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Early Triassic; late Olenekian.
**DISTRIBUTION AND FORMATIONS** Eastern China; upper Jialingjiang.
**HABITAT** Continental nearshore.



*Hupehsuchus nanchangensis* and *Eretmorhipis* (right)



*Hupehsuchus nanchangensis*



**NOTES** Shared its habitat with *Nanchangosaurus*, *Eohupehsuchus*, *Parahupehsuchus*, *Eretmorhipis*, *Chaohusaurus zhangjiawanensis*.

## PARAHUPEHSUCHINES

### SMALL HUPEHSUCHIDS FROM THE EARLY TRIASSIC OF ASIA

**ANATOMICAL CHARACTERISTICS** Trunks elongated, very massively constructed.
**NOTES** Without the skull of *Parahupehsuchus*, is not clear whether it and *Eretmorhipis* belong in same subfamily.

### *Parahupehsuchus longus*

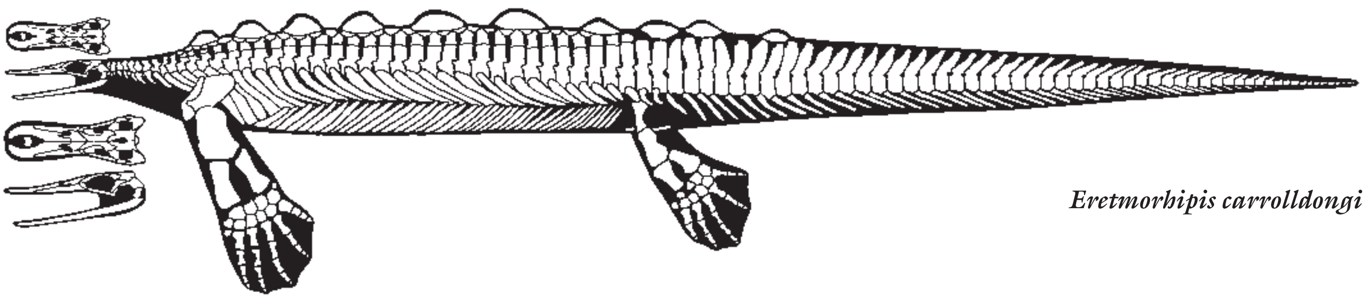
**1 m (3.3 ft) TL, 2 kg (4.5 lb)**

**FOSSIL REMAINS** Majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Limbs not large.
**AGE** Early Triassic; late Olenekian.
**DISTRIBUTION AND FORMATIONS** Eastern China; upper Jialingjiang.
**HABITAT** Continental nearshore.
**HABITS** Insufficient information.
**NOTES** Shared its habitat with *Nanchangosaurus*, *Eohupehsuchus*, *Hupehsuchus*, *Eretmorhipis*, *Chaohusaurus zhangjiawanensis*.

### *Eretmorhipis carrolldongi*

**0.93 m (3 ft) TL, 2 kg (4.5 lb)**

**FOSSIL REMAINS** Skull and two skeletons.
**ANATOMICAL CHARACTERISTICS** Head lightly built, small, flattened, subrectangular in top view with duck-like beak that includes central floating bone between beak prongs, orbits small, mechanoreceptors apparently on beak. Tail rather rigid. Forepaddle especially large.
**AGE** Early Triassic; late Olenekian.



*Eretmorhipis carrolldongi*

**DISTRIBUTION AND FORMATIONS** Eastern China; upper Jialingjiang.
**HABITAT** Continental nearshore.
**HABITS** Limbs about as important for swimming as axial undulations. Apparently used electrical field mechanoreceptors to detect small prey items, especially arthropods, probably at night.
**NOTES** Shared its habitat with *Nanchangosaurus*, *Eohupehsuchus*, *Hupehsuchus*, *Parahupehsuchus*, *Chaohusaurus zhangjiawanensis*. Head in particular remarkably convergent with that of the duck-billed platypus. Shows that very sophisticated reptilian nocturnal aquatic hunter of small items evolved quickly after P/T extinction, but apparently failed to do so again during Mesozoic.

# ICHTHYOSAURIFORMES

**SMALL TO GIGANTIC ICHTHYOSAUROMORPHS FROM THE EARLY TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Fairly uniform. All streamlined, fish- or cetacean-like. Snouts almost always narrow, scleral rings may be universal, teeth sometimes have bulbous roots. Neck very short. Trunks consist of a very large number of vertebrae and ribs, trunks never broader than deep and never extremely deep. Tail never very long, aft downward flexure supported a soft upper tail fin. Scapula short, rounded. Hydrodynamically streamlined, transitional anguilliform-carangiform to thunniform swimmers. Very small, fine scales formed a smooth skin texture.
**HABITAT** Coastal nearshore to deep oceans. Probably all gave live birth.
**HABITS** Swimming performance good to extremely high. Ambush and/or pursuit fishers and hunters of small to big game, some crushers.

## OMPHALOSAURIDS

**SMALL ICHTHYOSAURIFORMES FROM THE MIDDLE TRIASSIC OF NORTH AMERICA AND ASIA**

**ANATOMICAL CHARACTERISTICS** Teeth irregularly placed, small buttons. Trunk moderately long. Tall vertebrae at modest downward flexure of aft tail supported a modest upper tail fin. Pelvis attached to vertebral column. Transitional anguilliform-carangiform swimmers.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.
**HABITAT** Coastal shallows.
**HABITS** Swimming performance good. Ambush and pursuit fishers of small and medium-sized game.

### *Omphalosaurus nevadanus*

**2 m (6 ft) TL, 25 kg (50 lb)**

**FOSSIL REMAINS** Minority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Middle Triassic; Anisian.
**DISTRIBUTION AND FORMATIONS** Nevada; Prida.
**HABITAT** Continental shallows.
**NOTES** The placement of other poorly preserved specimens in the genus is uncertain.

### *Tholodus schmidi*

**1.5 m (5 ft) TL, 10 kg (20 lb)**

**FOSSIL REMAINS** Partial remains.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; lower Muschelkalk.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Cyamodus tarnowitzensis*, *Contectopalatus*.

## NASOROSTRANS

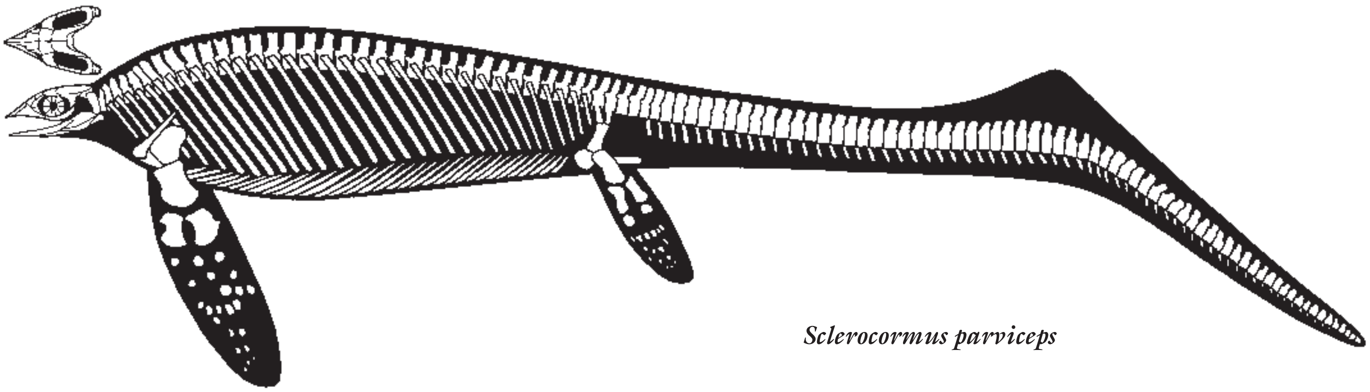
**SMALL ICHTHYOSAURIFORMES FROM THE EARLY TRIASSIC OF ASIA**

**ANATOMICAL CHARACTERISTICS** Heads short, broad, very triangular, with a very short, pointed snout and large temporal region, lower jaw shallow, toothless. Trunk moderately long, ribs and especially gastralia robust. Tall vertebrae at modest downward flexure of aft tail supported a modest upper tail fin. Pelvis attached to vertebral column. Flipper elements from wrist and ankle below very poorly ossified. Transitional anguilliform-carangiform swimmers.
**HABITAT** Coastal shallows.
**HABITS** Swimming performance good. Appear to have been suction feeders.

### *Sclerocormus parviceps*

**1.5 m (5 ft) TL, 9 kg (20 lb)**

**FOSSIL REMAINS** Skull and skeleton severely flattened top to bottom, possible juvenile skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head very small. Tail fairly long. Foreflipper very large and larger than aft.
**AGE** Early Triassic; late Olenekian.
**DISTRIBUTION AND FORMATIONS** Eastern China; upper Nanlinghu.



*Sclerocormus parviceps*

**HABITAT** Continental shallows.
**NOTES** *Cartorhynchus lenticarpus* is probably the juvenile of this or a closely related species. Shared its habitat with *Majiashanosaurus*, *Chaohusaurus geishanensis.*

## ICHTHYOPTERYGIANS

### SMALL TO GIGANTIC ICHTHYOSAURIFORMES FROM THE EARLY TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL

**ANATOMICAL CHARACTERISTICS** Snouts almost always narrow. Vertebral centra spool shaped. Limbs are clawless full flippers with increased number of distal elements. Transitional anguilliform-carangiform to thunniform swimmers.
**HABITAT** Coastal nearshore to deep oceans.
**HABITS** Swimming performance good to extremely high. Ambush and/or pursuit fishers and hunters of small to big game. Some crushers, some may have been suckers.

## UTATSUSAURIANS

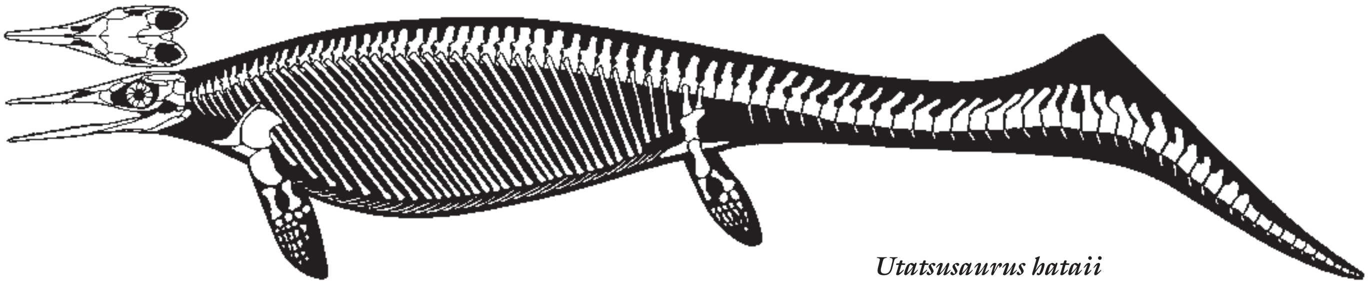
### SMALL ICHTHYOPTERYGIANS FROM THE EARLY AND POSSIBLY MIDDLE TRIASSIC OF NORTH AMERICA

**ANATOMICAL CHARACTERISTICS** Snouts at least somewhat spike shaped. Trunks moderately long. Tall vertebrae at modest downward flexure of aft tail supported a modest upper tail fin. Pelvis attached to vertebral column. Transitional anguilliform-carangiform swimmers.
**HABITAT** Coastal shallows.
**HABITS** Swimming performance good. Ambush and pursuit fishers of small and medium-sized game.

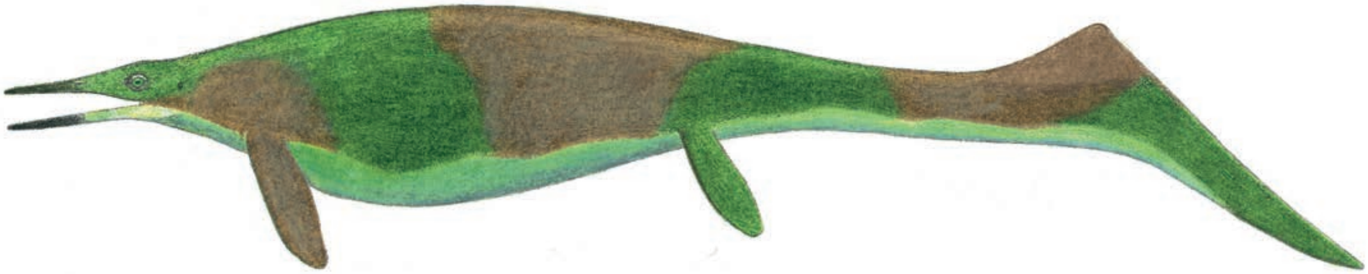
### *Utatsusaurus hataii*

**2.5 m (8 ft) TL, 45 kg (100 lb)**

**FOSSIL REMAINS** Skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Snout long and somewhat spike shaped, teeth very numerous and small. Flippers similar in size, distal flipper elements poorly ossified.
**AGE** Early Triassic.



*Utatsusaurus hataii*



**DISTRIBUTION AND FORMATIONS** Central Japan; Osawa.
**HABITAT** Continental shallows.

### *Parvinatator wapitiensis*

**1 m (3.3 ft) TL, 3 kg (6.5 lb)**

**FOSSIL REMAINS** Skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Snout spikelike, orbit very large, aft lower jaw massive, teeth moderate in number and fairly large. Distal flipper elements ossified, foreflipper swept back distally.
**AGE** Late Early or Middle Triassic.
**DISTRIBUTION AND FORMATIONS** British Columbia; Sulphur Mountain.
**HABITAT** Continental shallows.
**NOTES** Exact stratigraphic level of taxon not certain.

*Parvinatator wapitiensis*

## XINMINOSAURS

**SMALL ICHTHYOPTERYGIANS FROM THE MIDDLE TRIASSIC OF ASIA**

**ANATOMICAL CHARACTERISTICS** Midteeth form a flattened pavement. Trunks moderately long. Tall vertebrae at modest downward flexure of aft tail supported a modest upper tail fin. Pelvis attached to vertebral column. Transitional anguilliform-carangiform swimmers.
**HABITAT** Coastal shallows.
**HABITS** Swimming performance good. Mollusk crushers, also perhaps ambush and pursuit fishers of small and medium-sized game.
**NOTES** Absence from at least some other seas may reflect lack of sampling.

### *Xinminosaurus catactes*

**2.3 m (7.5 ft) TL, 30 kg (65 lb)**

**FOSSIL REMAINS** Disrupted skull and skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Anterior jaws may be toothless. Distal paddle elements ossified, fore and aft paddles similarly small.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; upper Guanling.
**NOTES** Shared its habitat with *Largocephalosaurus*, *Sinosaurosphargis*, *Panzhousaurus*, *Wumengosaurus*, *Nothosaurus yangjuanensis*, *Barracudasauroides*.

## EOICHTHYOSAURS

**SMALL TO GIGANTIC ICHTHYOSAURIFORMES FROM THE EARLY TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**HABITAT** Coastal nearshore to deep oceans.
**HABITS** Swimming performance good to extremely high. Ambush and/or pursuit fishers and hunters of small to big game, some crushers.

## GRIPPIIDS

### SMALL EOICHTHYOSAURS FROM THE MIDDLE TRIASSIC OF THE NORTHERN HEMISPHERE

**ANATOMICAL CHARACTERISTICS** Heads rather short, snouts short, deep aft because orbits very large. Trunks moderately long. Tall vertebrae at modest downward flexure of aft tail supported a modest upper tail fin. Transitional anguilliform-carangiform swimmers.
**HABITAT** Coastal shallows.
**HABITS** Swimming performance good. Ambush and pursuit fishers of small game.
**NOTES** Grippiids show that truly marine swimmers evolved just a few million years after the P/T extinction.

### *Gulosaurus helmi*
**Adult size uncertain**

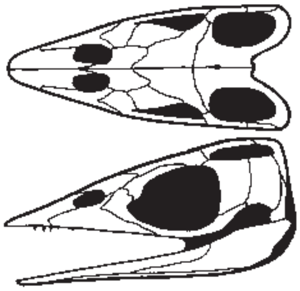
**FOSSIL REMAINS** Skull and partial skeleton, juvenile.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Triassic; Olenekian.
**DISTRIBUTION AND FORMATIONS** British Columbia; middle Sulphur Mountain.
**HABITAT** Continental shallows.

### *Grippia longirostris*
**1.5 m (5 ft) TL, 8 kg (18 lb)**

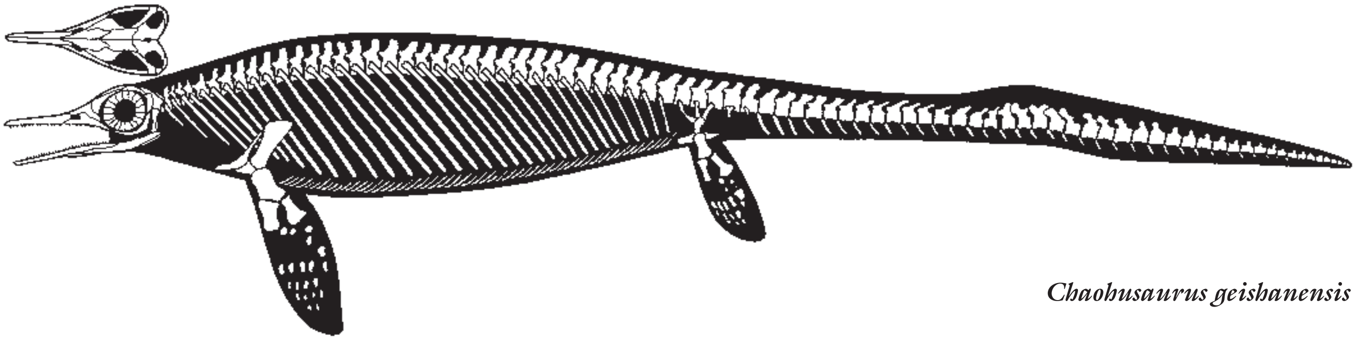
**FOSSIL REMAINS** Partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Snout not slender, only a few small teeth near front of upper jaw.
**AGE** Early Triassic; late Olenekian.
**DISTRIBUTION AND FORMATIONS** Svalbard; lower Vikinghogda.
**HABITAT** Open continental shelf, polar.

### *Chaohusaurus zhangjiawanensis*
**0.9 m (3 ft) TL, 1.8 kg (4 lb)**

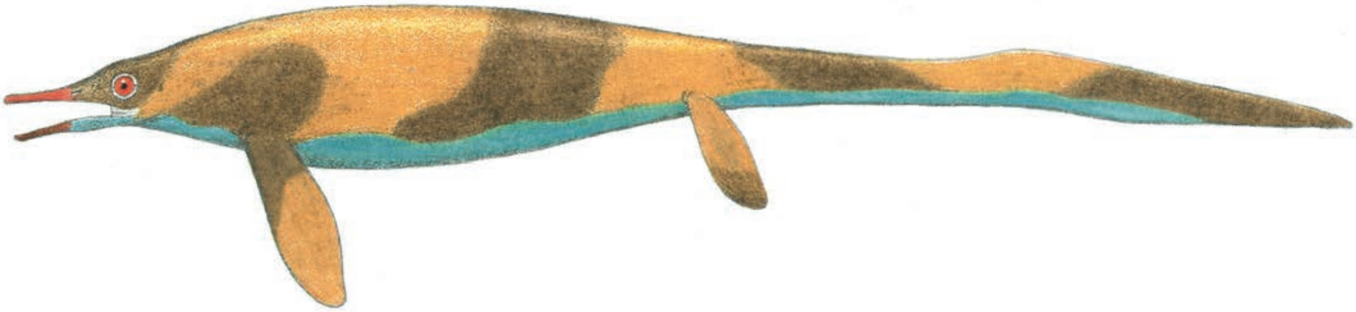
**FOSSIL REMAINS** Two partial skulls and complete skeletons, severely flattened top to bottom, including probable fetuses.
**ANATOMICAL CHARACTERISTICS** Foreflipper large, much larger than aft, distal elements in both poorly ossified.
**AGE** Early Triassic; late Olenekian.
**DISTRIBUTION AND FORMATIONS** Eastern China; upper Jialingjiang.
**HABITAT** Continental shallows.
**NOTES** Presence of small apparent fetal remains in and exiting adult skeleton indicates live birth, headfirst. Shared its habitat with *Nanchangosaurus*, *Eohupehsuchus*, *Hupehsuchus*, *Parahupehsuchus*, *Eretmorhipis*.



*Grippia longirostris*



*Chaohusaurus geishanensis*



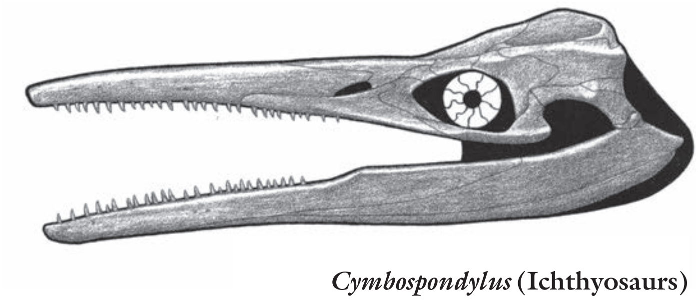
### *Chaohusaurus geishanensis*

**0.9 m (3 ft) TL, 1.8 kg (4 lb)**

FOSSIL REMAINS A number of skulls and skeletons.
ANATOMICAL CHARACTERISTICS Snout slender, teeth fairly numerous, small. Foreflipper large, much larger than aft, distal elements in both poorly ossified.
AGE Middle Triassic; late Olenekian.
DISTRIBUTION AND FORMATIONS Eastern China; upper Nanlinghu.
HABITAT Continental shallows.
NOTES May include *C. chaoxianensis* and *C. brevifemoralis*. Shared its habitat with *Majiashanosaurus*, *Sclerocormus.*

## ICHTHYOSAURS

**SMALL TO GIGANTIC EOICHTHYOSAURS FROM THE EARLY TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL**



***Cymbospondylus* (Ichthyosaurs)**

ANATOMICAL CHARACTERISTICS Pelvis not attached to vertebral column, upper pelvic element a splint. Flippers better developed, with shortened lower arm and increased distal complexes.
HABITAT Coastal nearshore to deep oceans.
HABITS Swimming performance good to extremely high. Ambush and/or pursuit fishers and hunters of small to big game, some crushers.
NOTES Includes the largest and the fastest sea reptiles.

## CYMBOSPONDYLIDS

**LARGE TO GIGANTIC ICHTHYOSAURS FROM THE EARLY TO MIDDLE TRIASSIC OF NORTH AMERICA AND EUROPE**

ANATOMICAL CHARACTERISTICS Heads solidly constructed, snouts long, temporal region greatly expanded. Trunks elongated and very shallow. Tall vertebrae at modest downward flexure of aft tail supported a modest upper tail fin. Distal flipper elements poorly ossified. Hydrodynamically well-streamlined, transitional anguilliform-carangiform swimmers.
HABITAT Coastal to deep ocean.
HABITS Swimming performance good to very good. Pursuit fishers and hunters of medium-sized and especially big game.
NOTES First large, big-game-hunting marine reptiles. Placement of many genera in family questionable. Absence from at least some other seas may reflect lack of sufficient sampling.

### *Quasianosteosaurus vikinghoegdai*

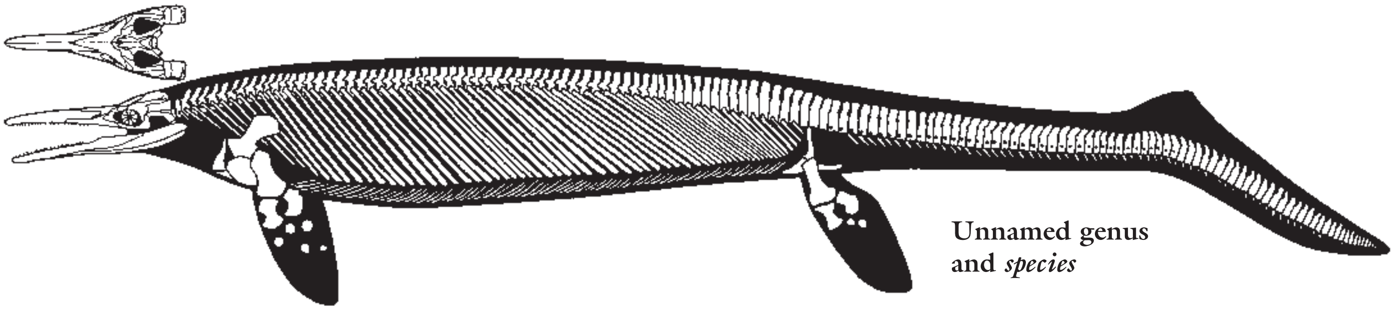
**5 m (16 ft) TL, 500 kg (1,000 lb)**

FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Triassic; late Olenekian.
DISTRIBUTION AND FORMATIONS Svalbard; upper Sticky Keep.
HABITAT Open continental shelf, polar.
NOTES Earliest known large ichthyosaur and sea reptile.

### Unnamed genus and species

**9.6 m (31 ft) TL, 2.8 tonnes**

FOSSIL REMAINS Nearly complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Head medium sized, moderately broad, snout very long, robust, teeth numerous, fairly small.
AGE Middle Triassic; late Anisian.



**Unnamed genus and *species***

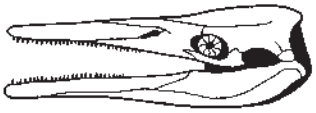
Unnamed genus and *species*

**DISTRIBUTION AND FORMATIONS** Nevada; upper Favret.
**HABITAT** Continental shelf.
**HABITS** Swimming performance good.
**NOTES** Has long been *Cymbospondylus petrinus*, but original specimens too fragmentary to base a genus and species on. *C. nichollsi* may be young of this or other species from the same level of the Favret Formation. A partial skull may be an individual 14 m (46 ft) long. Shared its habitat with *Augustasaurus*, *Phalarodon*, *Thalattoarchon*, unnamed genus *duelferi*, unnamed genus *youngorum*.

### Unnamed genus *youngorum*

**14 m (42 ft) TL, 9 tonnes**

**FOSSIL REMAINS** Skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head moderately broad, snout long, robust, teeth numerous, fairly small.
**AGE** Middle Triassic; late Anisian.
**DISTRIBUTION AND FORMATIONS** Nevada; upper Favret.
**HABITAT** Continental shelf.
**NOTES** Placement in same genus as prior unnamed taxon incorrect because of very different shoulder girdles, may not be member of same family. Earliest known gigantic sea reptile, but claim of mass of 45 tonnes is greatly exaggerated.



unnamed genus *youngorum*

### Unnamed genus *duelferi*

**5 m (17 ft) TL, 400 kg (900 lb)**

**FOSSIL REMAINS** Skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head moderately broad, snout long, robust, teeth fairly large.
**AGE** Middle Triassic; late Anisian.
**DISTRIBUTION AND FORMATIONS** Nevada; upper Favret.
**HABITAT** Continental shelf.
**NOTES** Placement in same genus as above unnamed genus and species incorrect because of very different shoulder girdles, may not be member of same family.

### Unnamed genus *buchseri*

**8 m (26 ft) TL, 1.5 tonnes**

**FOSSIL REMAINS** Majority of skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Foreflipper fairly large.
**AGE** Middle Triassic; latest Anisian and/or earliest Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland; Besano.
**HABITAT** Island archipelago shallows.
**NOTES** Original placement in *Cymbospondylus* incorrect, nearly identical shoulder girdles indicate is close relative of above unnamend genus and species. Shared its habitat with *Askeptosaurus*, *Helveticosaurus*, *Paraplacodus*, *Serpianosaurus*, *Wimanius*, *Besanosaurus*, *Mixosaurus cornalianus*, *M.? kuhnschnyderi*.

### *Thalattoarchon saurophagis*

**8.6 m (28 ft) TL, 2 tonnes**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head robustly constructed, teeth large.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Nevada; upper Favret.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Augustasaurus*, unnamed genus and species, unnamed genus *duelferi*, unnamed genus *youngorum*, *Phalarodon*. First known archpredatory marine reptile.

### *Phantomosaurus neubigi*

**6 m (20 ft) TL, 700 kg (1,500 lb)**

**FOSSIL REMAINS** Partial skull and skeleton, badly damaged.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Middle Triassic; late Anisian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; upper Muschelkalk.

**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Placodus*, *Nothosaurus mirablis*, *N. giganteus*, *Pistosaurus.*

## MIXOSAURIDS

**SMALL TO MEDIUM-SIZED ICHTHYOSAURS FROM THE MIDDLE TO LATE TRIASSIC OF THE NORTHERN HEMISPHERE**

**ANATOMICAL CHARACTERISTICS** Heads large, snouts long and slender. Tall vertebrae at modest downward flexure of aft tail supported a modest upper tail fin. Distal flipper elements ossified, foreflippers much larger than aft. Dorsal fin may be present. Transitional anguilliform-carangiform swimmers.
**HABITAT** Coastal shallows.
**HABITS** Swimming performance good. Ambush and pursuit fishers of small game, some crushers.
**NOTES** A poorly preserved dorsal fin may indicate presence on at least some basal ichthyosaurs. Absence from Southern Hemisphere may reflect lack of sufficient sampling.

### *Contectopalatus atavus*

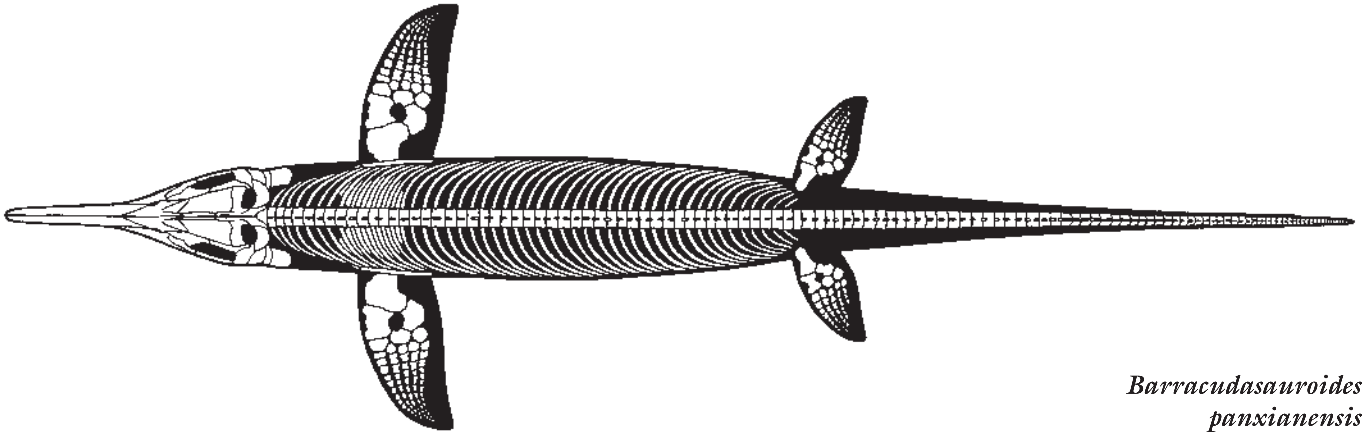
**5 m (16 ft) TL, 400 kg (900 lb)**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Head possibly very narrow, tall subtriangular midline crest atop temporal region, teeth medium sized.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; lower Muschelkalk.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Cyamodus tarnowitzensis*, *Tholodus.*

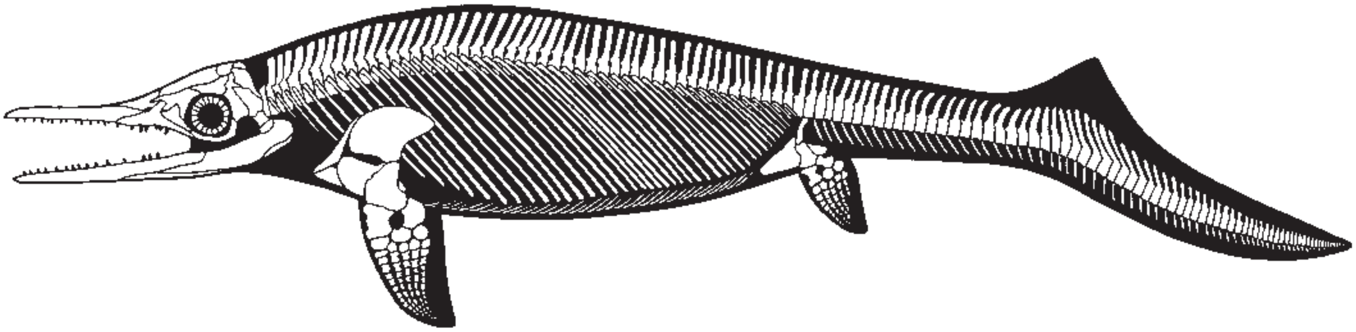
### *Barracudasauroides panxianensis*

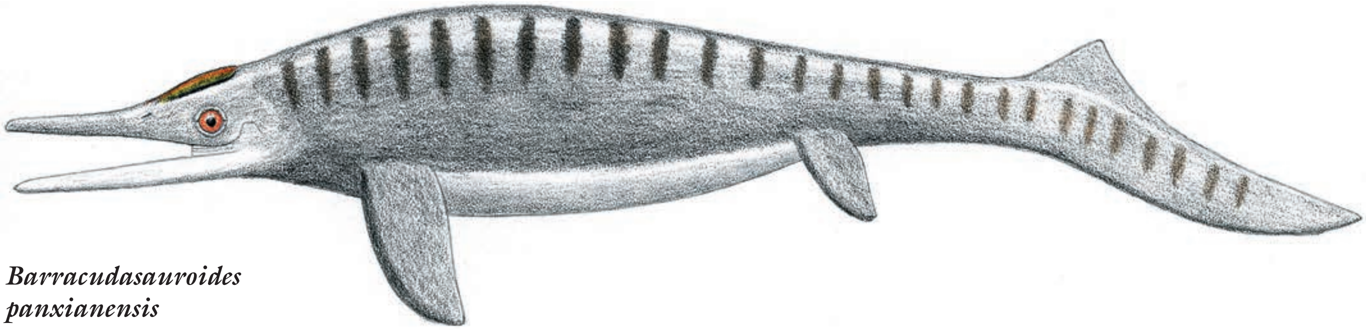
**1.23 m (4 ft) TL, 8 kg (18 lb)**

**FOSSIL REMAINS** Three nearly complete or partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head robust, orbits very large, low midline crest atop temporal region, teeth moderate in number and robust.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; upper Guanling.
**HABITAT** Continental shallows.
**HABITS** Hunted larger game.

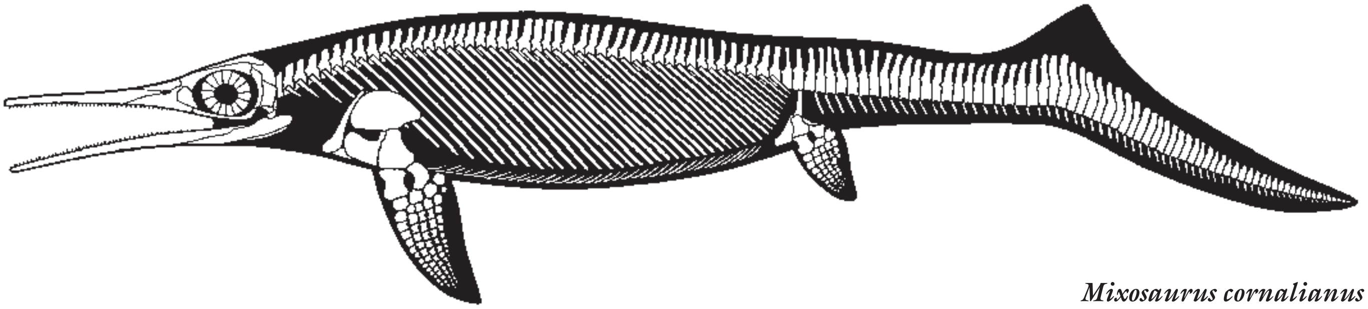


***Barracudasauroides panxianensis***

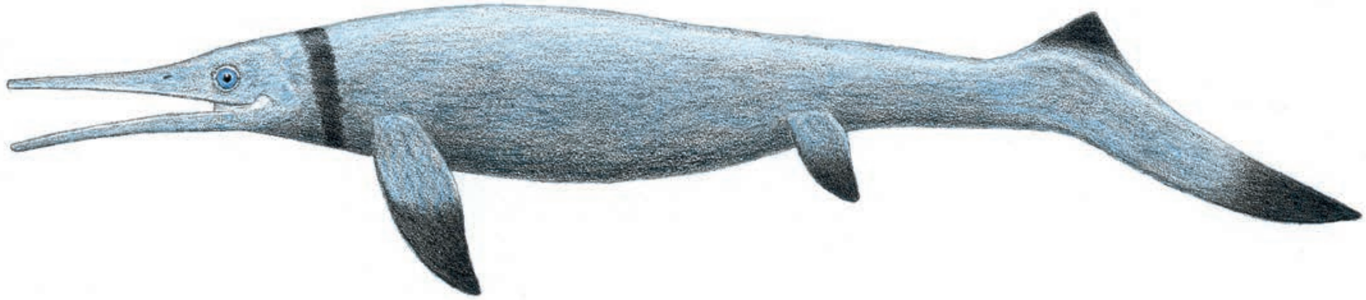




*Barracudasauroides panxianensis*



*Mixosaurus cornalianus*



**NOTES** Shared its habitat with *Largocephalosaurus*, *Sinosaurosphargis*, *Panzhousaurus*, *Wumengosaurus*, *Nothosaurus yangjuanensis*, *Xinminosaurus*.

### *Mixosaurus cornalianus*

**1.85 m (6 ft) TL, 24 kg (50 lb)**

**FOSSIL REMAINS** Numerous skulls and skeletons, including possible fetuses, soft tissues.
**ANATOMICAL CHARACTERISTICS** Head not robustly constructed, snout quite long and slender, no crest atop temporal region, teeth numerous and small.
**AGE** Middle Triassic; latest Anisian and earliest Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland-Italy border; Besano.
**HABITAT** Island archipelago shallows.
**NOTES** The classic early small ichthyosaur. Possible fetuses may indicate live birth. Dorsal fin may be present on a specimen. Shared its habitat with *Askeptosaurus*, *Helveticosaurus*, *Paraplacodus*, *Serpianosaurus*, *Wimanius*, *Besanosaurus*, unnamed genus *buchseri*, *M.? kuhnschnyderi*.

### *Mixosaurus* (or *Sangiorgiosaurus*) *kuhnschnyderi*

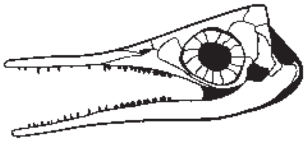
**1 m (3.3 ft) TL, 4 kg (9 lb)**

**FOSSIL REMAINS** Skull and skeletons, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** A few aft teeth are stout knobs.
**AGE** Middle Triassic; latest Anisian and earliest Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland-Italy border; Besano.
**HABITAT** Island archipelago shallows.
**HABITS** Also crushed small mollusks.

### *Phalarodon fraasi*

**1.25 m (4 ft) TL, 7 kg (15 lb)**

**FOSSIL REMAINS** A few skulls and skeletons, complete to partial.
**ANATOMICAL CHARACTERISTICS** Snout fairly long and shallow, orbits very large, tips of jaws toothless, front teeth small robust spikes, aft teeth somewhat larger blunt knobs.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Nevada; upper Favret, lower Prida.
**HABITAT** Continental shallows.
**HABITS** Also crushed mollusks.
**NOTES** Probably includes *P. callawayi*. Is not certain whether this species had a midline aft head crest. Shared its habitat with *Augustasaurus*, unnamed genus and species, unnamed genus *duelferi*, unnamed genus *youngorum*, *Thalattoarchon*.

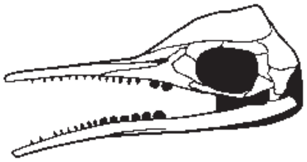


*Phalarodon fraasi*

### *Phalarodon? nordenskioeldii*

**1.5 m (5 ft) TL, 10 kg (20 lb)**

**FOSSIL REMAINS** A few partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Snout fairly long and shallow, orbits very large; large, long, subtriangular midline crest atop temporal region, tips of jaws toothless, front teeth small robust spikes, aft teeth markedly larger blunt knobs.
**AGE** Late Triassic; early Carnian.
**DISTRIBUTION AND FORMATIONS** Svalbard; Tschermakfjellet.
**HABITAT** Open continental shelf, polar.
**HABITS** Specialized for crushing mollusks.
**NOTES** Whether this species belongs in the much earlier and distinctive *Phalarodon* is problematic.



*Phalarodon? nordenskioeldii*

### *Wimanius odontopalatus*

**1 m (3.3 ft) TL, 4 kg (9 lb)**

**FOSSIL REMAINS** Majority of skull.
**ANATOMICAL CHARACTERISTICS** Snout slender, orbits very large, aft skull deep, teeth numerous and rather small.
**AGE** Middle Triassic; latest Anisian and earliest Ladinian.
**DISTRIBUTION AND FORMATIONS** Switzerland-Italy border; Besano.
**HABITAT** Island archipelago shallows.
**NOTES** May be in its own family. Shared its habitat with *Askeptosaurus*, *Helveticosaurus*, *Paraplacodus*, *Serpianosaurus*, *Besanosaurus*, unnamed genus *buchseri*, *Mixosaurus cornalianus*, *M.? kuhnschnyderi*.

## TORETOCNEMIDS

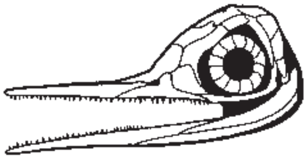
**SMALL TO LARGE ICHTHYOSAURS FROM THE MIDDLE TO LATE TRIASSIC OF NORTH AMERICA AND ASIA**

**ANATOMICAL CHARACTERISTICS** Heads large, snouts long and slender, orbits very large. Aft head deep, teeth numerous and small. Tall vertebrae at modest downward flexure of aft tail supported a modest upper tail fin. Distal flipper elements ossified, flippers fairly large, fore not much larger than aft. Transitional anguilliform-carangiform swimmers.
**HABITAT** Coastal shallows.
**HABITS** Swimming performance good. Ambush and pursuit fishers of small game.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

### *Qianichthyosaurus xingyiensis*

**1.3 m (4 ft) TL, 10 kg (20 lb)**

**FOSSIL REMAINS** Two skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Middle Triassic; late Ladinian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; lower Falang.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with *Keichousaurus*, *Nothosaurus youngi*, *Lariosaurus*, *Qianxisaurus*, *Wangosaurus*. May be the direct ancestor of *Qianichthyosaurus zhoui*.



*Qianichthyosaurus xingyiensis*

### *Qianichthyosaurus zhoui*

**2 m (6.5 ft) TL, 35 kg (75 lb)**

**FOSSIL REMAINS** Numerous skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Late Triassic; Carnian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; upper Falang.
**HABITAT** Continental nearshore. Shared its habitat with *Anshunsaurus huangguoshuensis*, *Miodentosaurus*, *Yunguisaurus*, *Guanlingsaurus*, *Guizhouichthyosaurus*, unnamed genus *orientalis*.

### *Toretocnemus californicus*

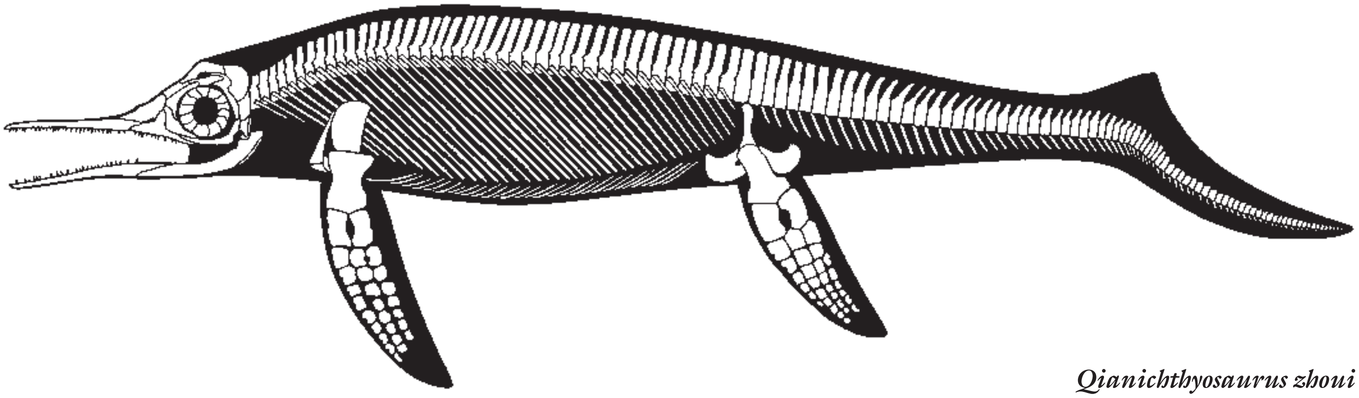
**2 m (6.5 ft) TL, 35 kg (75 lb)**

**FOSSIL REMAINS** Skeleton lacking skull.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Triassic; Carnian.
**DISTRIBUTION AND FORMATIONS** Northern California; Hosselkus Limestone.
**HABITAT** Continental shallows.
**NOTES** May include *T. zitelli*.

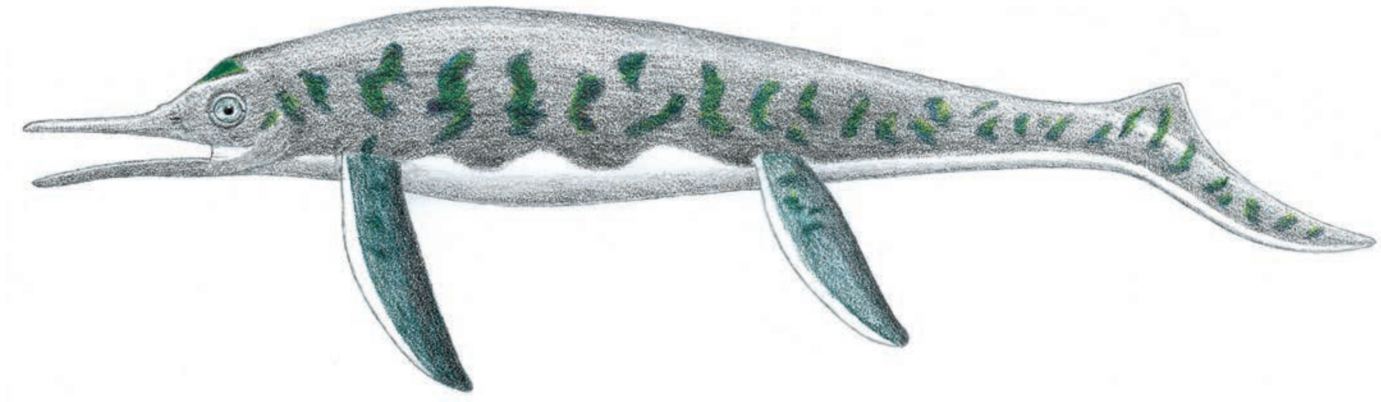
### *Besanosaurus leptorhynchus*

**6 m (20 ft) TL, 1 tonne**

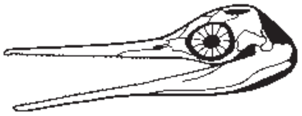
**FOSSIL REMAINS** A few specimens from nearly complete to partial skull and skeleton, other skeleton severely disrupted, and partial probable fetus.
**ANATOMICAL CHARACTERISTICS** As for group.



*Qianichthyosaurus zhoui*



**AGE** Middle Triassic; latest Anisian and earliest Ladinian.
**DISTRIBUTION AND FORMATIONS** Northern Italy; Besano.
**HABITAT** Continental coastal.
**NOTES** Includes *Mikadocephalus.* Shared its habitat with *Askeptosaurus*, *Helveticosaurus*, *Paraplacodus*, *Serpianosaurus*, *Wimanius*, unnamed genus *buchseri*, *Mixosaurus cornalianus*, *M.? kuhnschnyderi*.



*Besanosaurus leptorhynchus*

## MEGAMARINASAURIDS

### GIGANTIC ICHTHYOSAURS FROM THE LATE TRIASSIC OF NORTH AMERICA

**ANATOMICAL CHARACTERISTICS** Trunks shallow, downward flexure of aft tail modest. Distal flipper elements probably unossified. Transitional anguilliform-carangiform swimmers.

**NOTES** Usually considerd shastasaurids, but differences in shoulder girdle indicate otherwise. Length of snout and presence/absence of teeth not known. Estimates that fragmentary remains indicate that some shastasaurs reached 26 m (85 ft) and the mass of blue whales are highly exaggerated. Absence from at least some other seas may reflect lack of sufficient sampling.

### Unnamed genus *sikanniensis*

**16.6–17.9 m (54–59 ft) TL, 16 tonnes**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head very large.
**AGE** Late Triassic; middle Norian.
**DISTRIBUTION AND FORMATIONS** British Columbia; upper Pardonet.
**HABITAT** Continental coastal.
**NOTES** Belongs to neither much earlier and significantly different genus *Shastasaurus*, nor earlier and very different *Shonisaurus*, both of which this species has been placed in. Shared its habitat with *Macgowania*, *Hudsonelpidia*. The longest and most massive known sea reptile—or nondinosaur "reptile"—but greatly exaggerated claims of 21 m (70 ft) and over 80 tonnes stem from major misreadings of specimen measurements; uncertain total length depends in part on unknown length of snout.

## GUANLINGASAURIDS

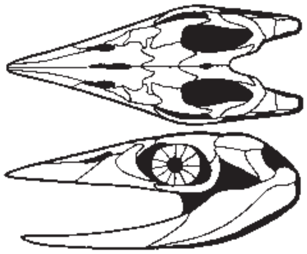
### LARGE ICHTHYOSAURS FROM THE LATE TRIASSIC OF NORTH AMERICA

**ANATOMICAL CHARACTERISTICS** Snouts short and triangular in top view, aft head broad, toothless. Trunks elongated and very shallow, downward flexure of aft tail slight. Distal flipper elements poorly ossified. Anguilliform swimmers.
**HABITS** May have been suction feeders. Swimming performance good.
**NOTES** Usually considerd shastasaurids, but differences in aft skull and shoulder girdle indicate otherwise. Feeding mode disputed. Absence from at least some other seas may reflect lack of sufficient sampling.

### *Guanlingsaurus liangae*

**8.3 (27 ft) TL, 2.5 tonnes**

**FOSSIL REMAINS** A few skulls and skeletons complete to nearly so, adult and juvenile, skeletons severely crushed top to bottom.
**ANATOMICAL CHARACTERISTICS** Trunk very shallow. Foreflippers long, hind flippers medium sized.
**AGE** Late Triassic; Carnian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; upper Falang.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with *Anshunsaurus huangguoshuensis*, *Miodentosaurus*, *Yunguisaurus*, *Qianichthyosaurus zhoui*, *Guizhouichthyosaurus*, unnamed genus *orientalis*.



*Guanlingsaurus liangae*

## SHONISAURIDS

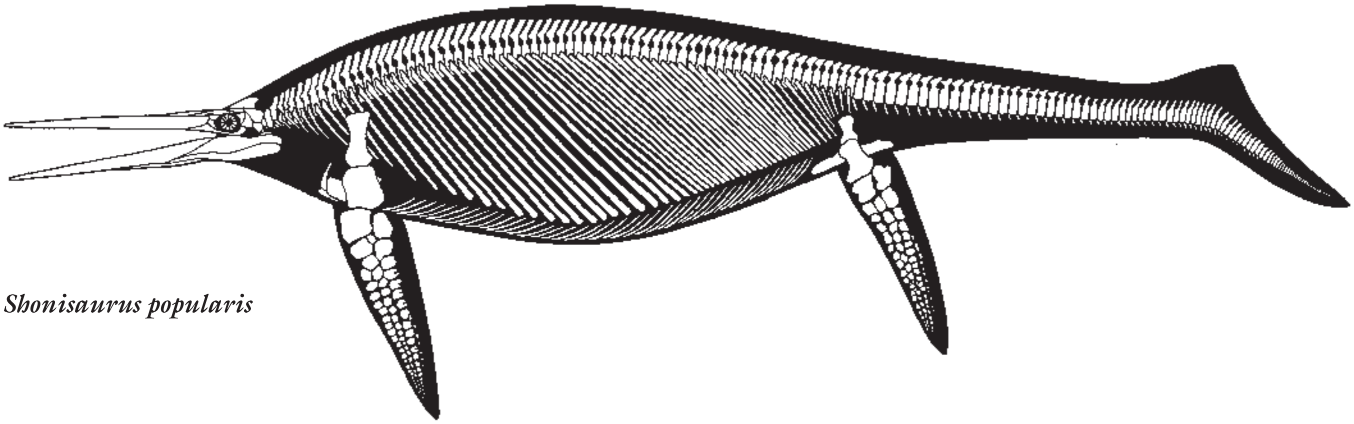
### GIGANTIC ICHTHYOSAURS FROM THE LATE TRIASSIC OF NORTH AMERICA

**ANATOMICAL CHARACTERISTICS** Heads long, shallow, not lightly built, snouts very long, orbits modest sized, lower jaw a little deeper than skull, teeth few, limited to front of jaws, small. Trunk fairly deep, downward flexure of aft tail modest.
**HABITS** Fishers of medium-sized game. Swimming performance moderate.
**NOTES** Not shastasaurids, as has been proposed.

### *Shonisaurus popularis*

**13.7 m (45 ft) TL, 16 tonnes**

**FOSSIL REMAINS** Over three dozen partial specimens.
**ANATOMICAL CHARACTERISTICS** Flippers fairly long, fore a little larger than aft, tail not large.
**AGE** Late Triassic; latest Carnian, possibly earliest Norian.
**DISTRIBUTION AND FORMATIONS** Nevada; middle Luning.
**HABITAT** Continental coastal.
**NOTES** The classic gigantic early ichthyosaur. Past restorations have tended to exaggerate the depth of the body, in part because the dorsal column was posed too straight while the ribs were oriented too vertically. May compete with longer but more slenderly built unnamed genus *sikanniensis* as most massive known pelagic reptile, but markedly higher size estimates for known specimens are unlikely.



*Shonisaurus popularis*

## SHASTASAURIDS

**LARGE TO GIGANTIC ICHTHYOSAURS FROM THE LATE TRIASSIC OF NORTH AMERICA AND ASIA**

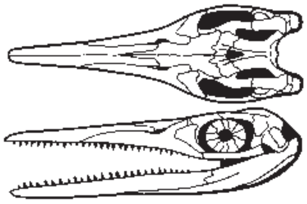
**ANATOMICAL CHARACTERISTICS** Snouts slender and pointed. Trunks elongated and shallow, tail fairly long, aft portion flexed more downward than usual in basal ichthyosaurs. Distal flipper elements ossified. Anguilliform swimmers.
**HABITAT** Coastal, possibly deeper ocean.
**HABITS** Swimming performance good.
**NOTES** Often considered to contain short-snouted, toothless guanlingsaurs, but differences in aft skull and shoulder girdle indicate otherwise. Absence from at least some other seas may reflect lack of sufficient sampling.

### *Shastasaurus pacificus*
**7 m (23 ft) TL, 1.5 tonnes**

**FOSSIL REMAINS** Partial skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Triassic; late Carnian.
**DISTRIBUTION AND FORMATIONS** Northern California; middle Hosselkus Limestone.
**HABITAT** Continental coastal.
**NOTES** Shared its habitat with *Nectosaurus*, *Thalattosaurus*, *Toretocnemus*?

### *Guizhouichthyosaurus tangae*
**10 m (33 ft) TL, 4 tonnes**

**FOSSIL REMAINS** A few complete and partial skulls, and skeletons severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Head elongated, snout very long and slender, robust, medium-sized teeth numerous and line most of jaws. Very high number of vertebrae, trunk very shallow. Flippers elongated, narrow.
**AGE** Late Triassic; Carnian.
**DISTRIBUTION AND FORMATIONS** Southeastern China; upper Falang.
**HABITAT** Continental nearshore.
**NOTES** Placement in shastasaurids not certain. Shared its habitat with *Anshunsaurus huangguoshuensis*, *Miodentosaurus*, *Yunguisaurus*, *Qianichthyosaurus zhoui*, *Guanlingsaurus*, unnamed genus *orientalis*.



***Guizhouichthyosaurus tangae***

## NONPARVIPELVIAN ICHTHYOSAUR MISCELLANEA

### *Californosaurus perrini*
**3 m (10 ft) TL, 100 kg (200 lb)**

**FOSSIL REMAINS** Majority of skeleton lacking skull.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Triassic; middle Carnian.
**DISTRIBUTION AND FORMATIONS** Northern California; lower Hosselkus Limestone.
**HABITAT** Continental coastal.
**HABITS** Swimming performance very good or excellent. Fisher of small to medium-sized game.

## PARVIPELVIANS

**SMALL TO GIGANTIC ICHTHYOSAURS FROM THE LATE TRIASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Fairly uniform. Heads narrow. Trunks compact, gastralia do not continue aft to pelvis. Slender vertebrae of aft tail sharply flexed downward, supported large, soft upper fin that was dorsal half of half-moon-shaped tail fluke. Shoulder and pelvic girdles reduced. Lower flipper elements ossified and reduced to blocks that formed part of a distal pavement flipper complex. Prominent dorsal fin present. Highly hydrodynamically streamlined, carangiform to thunniform swimmers.
**HABITAT** Coastal nearshore to deep oceans.
**HABITS** Swimming performance very good to extremely high. Pursuit fishers and hunters of small to big game.
**NOTES** The fastest fish- and cetacean-like sea reptile.

## MACGOWANIIDS

**MEDIUM-SIZED PARVIPELVIANS FROM THE LATE TRIASSIC OF NORTH AMERICA**

**ANATOMICAL CHARACTERISTICS** Snout rather short, fairly sharp tipped, teeth numerous, medium sized. Carangiform swimmers.
**HABITAT** Coastal.
**HABITS** Swimming performance very good. Fishers of small to medium-sized game.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

### *Macgowania janiceps*

**3.5 m (11 ft) TL, 125 kg (275 lb)**

**FOSSIL REMAINS** Skull and partial skeleton, badly damaged.
**ANATOMICAL CHARACTERISTICS** As for group.
**AGE** Late Triassic; middle Norian.
**DISTRIBUTION AND FORMATIONS** British Columbia; upper Pardonet.
**HABITAT** Continental coastal.
**NOTES** Shared its habitat with unnamed genus *sikanniensis*, *Hudsonelpidia*.

## HUDSONELPIDIDS

**SMALL PARVIPELVIANS FROM THE LATE TRIASSIC OF NORTH AMERICA**

**ANATOMICAL CHARACTERISTICS** Snout rather short, fairly sharp tipped. Flippers appear rather small. Carangiform swimmers.
**HABITAT** Coastal.
**HABITS** Swimming performance very good. Fishers of small to medium-sized game.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

### *Hudsonelpidia brevirostris*

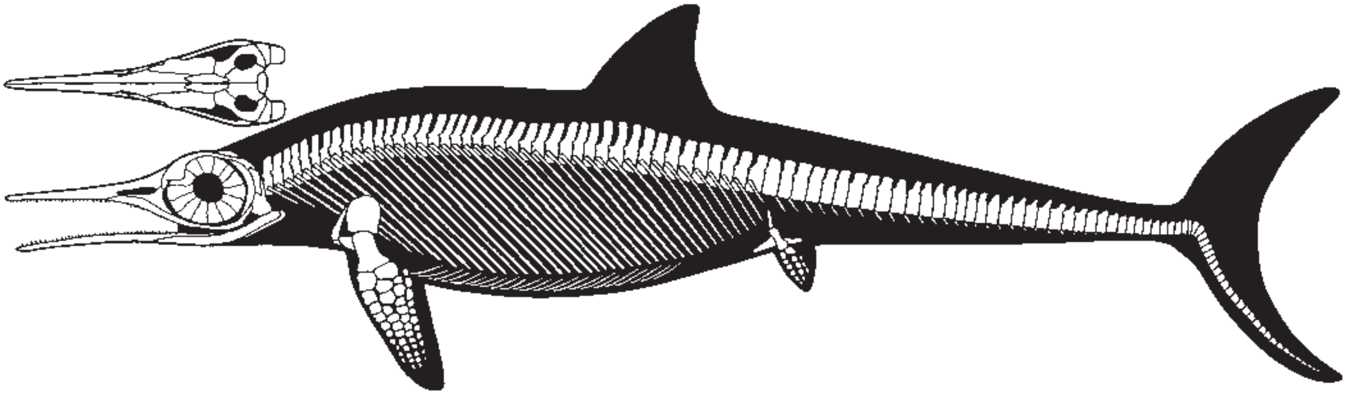
**Adult size uncertain**

**FOSSIL REMAINS** Skull and partial skeleton, badly damaged, probably juvenile.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Late Triassic; middle Norian.
**DISTRIBUTION AND FORMATIONS** British Columbia; upper Pardonet.
**HABITAT** Continental coastal.
**NOTES** Shared its habitat with unnamed genus *sikanniensis*, *Macgowania*.

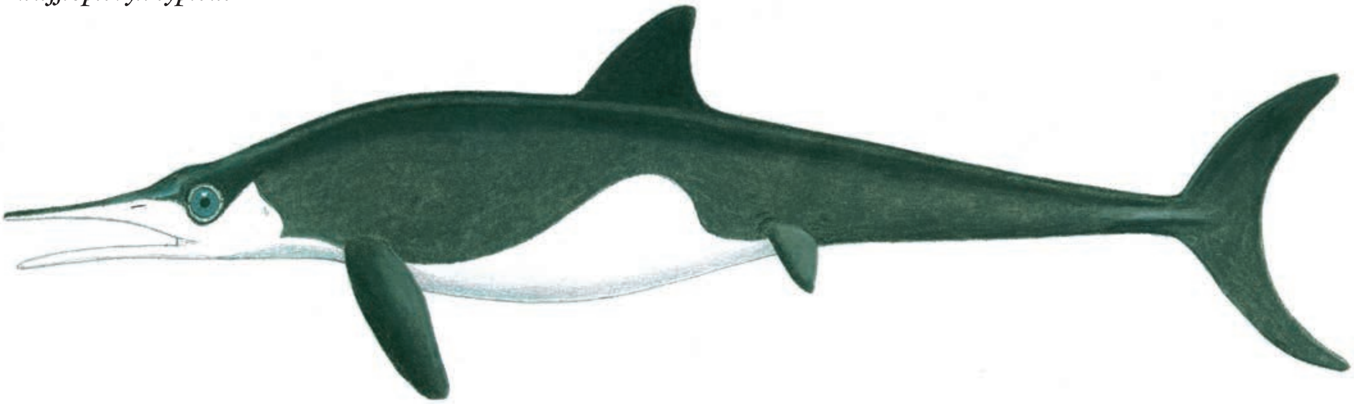
## HAUFFIOPTERYGIANS

**MEDIUM-SIZED PARVIPELVIANS FROM THE EARLY JURASSIC OF EUROPE**

**ANATOMICAL CHARACTERISTICS** Heads large, orbits extremely large, teeth numerous and small. Transitional carangiform-thunniform swimmers.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.
**HABITAT** Coastal.
**HABITS** Swimming performance very good. Fishers of small to medium-sized game.



*Hauffiopteryx typicus*



**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

### *Hauffiopteryx typicus*

**2.9 m (9.5 ft) TL, 110 kg (250 lb)**

**FOSSIL REMAINS** A number of complete skulls and skeletons, adult and juvenile.
**ANATOMICAL CHARACTERISTICS** Flippers medium sized, fore much larger than aft.
**AGE** Early Jurassic; late Pliensbachian to early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany, Switzerland, southern England; Posidonienschiefer, unnamed.
**NOTES** *H. altera* probably a juvenile of this species. Shared its habitat with *Meyerasaurus*, *Hauffiosaurus*, *Seeleyosaurus*, *Hydrorion*, unnamed genus *trigonodon*, *Suevoleviathan*, *Eurhinosaurus*, *Stenopterygius*, *Mystriosaurus*, *Platysuchus*, *Macrospondylus*, *Hauffiopteryx altera*.

## TEMNODONTOSAURIDS

**MEDIUM-SIZED TO GIGANTIC PARVIPELVIANS FROM THE EARLY JURASSIC OF EUROPE**

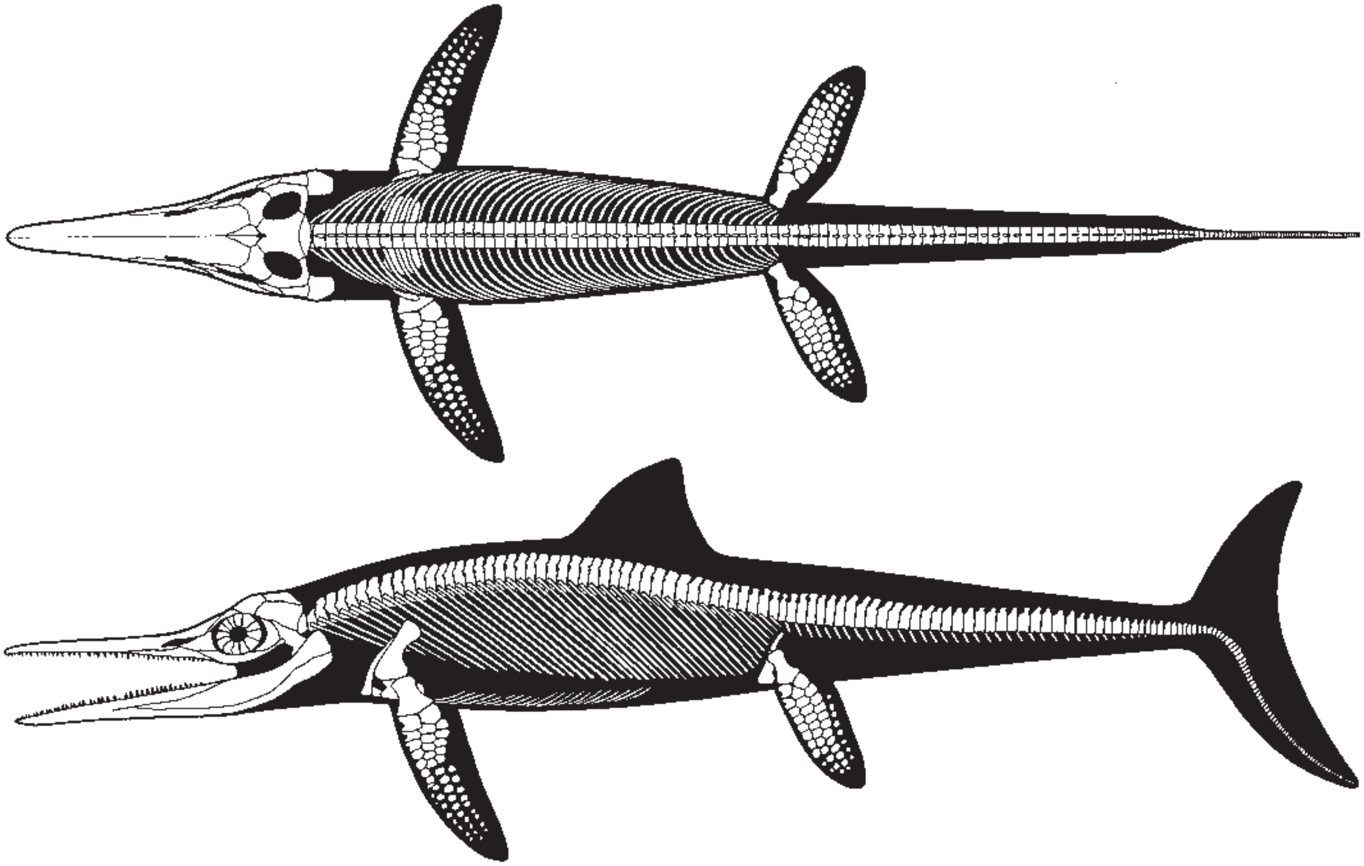
**ANATOMICAL CHARACTERISTICS** Heads large, massively constructed, snouts very long, robust, orbits very large, temporal region greatly expanded, teeth numerous. Trunks long. Tails fairly long. Flippers medium sized, fore considerably larger than aft, pavement elements often poorly ossified. Carangiform swimmers.
**HABITAT** Island archipelago shallows.
**HABITS** Swimming performance very good. Pursuit fishers and hunters of medium-sized and especially big game.
**NOTES** Had the largest eyes among known sea reptiles and possibly all animals. Absence from at least some other seas probably reflects lack of sufficient sampling.

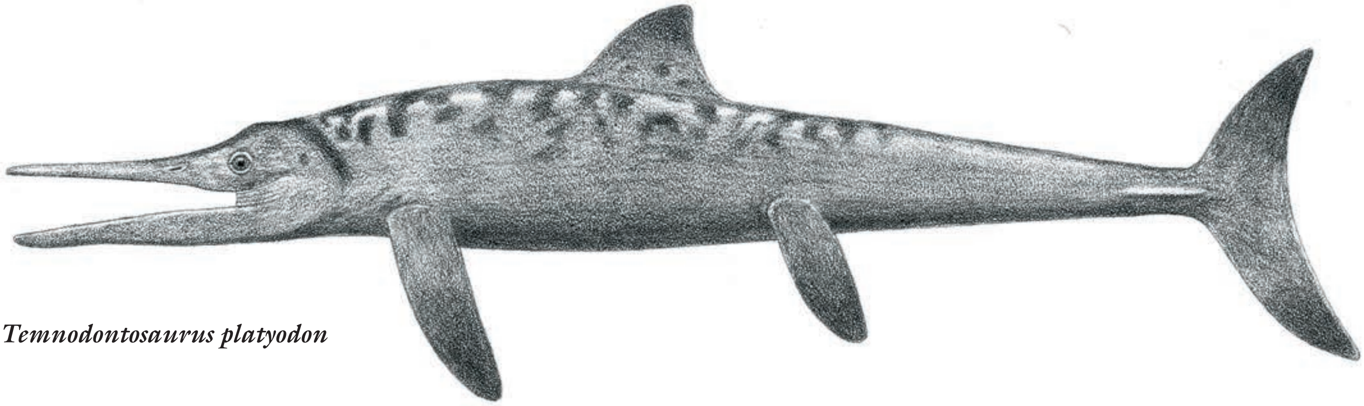
### *Temnodontosaurus platyodon*

**8.5 m (28 ft) TL, 2.6 tonnes**

**FOSSIL REMAINS** Skulls and skeletons, complete to partial, some juvenile.
**ANATOMICAL CHARACTERISTICS** Head very large, very massive including snout, teeth medium sized. Trunk fairly robust. Forefin somewhat larger than aft.

*Temnodontosaurus platyodon*





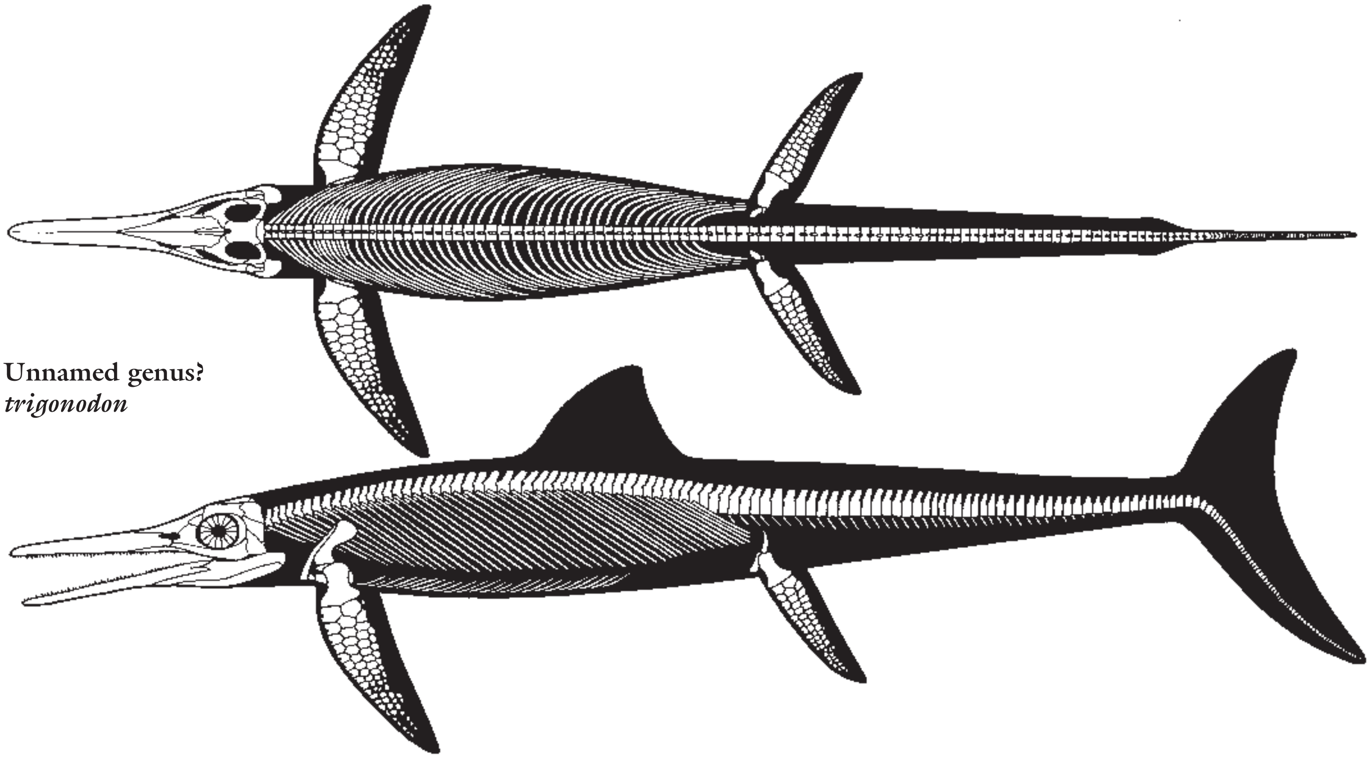
*Temnodontosaurus platyodon*

**AGE** Early Jurassic; late Hettangian and early Sinemurian.
**DISTRIBUTION AND FORMATIONS** Southern England; upper Blue Lias.
**HABITAT** Island archipelago shallows.
**NOTES** *T. risor* may be the juvenile of this species. Shared its habitat with *Excalibosaurus*, *Plesiosaurus*, *Eretmosaurus*, *Leptonectes tenuirostris*, *Ichthyosaurus communis*, unnamed genus *eurycephalus*.

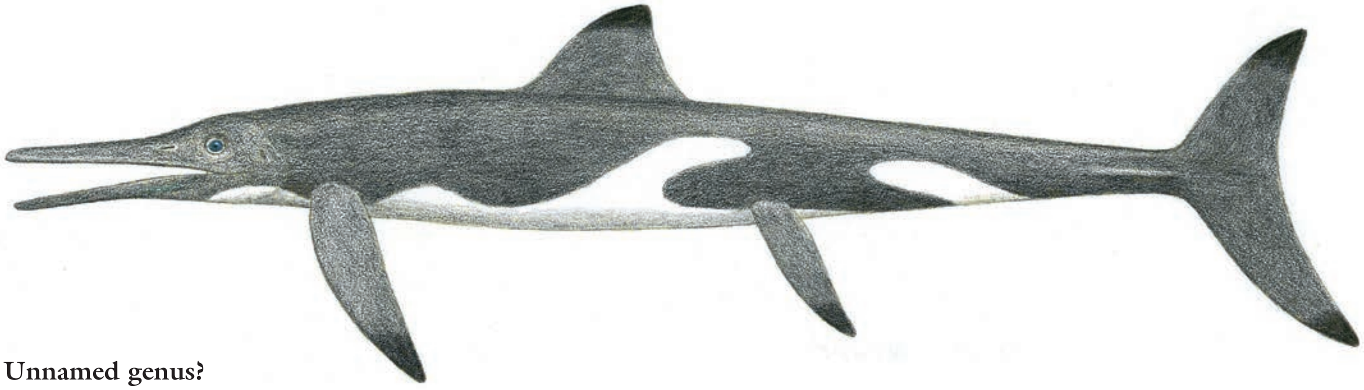
### Unnamed genus? *trigonodon*

**11.2 m (37 ft) TL, 4.5 tonnes**

**FOSSIL REMAINS** Skulls and skeletons, complete to partial.
**ANATOMICAL CHARACTERISTICS** Head not massive, snout rather slender, teeth small. Trunk shallower. Forefin somewhat larger than aft.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany, northern, eastern France, central England?; Posidonienschiefer, unnamed, Whitby Mudstone?
**NOTES** Placement in much earlier *Temnodontosaurus* is problematic, may be more than one species. Eye nearly 0.3 m (1 ft) across. Newly found complete English specimen 10 m (32.8 ft) long assigned to this species is not the largest. Shared its habitat with *Meyerasaurus*, *Hauffiosaurus*, *Seeleyosaurus*, *Hydrorion*, *Hauffiopteryx*,



**Unnamed genus?**
***trigonodon***



**Unnamed genus?**
***trigonodon***

*Suevoleviathan*, *Eurhinosaurus*, *Stenopterygius*, *Mystriosaurus*, *Platysuchus*, *Macrospondylus.*

### Unnamed genus? *crassimanus*

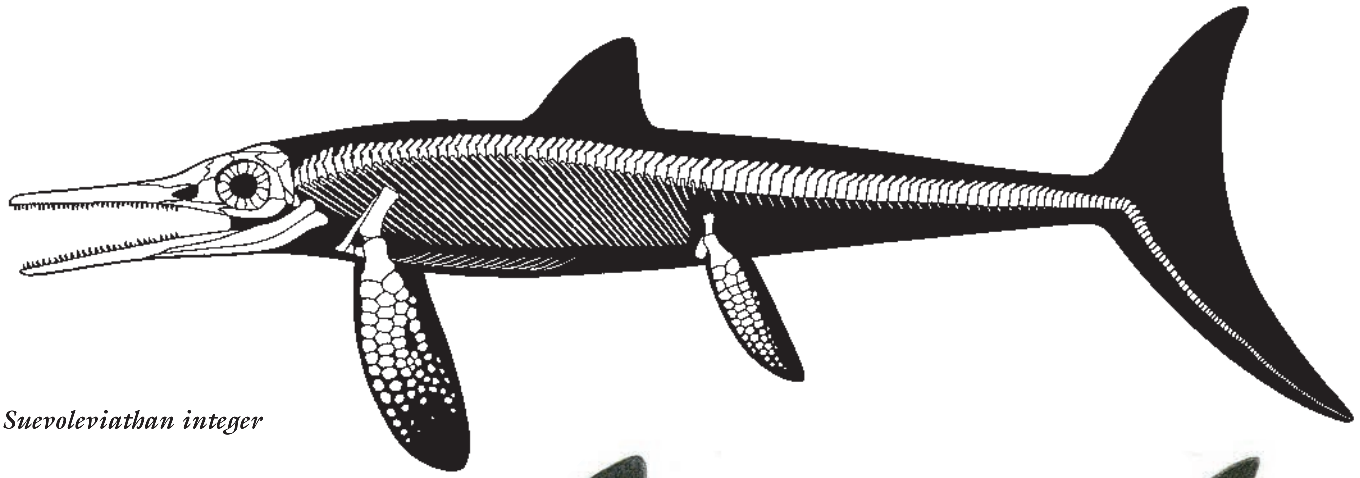
**9 m (30 ft) TL, 3 tonnes**

FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Head very large. Trunk rather slender. Flippers rather small, fore much larger than aft.
AGE Early Jurassic; middle Toarcian.
DISTRIBUTION AND FORMATIONS Northeastern England; middle Whitby Mudstone.
HABITAT Island archipelago shallows.
NOTES Placement in much earlier *Temnodontosaurus* is problematic, may not be same genus as *trigonodon*.

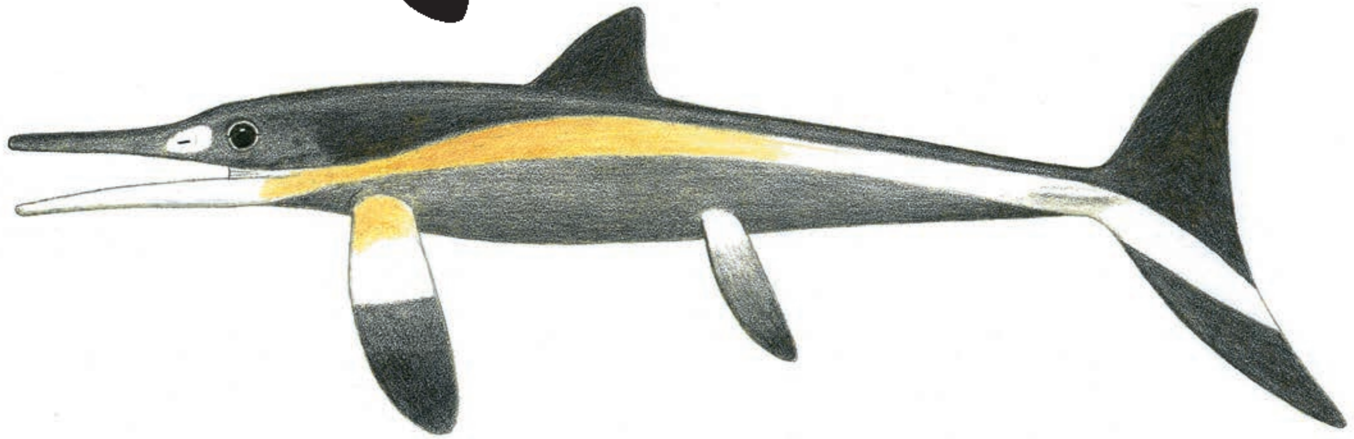
### *Suevoleviathan integer*

**3.9 m (13 ft) TL, 220 kg (480 lb)**

FOSSIL REMAINS Skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Head massive, teeth medium sized. Foreflipper large.
AGE Early Jurassic; early Toarcian.
DISTRIBUTION AND FORMATIONS Southern Germany; Posidonienschiefer.
NOTES *S. disinteger* is probably a growth stage of this species. Shared its habitat with *Meyerasaurus*, *Hauffiosaurus*, *Seeleyosaurus*, *Hydrorion*, *Hauffiopteryx*, unnamed genus *trigonodon*, *Eurhinosaurus*, *Stenopterygius*, *Mystriosaurus*, *Platysuchus*, *Macrospondylus.*



*Suevoleviathan integer*



## LEPTONECTIDS

### MEDIUM-SIZED TO GIGANTIC PARVIPELVIANS FROM THE EARLY JURASSIC OF EUROPE

ANATOMICAL CHARACTERISTICS Heads very long because snout is very elongated into a slender bill, orbits large, head not deep aft, teeth numerous and small. Trunks fairly compact but not deep. Foreflippers markedly larger than aft. Carangiform swimmers.
HABITAT Coastal to deep oceans.
HABITS Swimming performance high to very high. Fishers of medium-sized game.
NOTES Convergent with billfish, classic high-speed carangiform swimmers. Absence from at least some other seas probably reflects lack of sufficient sampling.

### *Leptonectes? solei*

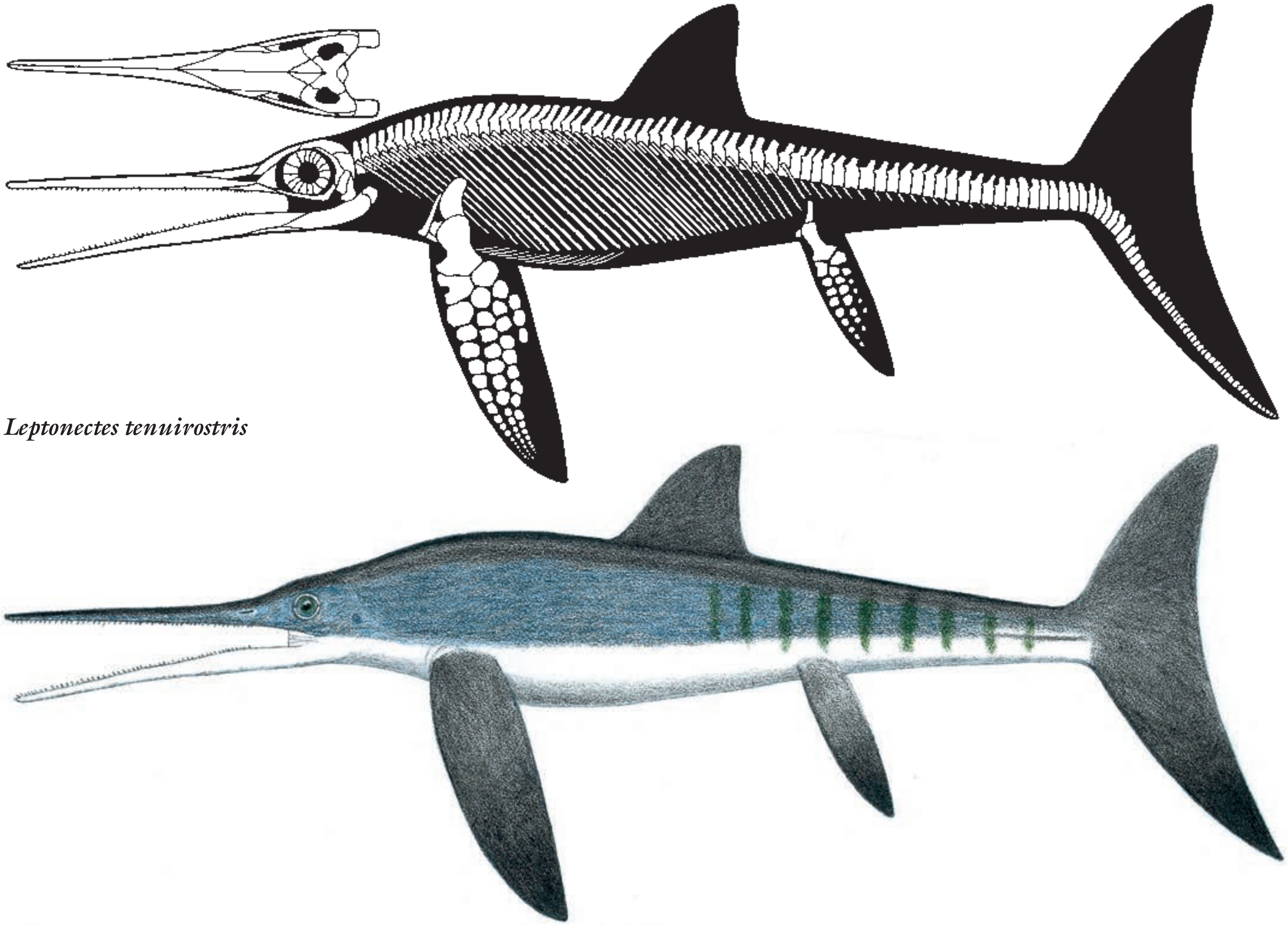
**7 m (23 ft) TL, 1.1 tonnes**

FOSSIL REMAINS Majority of two skulls and skeletons, severely flattened top to bottom.
ANATOMICAL CHARACTERISTICS Teeth highly numerous and small.
AGE Early Jurassic; early Pliensbachian.
DISTRIBUTION AND FORMATIONS Southern England; upper Charmouth Mudstone, upper Belemnite Marls.
HABITAT Island archipelago shallows.
NOTES *L. moorei* may be juvenile of this species. Shared its habitat with *Ichthyosaurus anningae*. May be the direct ancestor of *L. tenuirostris.*

### *Leptonectes tenuirostris*

**Adult size uncertain**

FOSSIL REMAINS Several skulls and skeletons, complete and partial.
ANATOMICAL CHARACTERISTICS Head large, upper and lower bills same length, teeth highly numerous and small. Tail rather short, lunate fluke very large. Foreflipper very large.
AGE Early Jurassic; early Sinemurian.
DISTRIBUTION AND FORMATIONS Southern England, Belgium; upper Blue Lias.
HABITAT Island archipelago shallows.
HABITS Highly maneuverable.
NOTES Whether adults reached 5 m (16 ft) is not certain. Shared its habitat with *Excalibosaurus*, *Plesiosaurus*, *Eretmosaurus*, *Temnodontosaurus*, *Ichthyosaurus communis*, unnamed genus *eurycephalus.*



*Leptonectes tenuirostris*

### *Leptonectes* unnamed species

**Adult size uncertain**

**FOSSIL REMAINS** Skull, probably juvenile.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Jurassic; late Pliensbachian.
**DISTRIBUTION AND FORMATIONS** Switzerland; unnamed.
**HABITAT** Island archipelago shallows.
**NOTES** Placement in much earlier *L. tenuirostris* highly problematic.

### *Wahlisaurus massare*

**Adult size uncertain**

**FOSSIL REMAINS** Skull and partial skeleton, possibly juvenile.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Jurassic; early Hettangian.
**DISTRIBUTION AND FORMATIONS** Central England; middle Scunthorpe Mudstone.
**HABITAT** Island archipelago shallows.

### Unnamed genus *nuertingensis*

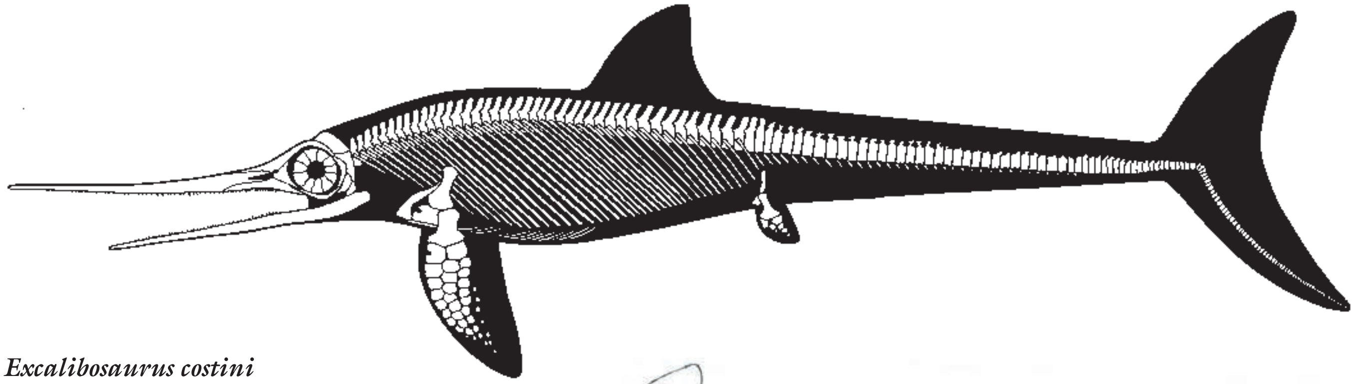
**10 m (33 ft) TL, 3 tonnes**

**FOSSIL REMAINS** Nearly complete skull and skeleton, severely flattened top to bottom, partial juvenile remains.
**ANATOMICAL CHARACTERISTICS** Upper jaw slightly longer than lower.
**AGE** Early Jurassic; middle Toarcian.
**DISTRIBUTION AND FORMATIONS** Eastern France; unnamed.
**HABITAT** Island archipelago shallows.
**NOTES** Slender snout indicates does not belong to *Temnodontosaurus*, *azerguensis* may be the juvenile of *nuertingensis*.

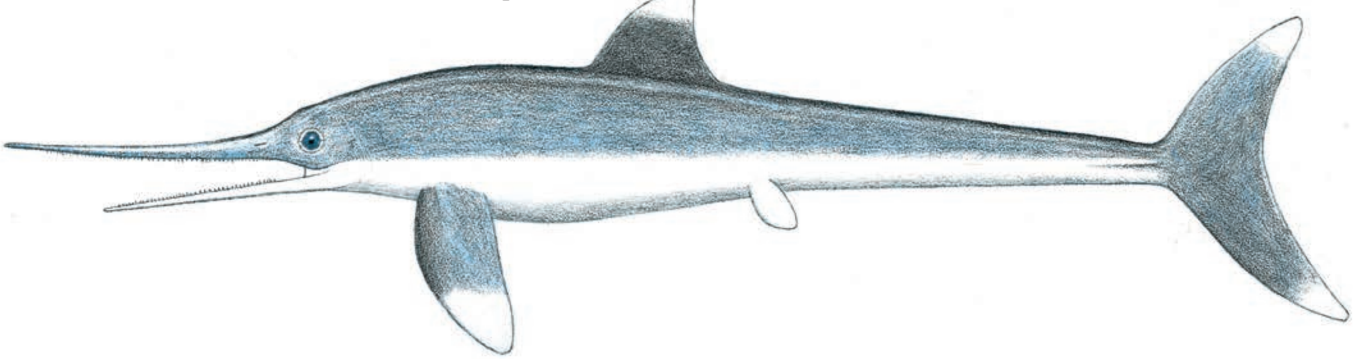
### *Excalibosaurus costini*

**6 m (20 ft) TL, 550 kg (1,200 lb)**

**FOSSIL REMAINS** Two skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Upper bill elongated into a slender sword much longer than lower.
**AGE** Early Jurassic; early Sinemurian.



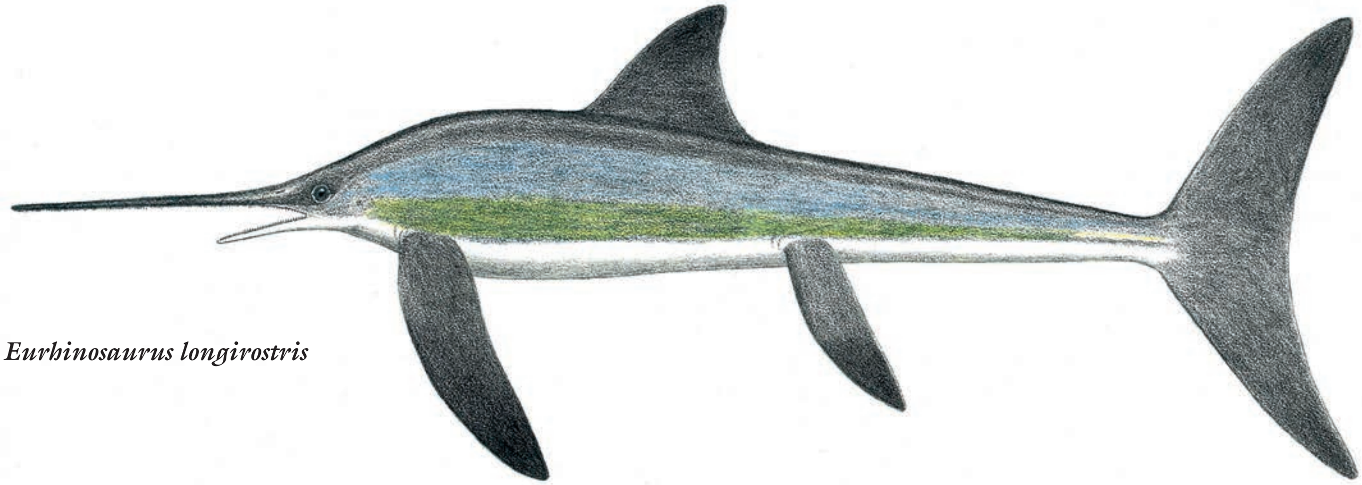
*Excalibosaurus costini*



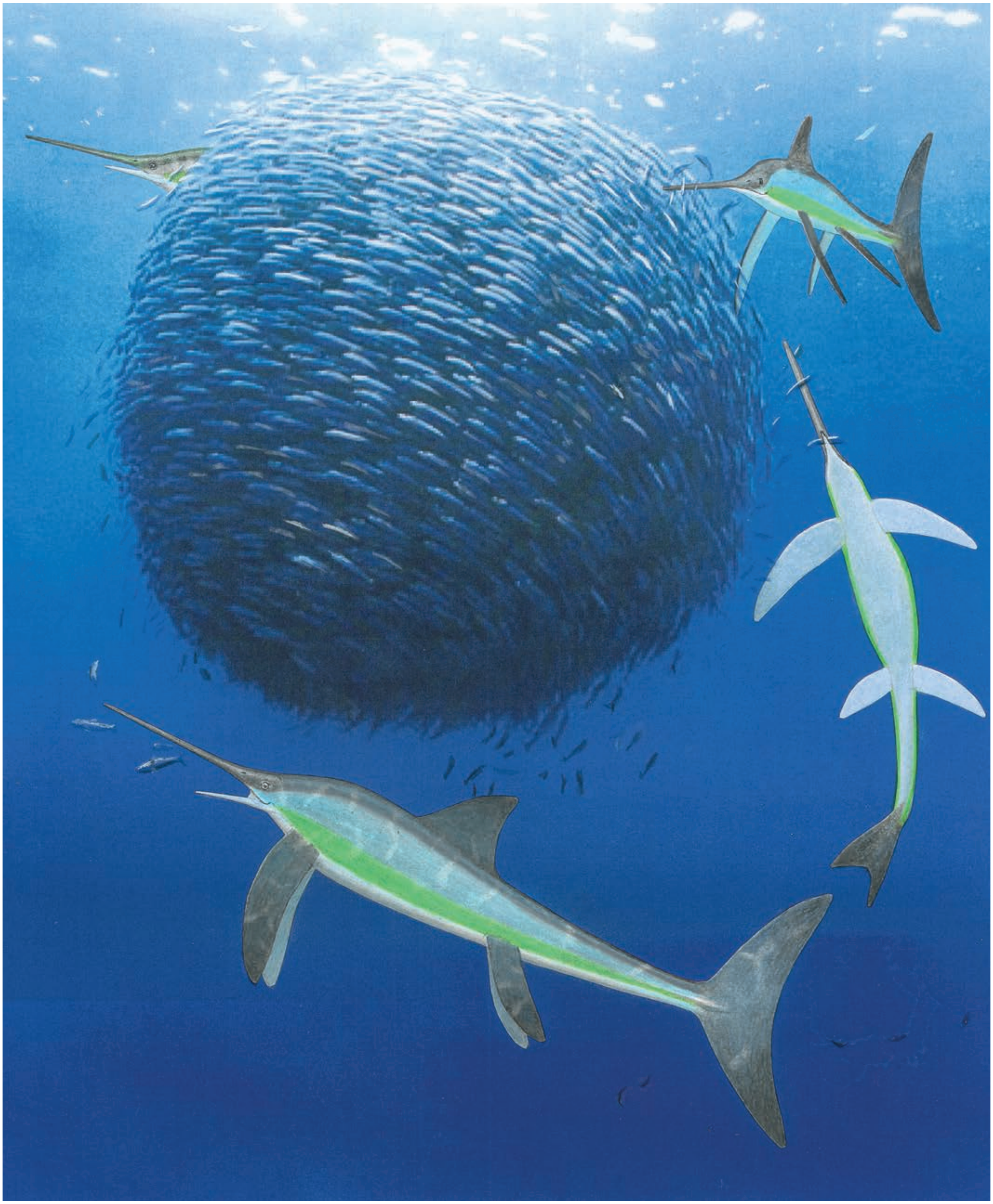
**DISTRIBUTION AND FORMATIONS** Southern England; upper Blue Lias.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Plesiosaurus*, *Eretmosaurus*, *Leptonectes tenuirostris*, *Temnodontosaurus*, *Ichthyosaurus communis*, unnamed genus *eurycephalus*.

### *Eurhinosaurus longirostris*
**3.4 m (11 ft) TL, 121 kg (260 lb)**

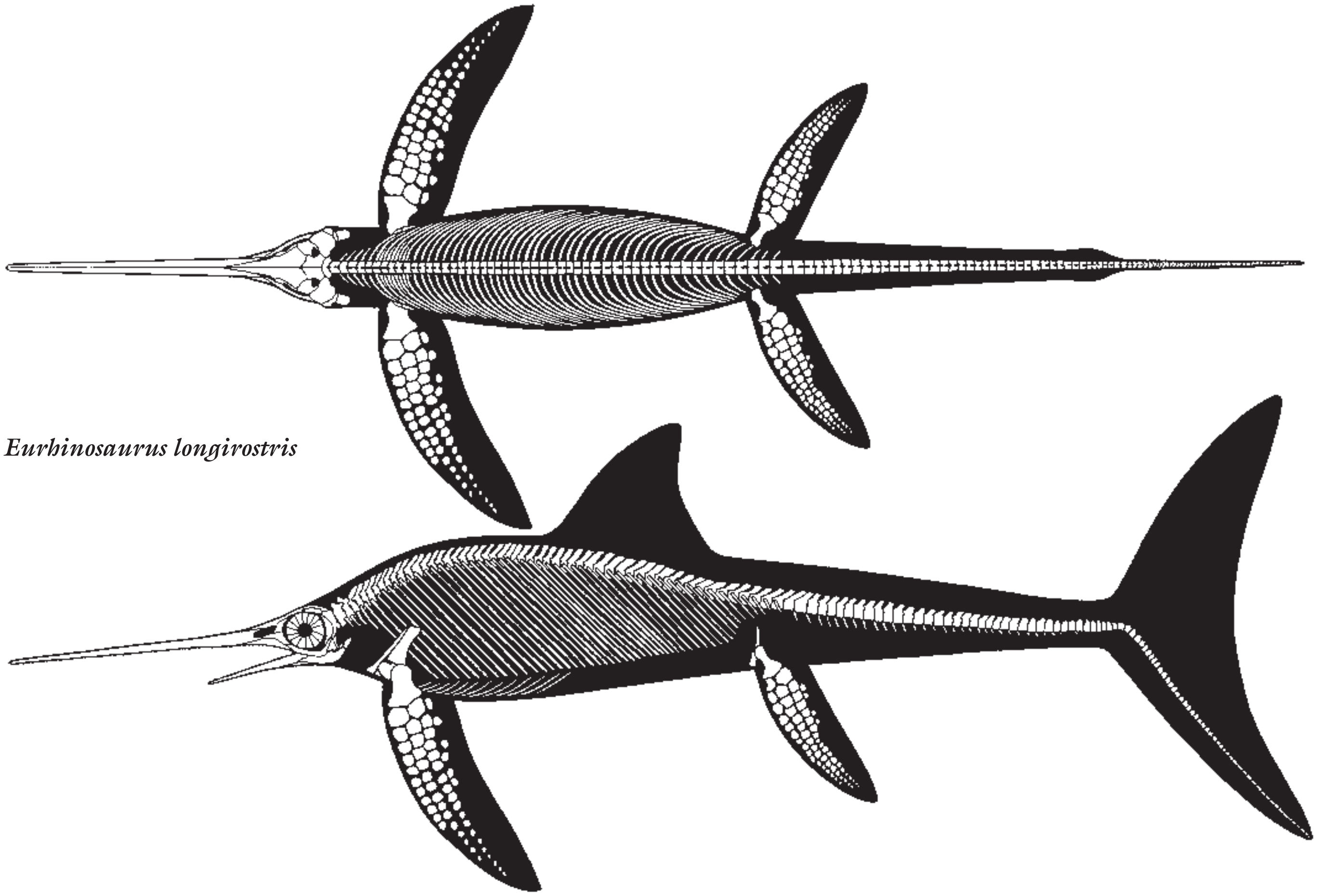
**FOSSIL REMAINS** A number of skulls and skeletons of varying completeness.
**ANATOMICAL CHARACTERISTICS** Upper bill elongated into a supersword many times longer than reduced lower bill, teeth very numerous and very small. Lunate fluke very large. Foreflipper very long.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Northeastern England, southern Germany, southeastern France, Switzerland; lower Whitby Mudstone, Posidonienschiefer.
**HABITAT** Island archipelago shallows.
**HABITS** Oversized flippers indicate high maneuverability combined with speed driven by oversized tail.
**NOTES** Shared its habitat with *Meyerasaurus*, *Hauffiosaurus*, *Rhomaleosaurus*, *Seeleyosaurus*, *Hydrorion*, *Hauffiopteryx*, unnamed genus *trigonodon*, *Suevoleviathan*, *Stenopterygius*, *Plagiophthalmosuchus*, *Mystriosaurus*, *Platysuchus*, *Macrospondylus*. The sea reptile closest to modern swordfish in form and swimming performance.



*Eurhinosaurus longirostris*



*Eurhinosaurus longirostris*



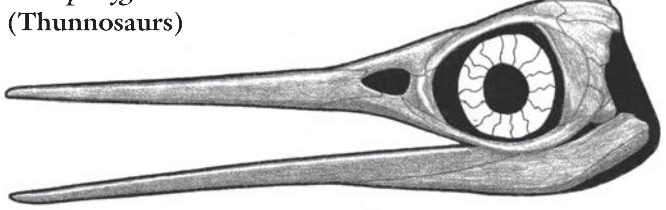
*Eurhinosaurus longirostris*

## THUNNOSAURS

**SMALL TO LARGE PARVIPELVIANS FROM THE EARLY JURASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Uniform. Trunks fairly to very compact. Foreflippers with at least six long lines of pavement elements. Carangiform to thunniform swimmers.
**HABITAT** Coastal shallows to deep oceans.
**HABITS** Swimming performance good to extremely high. Fishers of small to medium-sized game.
**NOTES** The only marine reptiles to evolve thunniform bodies.

*Stenopterygius*
**(Thunnosaurs)**



## ICHTHYOSAURIDS

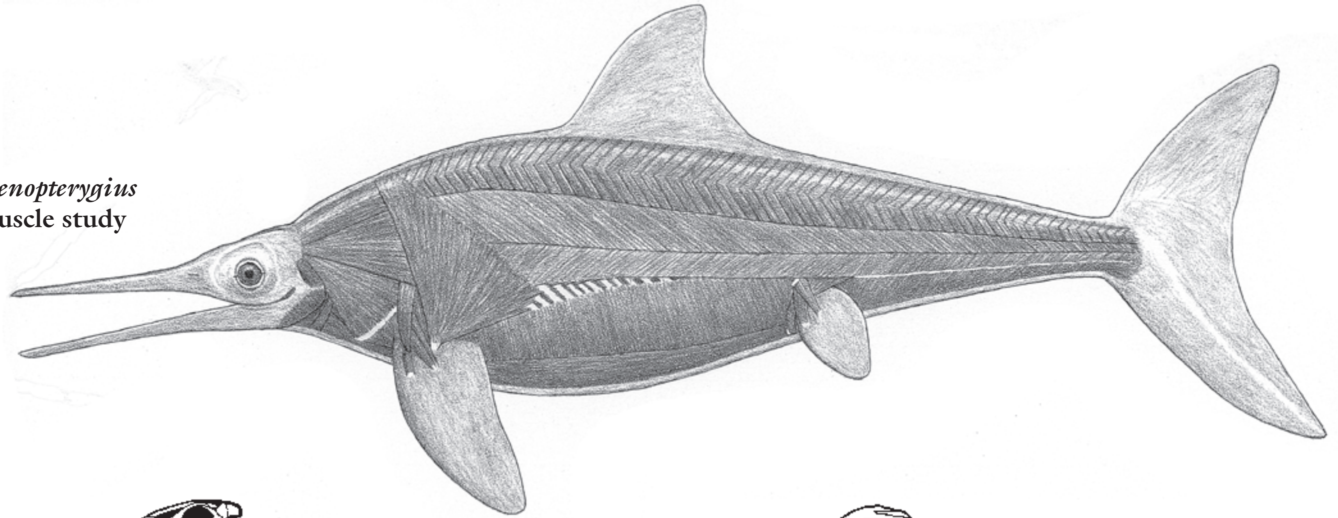
**SMALL TO MEDIUM-SIZED THUNNOSAURS FROM THE EARLY JURASSIC OF EUROPE**

**ANATOMICAL CHARACTERISTICS** Heads large, snouts long, narrow, orbits large, teeth fairly large. Flippers broad, foreflipper medium sized and much larger than hind. High-speed thunniform swimmers.
**HABITS** Swimming performance high to extremely high. Fishers of small game.
**NOTES** Absence from at least some other seas probably reflects lack of sufficient sampling.

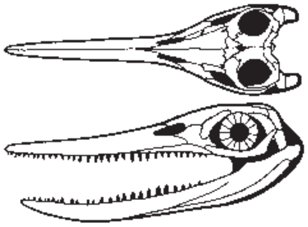
### *Protoichthyosaurus prostaxalis*

**2.5 m (8 ft) TL, 100 kg (220 lb)**

**FOSSIL REMAINS** Partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Snout very long, fairly robust, orbit medium sized, lower jaw fairly robust, upcurved, teeth numerous, stout, vertical.
**AGE** Early Jurassic; early Hettangian.



*Stenopterygius* muscle study



*Protoichthyosaurus prostaxalis*

**DISTRIBUTION AND FORMATIONS** Central England; lower Blue Lias, Hydraulic Limestone.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Eoplesiosaurus*, *Stratesaurus*, *Avalonnectes*, *Eurycleidus*, *Atychodracon*, *Thalassiodracon*.

### *Protoichthyosaurus? applebyi*

**2 m (6.5 ft) TL, 50 kg (110 lb)**

**FOSSIL REMAINS** Two skulls and majority of a skeleton.
**ANATOMICAL CHARACTERISTICS** Snout moderately long, fairly shallow, orbits large, lower jaw shallow, straight, teeth numerous, stout, vertical.

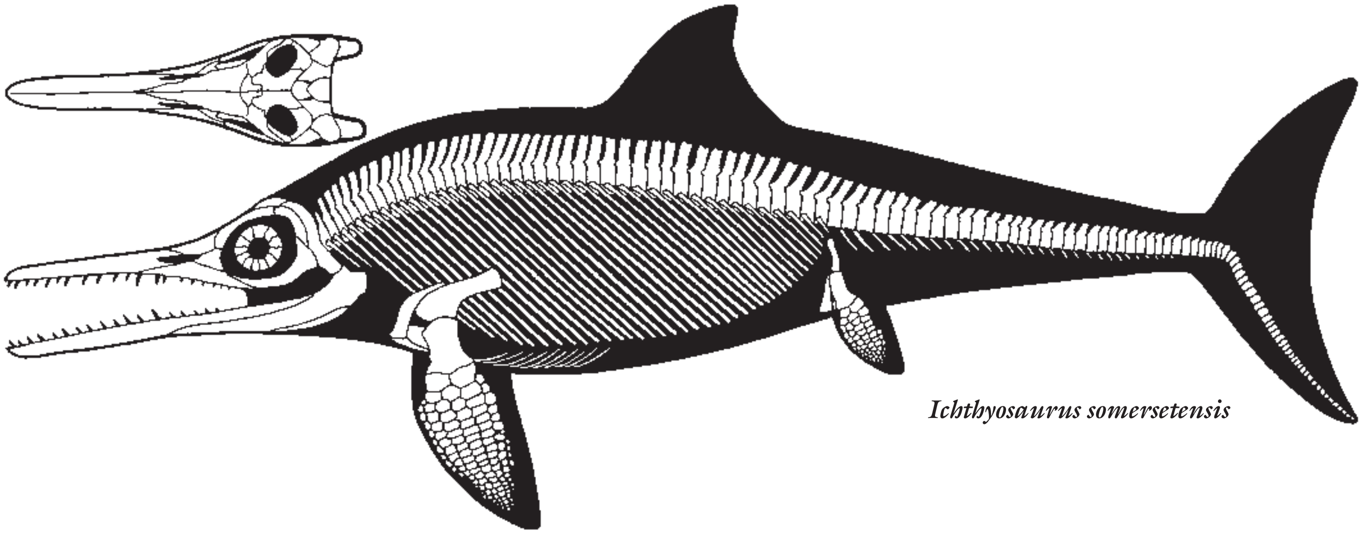
*Protoichthyosaurus? applebyi*

**AGE** Early Jurassic.
**DISTRIBUTION AND FORMATIONS** Southern England; unknown.
**HABITAT** Island archipelago shallows.
**HABITS** Probably favored somewhat large prey.
**NOTES** Whether this is in genus *Protoichthyosaurus* is problematic.

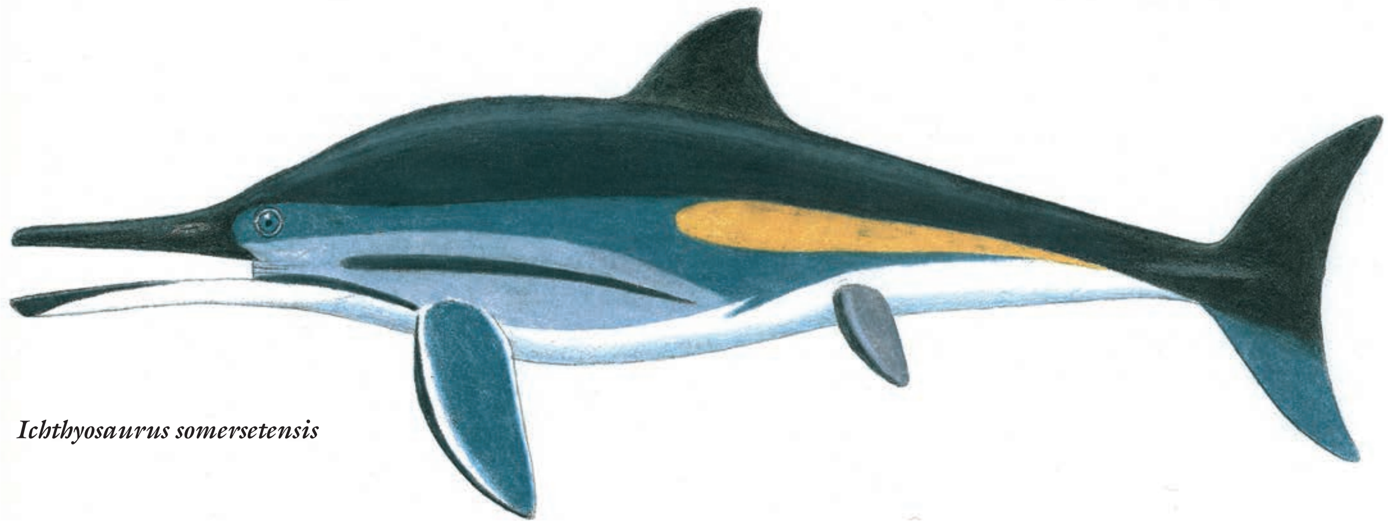
### *Ichthyosaurus somersetensis*

**3.2 m (10 ft) TL, 220 kg (480 lb)**

**FOSSIL REMAINS** A few complete and partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head fairly robust, teeth moderate in number, medium sized, not too stout, somewhat procumbent.
**AGE** Early Jurassic; Hettangian.



*Ichthyosaurus somersetensis*

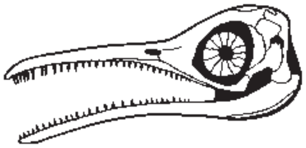


*Ichthyosaurus somersetensis*

**DISTRIBUTION AND FORMATIONS** Southern England; lower and/or middle Blue Lias.
**HABITAT** Island archipelago shallows.

### *Ichthyosaurus larkini*
**2 m (6.5 ft) TL, 50 kg (110 lb)**

**FOSSIL REMAINS** Three nearly complete skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Snout downcurved, teeth moderate in number, fairly large, stout, vertical.
**AGE** Early Jurassic; Hettangian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower and/or middle Blue Lias.
**HABITAT** Island archipelago shallows.



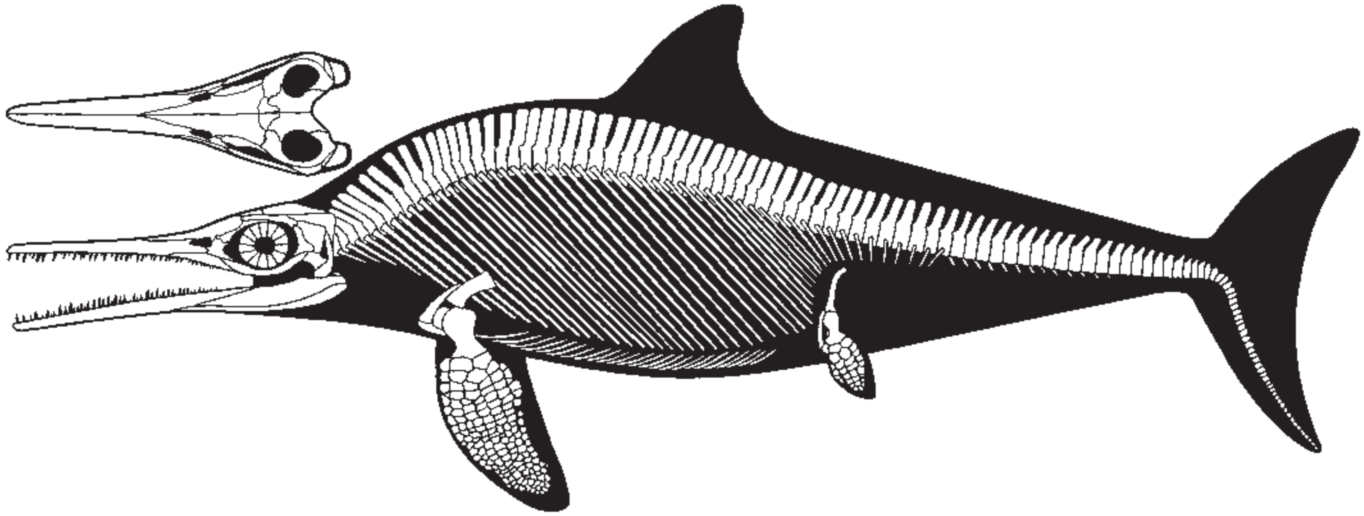
*Ichthyosaurus larkini*

### *Ichthyosaurus communis*
**2 m (6.5 ft) TL, 50 kg (110 lb)**

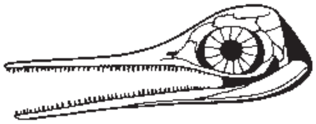
**FOSSIL REMAINS** A number of complete and partial skulls and skeletons, including probable fetuses.
**ANATOMICAL CHARACTERISTICS** Teeth numerous, rather small, vertical. Shoulder vertebrae spines tall.
**AGE** Early Jurassic; early Hettangian to early Sinemurian.
**DISTRIBUTION AND FORMATIONS** Southern England; middle to upper Blue Lias.
**HABITAT** Island archipelago shallows.
**NOTES** Assignment of some other species to this genus questionable. Presence of small fetus exiting skeleton of an adult indicates live birth tailfirst. Shared its habitat with *Excalibosaurus*, *Plesiosaurus*, *Eretmosaurus*, *Leptonectes tenuirostris*, unnamed genus *eurycephalus.*

### *Ichthyosaurus conybeari*
**1.6 m (5.3 ft) TL, 30 kg (65 lb)**

**FOSSIL REMAINS** Skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Teeth numerous, rather small, vertical.



**AGE** Early Jurassic; late Hettangian to early Pliensbachian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower to uppermost Blue Lias.
**HABITAT** Island archipelago shallows.

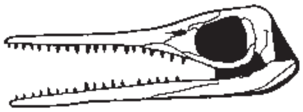


*Ichthyosaurus conybeari*

### *Ichthyosaurus anningae*

Adult size uncertain

**FOSSIL REMAINS** Nearly complete skull and skeleton, two skulls and partial skeletons, all immature.
**ANATOMICAL CHARACTERISTICS** Teeth moderate in number, fairly large, stout, vertical.
**AGE** Early Jurassic; early Pliensbachian.
**DISTRIBUTION AND FORMATIONS** Southern England; upper Charmouth Mudstone.
**HABITAT** Island archipelago shallows.
**HABITS** Probably favored somewhat large prey.
**NOTES** Shared its habitat with *Leptonectes solei.*



*Ichthyosaurus anningae*

### *Ichthyosaurus? breviceps*

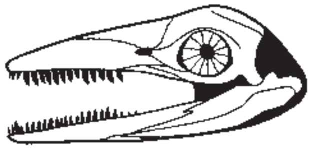
**1.6 m (5.3 ft) TL, 30 kg (65 lb)**

**FOSSIL REMAINS** Some complete skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head short, fairly deep, snout not shallow, eyes large, teeth not numerous and stout. Trunk vertebrae spines tall, body compact and highly thunniform. Foreflipper large.
**AGE** Early Jurassic.
**DISTRIBUTION AND FORMATIONS** Southern England; Blue Lias, level unknown.
**HABITAT** Island archipelago shallows.
**NOTES** Placement in *Ichthyosaurus* dubious.

### Unnamed genus *eurycephalus*

**5 m (16 ft) TL, 1 tonne**

**FOSSIL REMAINS** Skull.
**ANATOMICAL CHARACTERISTICS** Head quite deep along entire length, lower jaw fairly stout, teeth limited to front halves of jaws, quite large and robust.
**AGE** Early Jurassic; early Sinemurian.
**DISTRIBUTION AND FORMATIONS** Southern England; upper Blue Lias.
**NOTES** Deep snout, large teeth, etc., indicate does not belong in *Temnodontosaurus*, where is usually placed, may be closer to ichthyosaurids. Shared its habitat with that, *Excalibosaurus*, *Plesiosaurus*, *Eretmosaurus*, *Leptonectes tenuirostris*, *Ichthyosaurus communis.*



**Unnamed genus** *eurycephalus*

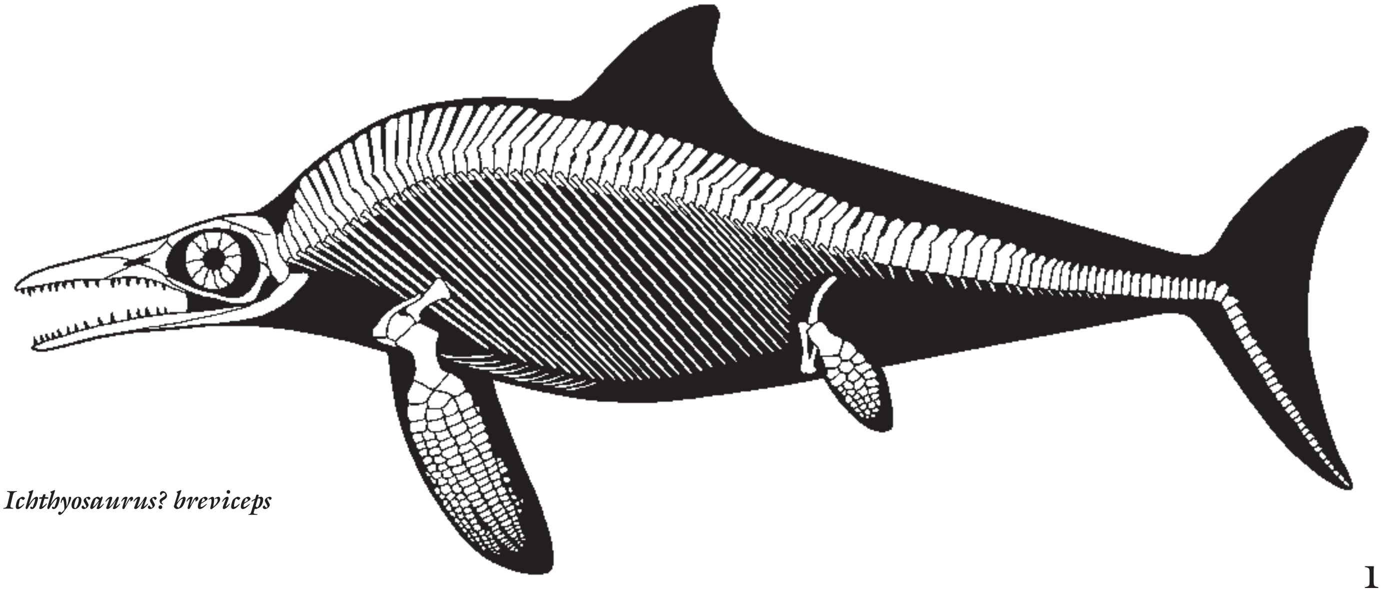
## MALAWANIANS

**SMALL THUNNOSAURS FROM THE EARLY CRETACEOUS OF THE MIDDLE EAST**

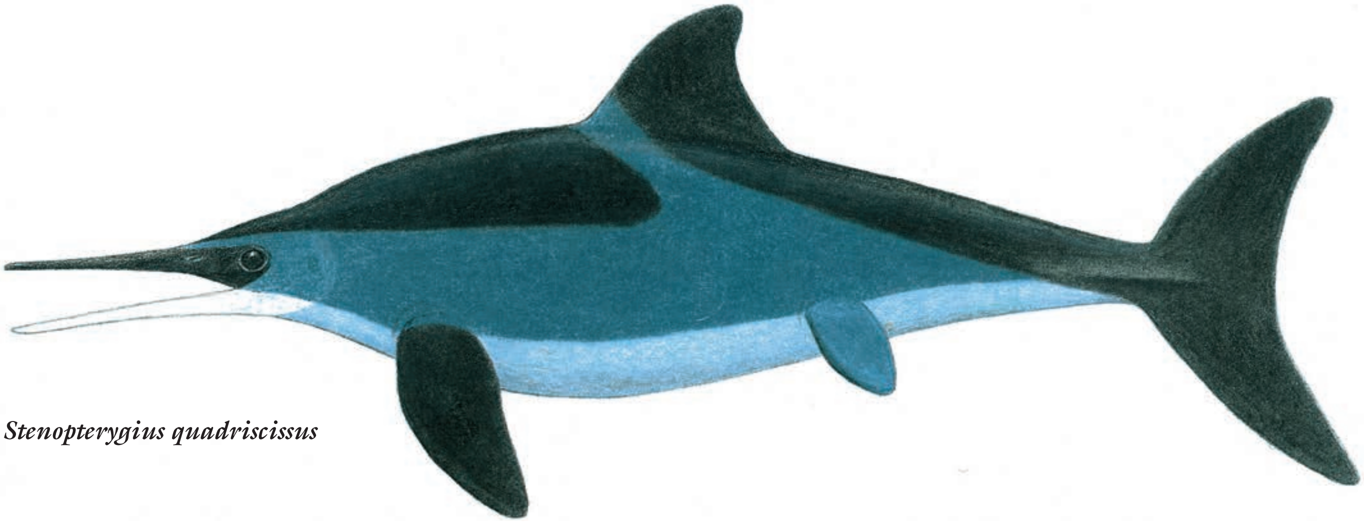
### *Malawania anachronus*

**2 m (6.5 ft) TL, 50 kg (110 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; late Hauterivian or Barremian.



*Ichthyosaurus? breviceps*



*Stenopterygius quadriscissus*

**DISTRIBUTION AND FORMATIONS** Iraq; unnamed.
**HABITAT** Continental shallows.
**NOTES** Placement in the much earlier ichthyosaurids is problematic.

## BARCROMIANS

**SMALL TO LARGE THUNNOSAURS FROM THE EARLY JURASSIC TO THE END OF THE MESOZOIC, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Uniform. Ventral pelvic elements fused to one another.
**HABITAT** Coastal shallows to deep oceans.
**HABITS** Swimming performance good to extremely high. Fishers of small to medium-sized game.

## STENOPTERYGIDS

**MEDIUM-SIZED BARCROMIANS FROM THE EARLY TO MIDDLE JURASSIC OF EUROPE AND SOUTH AMERICA**

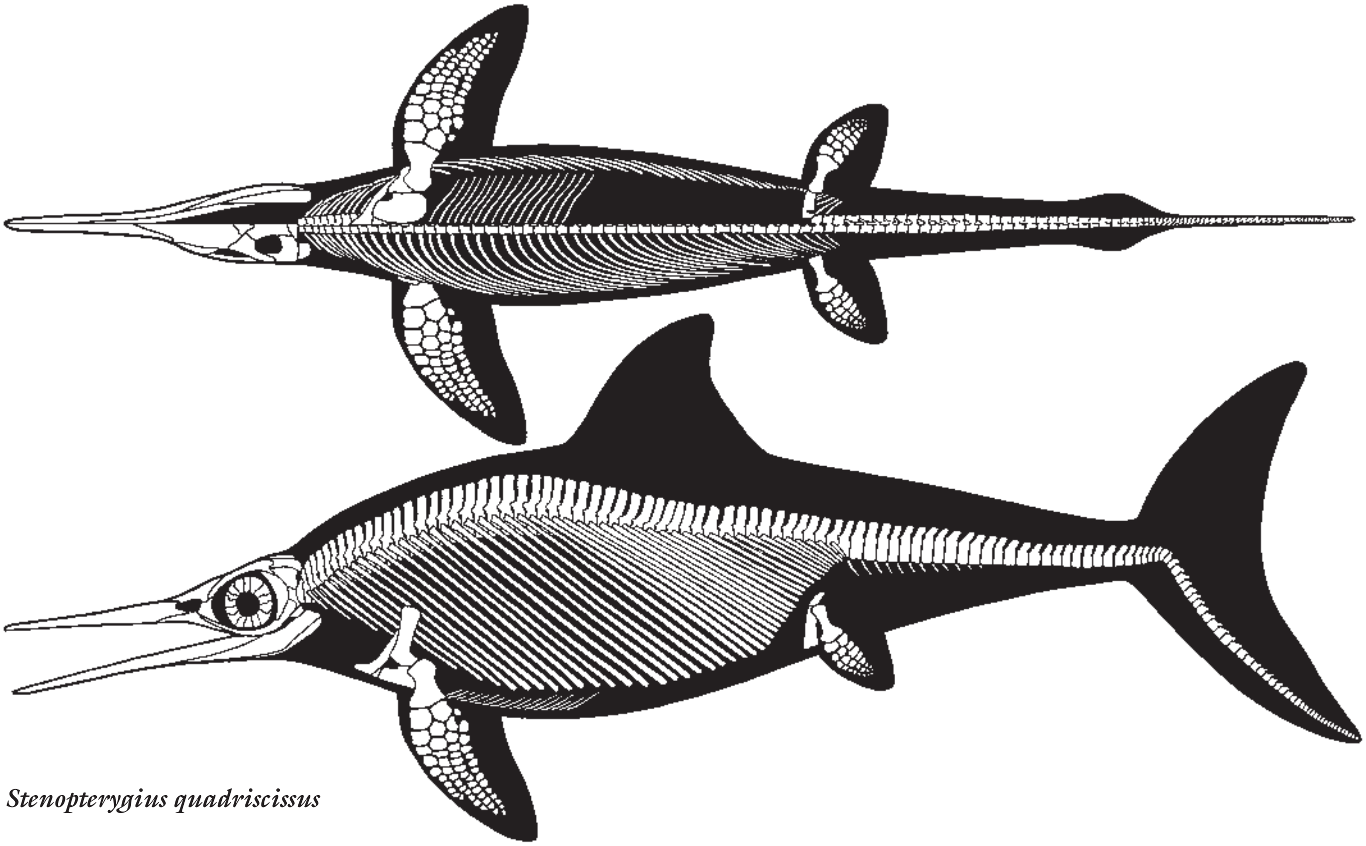
**ANATOMICAL CHARACTERISTICS** Very uniform. Heads large, snouts long, narrow, orbits large, teeth very reduced to absent, especially in adults. Trunk width less than two-thirds its own depth. Flippers broad, foreflippers medium sized and much larger than aft. High-speed thunniform swimmers.
**HABITS** Swimming performance very to extremely high. Fishers of small game.
**NOTES** Highly convergent with lamnid sharks, tuna, and dolphins, perhaps the acme of high-speed marine reptiles. Absence from at least some other seas probably reflects lack of sufficient sampling.

### *Stenopterygius quadriscissus*
**3.5 m (11.5 ft) TL, 270 kg (600 lb)**

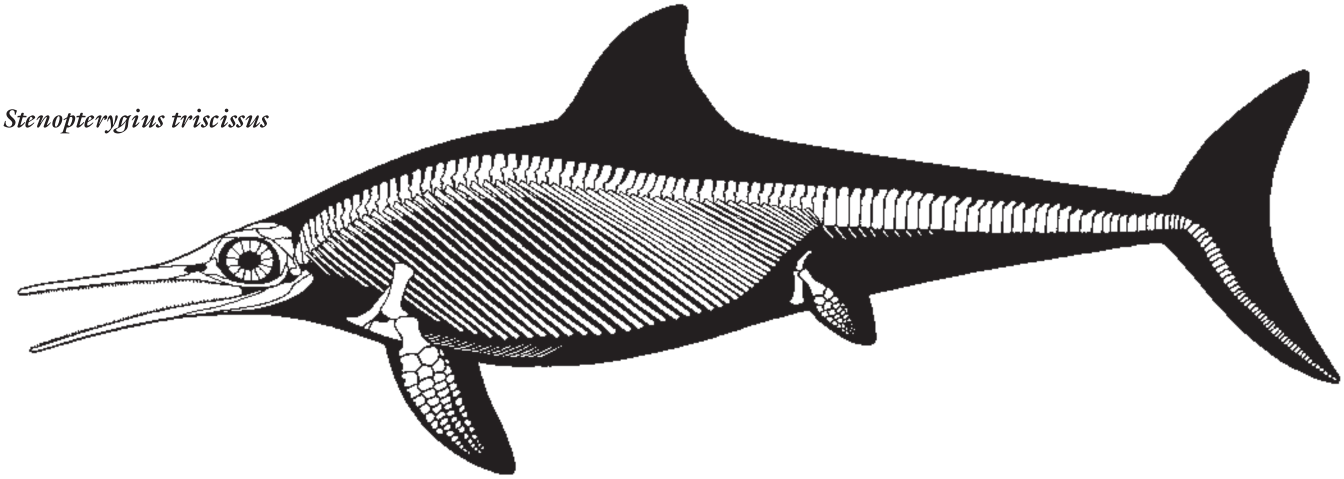
**FOSSIL REMAINS** A number of complete skulls and skeletons of various ages, some with preserved soft tissues.
**ANATOMICAL CHARACTERISTICS** Snout not very elongated, teeth functionally absent in adults. Body plump and highly thunniform, lower tail lobe not strongly elongated. Fins rather short.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Posidonienschiefer.
**HABITAT** Island archipelago shallows.
**NOTES** Internally positioned fetuses in this genus indicate live birth. The profile-skeletal is based on a specimen with a well-preserved body outline; preserved pigmentation patterns indicate countershading in at least some species of genus. Later examples shared their habitat with less numerous *S. triscissus* and *S. uniter*, and *Meyerasaurus*, *Hauffiosaurus*, *Seeleyosaurus*, *Hydrorion*, *Hauffiopteryx*, unnamed genus *trigonodon*, *Suevoleviathan*, *Eurhinosaurus*, *Mystriosaurus*, *Platysuchus*, *Macrospondylus*.

### *Stenopterygius triscissus*
**3.3 m (11 ft) TL, 210 kg (450 lb)**

**FOSSIL REMAINS** A number of complete skulls and skeletons of various ages.
**ANATOMICAL CHARACTERISTICS** Snout elongated, adult tooth reduction highly variable. Body not extremely plump, lower tail lobe not strongly elongated. Fins rather short.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany, southern England; Posidonienschiefer, unnamed.
**HABITAT** Island archipelago shallows.



*Stenopterygius quadriscissus*



*Stenopterygius triscissus*

**NOTES** Apparently did not appear as early as *S. quadriscissus* and may have been direct descendant of early examples of that.

### *Stenopterygius uniter*

**3.8 m (12.5 ft) TL, 310 kg (680 lb)**

**FOSSIL REMAINS** A number of complete skulls and skeletons of various ages.
**ANATOMICAL CHARACTERISTICS** Snout not very elongated, adult tooth reduction variable. Body not extremely plump, lower tail lobe long. Fins fairly long, slender, and sharp tipped.
**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Posidonienschiefer.
**HABITAT** Island archipelago shallows.
**HABITS** Large fins indicate most maneuverable swimmer of this genus.

**NOTES** Apparently did not appear as early as *S. triscissus* and may have been direct descendant of early examples of that or of *S. quadriscissus.*

### *Stenopterygius aaleniensis*

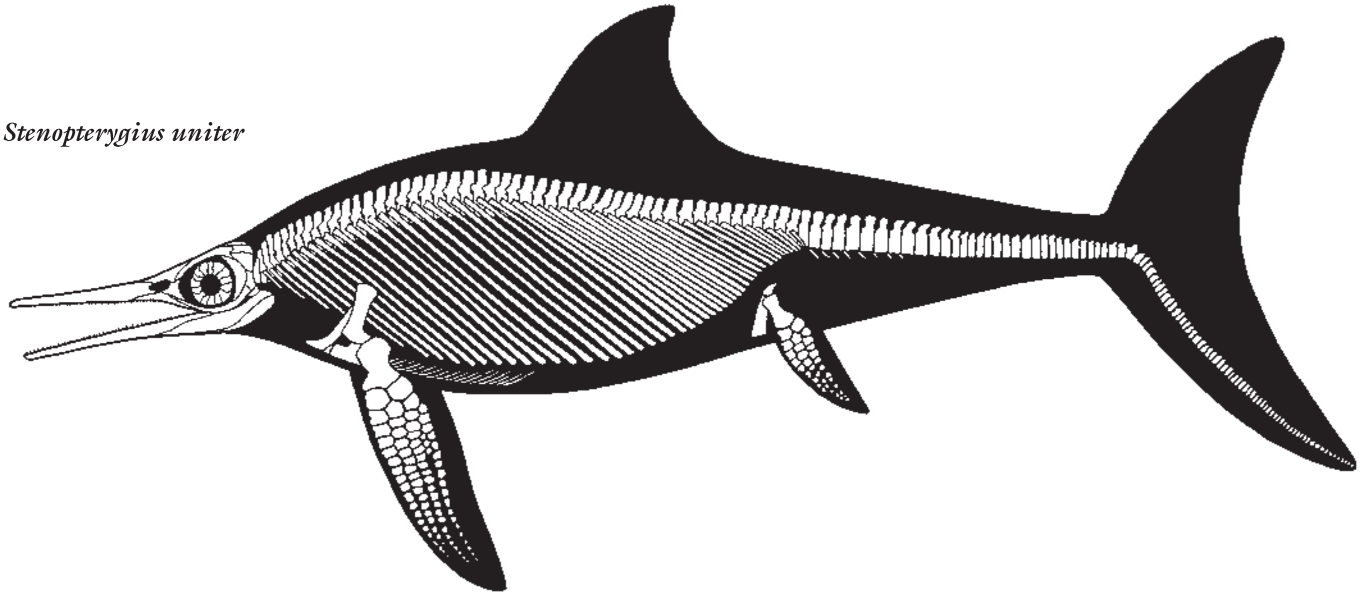
**3 m (10 ft) TL, 150 kg (330 lb)**

**FOSSIL REMAINS** Majority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Middle Jurassic; early Aalenian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; lowest Opalinuston.
**HABITAT** Island archipelago shallows.

### *Chacaicosaurus cayi*

**3.5 m (11.5 ft) TL, 270 kg (600 lb)**

**FOSSIL REMAINS** Skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Snout very long, moderately robust, tapering.



*Stenopterygius uniter*

*Chacaicosaurus cayi*

**AGE** Middle Jurassic; early Bajocian.
**DISTRIBUTION AND FORMATIONS** Southern Argentina; upper Los Molles.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Maresaurus* and *Mollesaurus*.

## OPHTHALMOSAURIDS

**SMALL TO LARGE BARCROMIANS FROM THE MIDDLE JURASSIC TO LATE CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Foreflipper pavements very highly developed. High-performance carangiform and thunniform swimmers.
**HABITAT** Coastal shallows to deep oceans.
**HABITS** Swimming performance good to extremely high. Fishers of small to medium-sized game.

## OPHTHALMOSAURID MISCELLANEA

### *Keilhauia nui*
**4 m (13 ft) TL, 300 kg (650 lb)**

**FOSSIL REMAINS** Partial skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; late Tithonian.
**DISTRIBUTION AND FORMATIONS** Svalbard; upper Agardhfjellet.
**HABITAT** Open continental shelf, polar.
**NOTES** Shared its habitat with *Pliosaurus*? *funkei*, *Colymbosaurus*? *svalbardensis*, *Spitrasaurus*, *Palvennia*, *Janusaurus*, *Cryopterygius*.

### *Palvennia hoybergeti*
**4 m (13 ft) TL, 300 kg (650 lb)**

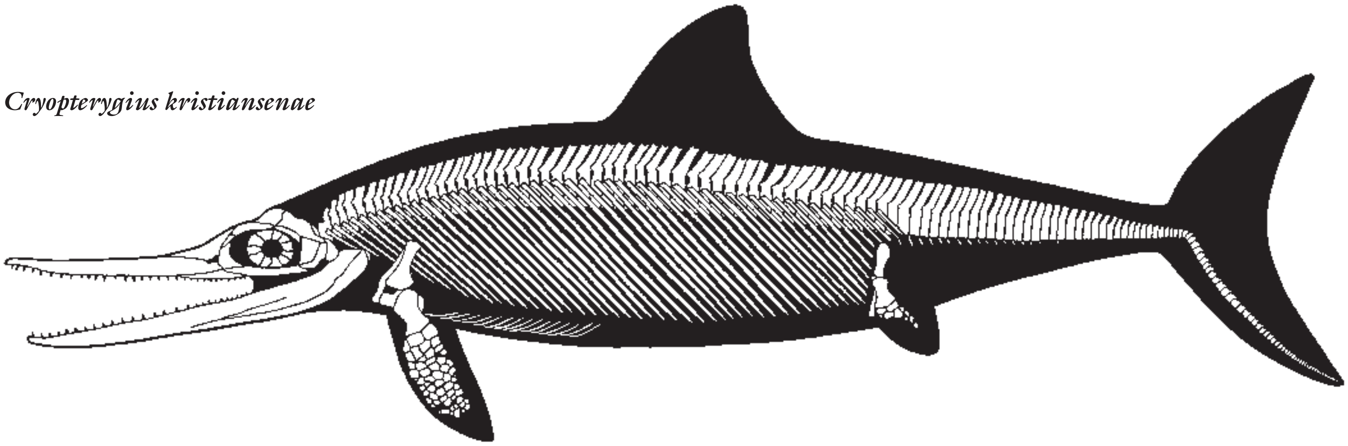
**FOSSIL REMAINS** Complete skull, partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Snout not elongated, rather sharp tipped, teeth numerous and rather small.
**AGE** Late Jurassic; late Tithonian.
**DISTRIBUTION AND FORMATIONS** Svalbard; upper Agardhfjellet.
**HABITAT** Open continental shelf, polar.

### *Janusaurus lundi*
**3 m (10 ft) TL, 135 kg (300 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth very small.
**AGE** Late Jurassic; late Tithonian.
**DISTRIBUTION AND FORMATIONS** Svalbard; upper Agardhfjellet.
**HABITAT** Open continental shelf, polar.

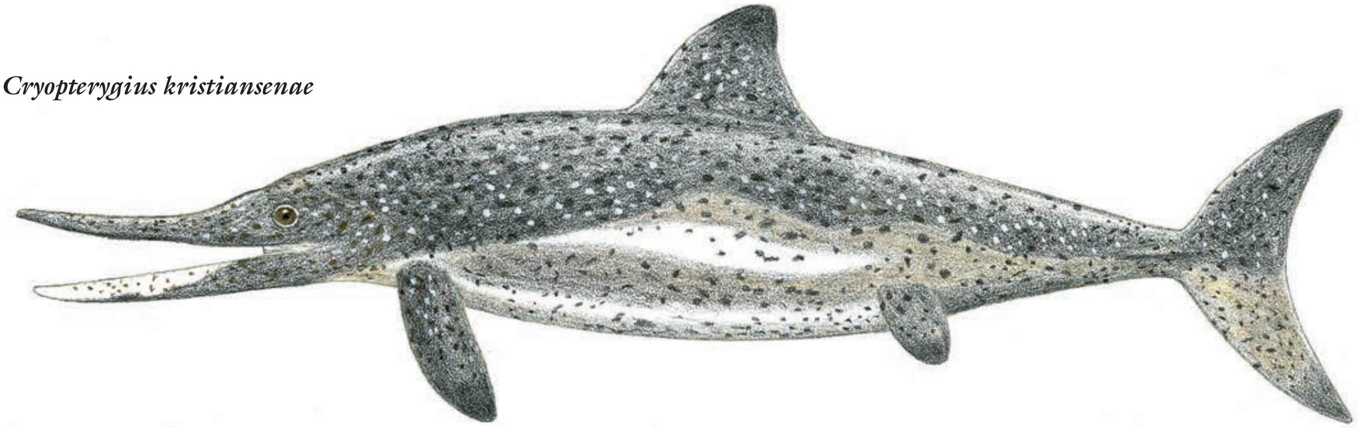
### *Cryopterygius kristiansenae*
**5.3 m (17 ft) TL, 400 kg (880 lb)**

**FOSSIL REMAINS** Nearly complete skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head large, snout quite long, teeth fairly numerous, rather small. Trunk fairly long. Flippers rather small. Transitional carangiform-thunniform swimmer.
**AGE** Late Jurassic; late Tithonian.
**DISTRIBUTION AND FORMATIONS** Svalbard; upper Agardhfjellet.
**HABITAT** Open continental shelf, polar.
**HABITS** Swimming performance modest.



*Cryopterygius kristiansenae*

*Cryopterygius kristiansenae*



### *Arthropterygius chrisorum*

**2 m (6.5 ft) TL, 40 kg (90 lb)**

**FOSSIL REMAINS** Skull and partial skeletons, adult to juvenile.
**ANATOMICAL CHARACTERISTICS** Snout rather short, orbit large, teeth numerous.
**AGE** Late Jurassic; Oxfordian or Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Northern Northwest Territories; Ringnes.
**HABITAT** Continental shelf.

### Unnamed genus or *Arthropterygius thalassonotus*

**3 m (10 ft) TL, 140 kg (300 lb)**

**FOSSIL REMAINS** Partial skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; late Tithonian.
**DISTRIBUTION AND FORMATIONS** Western Argentina; middle Vaca Muerta.
**HABITAT** Continental shelf.
**NOTES** This species belonging to earlier and also poorly preserved and remote *Arthropterygius* is problematic. Shared its habitat with *Dakosaurus andiniensis*, unnamed genus and species, *Sumpalla*?

### *Gengasaurus nicosiai*

**3 m (10 ft) TL, 135 kg (300 lb)**

**FOSSIL REMAINS** Skull disarticulated and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; late Kimmeridgian and/or earliest Tithonian.
**DISTRIBUTION AND FORMATIONS** Central Italy; unnamed.
**HABITAT** Island archipelago shallows.
**NOTES** Majority of skull is not visible.

## NANNOPTERYGINES

**MEDIUM-SIZED OPHTHALMOSAURIDS FROM THE LATE JURASSIC AND POSSIBLY EARLY CRETACEOUS OF EUROPE**

**ANATOMICAL CHARACTERISTICS** Heads fairly small, snouts rather short, narrow, orbits large, teeth small and numerous. Trunk fairly long. Flippers quite small.
**HABITS** Not highly maneuverable. Fishers of small game.
**NOTES** Had the smallest flippers of any known ichthyosaur. The purpose of such small steering and stabilizing surfaces is not clear. Fragmentary remains may indicate presence in Early Cretaceous. Absence from at least some other seas probably reflects lack of sufficient sampling.

### *Nannopterygius enthekiodon*

**4.2 m (13.8 ft) TL, 375 (800 lb)**

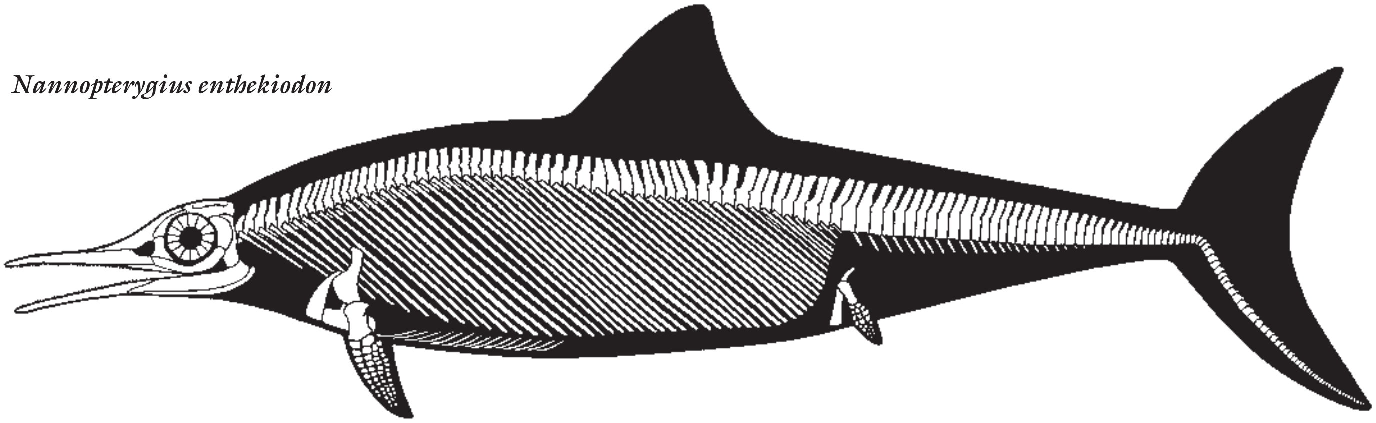
**FOSSIL REMAINS** Majority of two skulls and skeleton, other skeletal remains.
**ANATOMICAL CHARACTERISTICS** Transitional carangiform-thunniform.
**AGE** Late Jurassic; late Kimmeridgian or early Tithonian.
**DISTRIBUTION AND FORMATIONS** Southern England; middle Kimmeridge Clay.
**HABITAT** Island archipelago shallows.
**HABITS** Swimming performance modest.
**NOTES** Is possible that some specimens do not belong to *N. enthekiodon*. Shared its habitat with *Pliosaurus westburyensis*, *Grendelius mordax*.

### *Thalassodraco etchesi*

**3.5 m (10 ft) TL, 250 kg (500 lb)**

**FOSSIL REMAINS** Majority of skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** May have been more thunniform.
**AGE** Late Jurassic; early Tithonian.

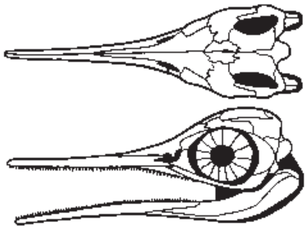
*Nannopterygius enthekiodon*



**DISTRIBUTION AND FORMATIONS** Southern England; middle Kimmeridge Clay.
**HABITAT** Island archipelago shallows.

**Unnamed genus *saveljeviensis***
**5 m (16 ft) TL, 800 kg (1,800 lb)**

**FOSSIL REMAINS** Majority of skull and partial skeleton, partial skull and skeletons, other remains, some juvenile.
**ANATOMICAL CHARACTERISTICS** May have been more thunniform.
**AGE** Late Jurassic; late middle to early late Tithonian.
**DISTRIBUTION AND FORMATIONS** Southwestern Russia; unnamed.
**HABITAT** Continental shelf.
**NOTES** *Nannopterygius yasykovi* may be a juvenile of this species. Placement in earlier *Nannopterygius* highly problematic.



**Unnamed genus *saveljeviensis***

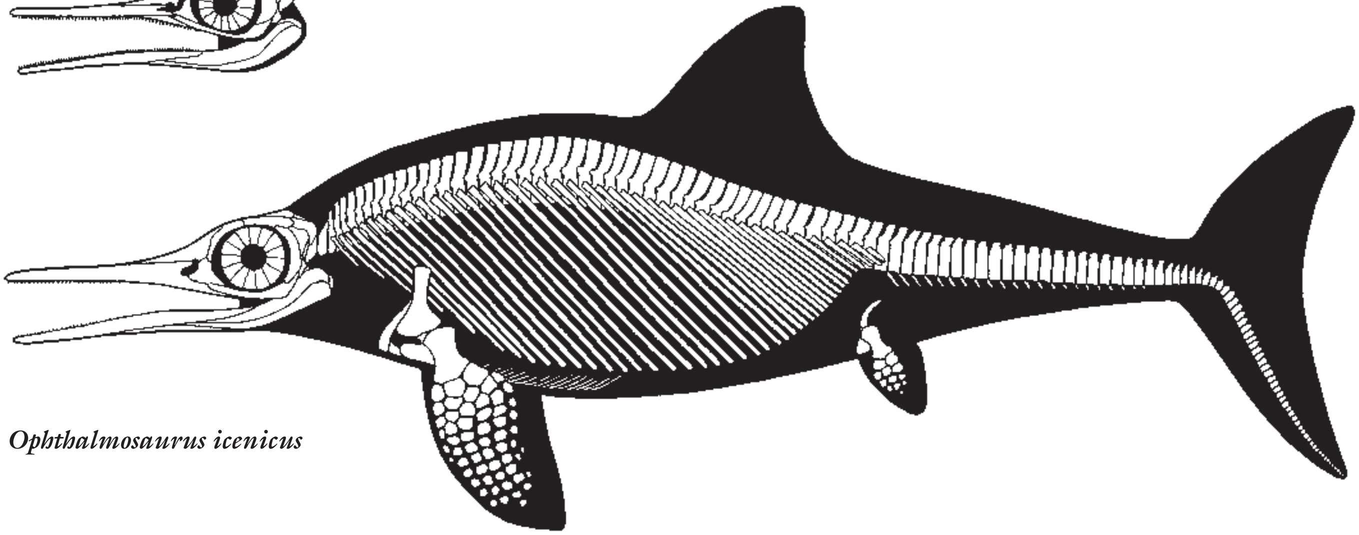
## OPHTHALMOSAURINES

**MEDIUM-SIZED TO LARGE OPHTHALMOSAURIDS FROM THE MIDDLE JURASSIC TO EARLY CRETACEOUS OF EUROPE AND THE AMERICAS**

**ANATOMICAL CHARACTERISTICS** Heads large, snouts long, narrow, orbits large, teeth reduced to absent, especially in adults. Body cross section nearly circular. Flippers broad, foreflippers medium sized and much larger than aft. High-speed thunniform swimmers.
**HABITS** Swimming performance very to extremely high. Fishers of small game.
**NOTES** Highly convergent with lamnid sharks, tuna, and dolphins. Absence from at least some other seas probably reflects lack of sufficient sampling.

***Ophthalmosaurus icenicus***
**6 m (20 ft) TL, 1.5 tonnes**

**FOSSIL REMAINS** Numerous incomplete specimens.
**ANATOMICAL CHARACTERISTICS** Teeth limited to front of jaws.



*Ophthalmosaurus icenicus*

AGE Middle Jurassic; middle Callovian.
DISTRIBUTION AND FORMATIONS Eastern England; lower Oxford Clay.
HABITAT Island archipelago shallows.
NOTES Assignment of a number of specimens to this species from other locations and times is highly problematic. Whether adults reached 6 m (20 ft) is not certain. Had the largest eyes, 0.25 m (0.6 ft) across, relative to its size of known sea reptiles. Shared its habitat with *Peloneustes*, *Pachycostasaurus*, *Simolestes*, *Liopleurodon*, *Cryptoclidus*, *Muraenosaurus*, *Tricleidus*, *Tyrannoneustes*, *Suchodus*, *Gracilineustes*.

### *Mollesaurus periallus*

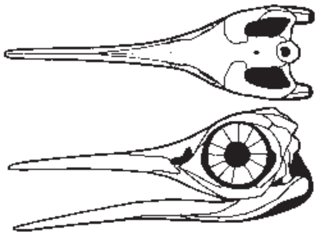
**5 m (16 ft) TL, 800 kg (1,800 lb)**

FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic; early Bajocian.
DISTRIBUTION AND FORMATIONS Central Argentina; upper Los Molles.
HABITAT Continental shelf.
NOTES Shared its habitat with *Chacaicosaurus* and *Maresaurus*.

### *Baptanodon natans*

**6 m (20 ft) TL, 1 tonne**

FOSSIL REMAINS Skull and partial skeletal remains.
ANATOMICAL CHARACTERISTICS Teeth functionally absent in adults.
AGE Late Jurassic; early Oxfordian.
DISTRIBUTION AND FORMATIONS Wyoming; upper Sundance.
HABITAT Interior seaway.
NOTES Shared its habitat with *Pantosaurus*, *Tatenectes*.



***Baptanodon natans***

### *Acamptonectes densus*

**4.5 m (15 ft) TL, 400 kg (900 lb)**

FOSSIL REMAINS Skull and partial skeleton, severely flattened top to bottom and otherwise disrupted.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous; Hauterivian.
DISTRIBUTION AND FORMATIONS Eastern England; Speeton Clay.
HABITAT Island archipelago shallows.

*Muiscasaurus catheti*
Adult size uncertain
FOSSIL REMAINS Skull and partial skeleton, partial skull and skeleton, both juvenile.
ANATOMICAL CHARACTERISTICS Teeth along entire length of jaws, rather small and numerous.
AGE Early Cretaceous; Barremian or Aptian.
DISTRIBUTION AND FORMATIONS Colombia; Paja.
HABITAT Continental shelf.
NOTES May be a platypterygiine.

## PLATYPTERYGIINES

**SMALL TO LARGE OPHTHALMOSAURIDS FROM THE LATE JURASSIC TO EARLY LATE CRETACEOUS, GLOBAL**

ANATOMICAL CHARACTERISTICS Trunks not highly compact. Foreflipper pavements uniquely developed. High-performance carangiform swimmers.
HABITAT Coastal shallows to deep oceans.
HABITS Swimming performance high to very high. Fishers of small to medium-sized game.
NOTES Thunniforms not yet identified among these often Cretaceous ichthyosaurs. Possess the most sophisticated forefins among marine tetrapods, if not vertebrates. Includes the last ichthyosaurs.

### *Sumpalla argentina*

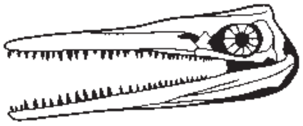
**2.1 m (7 ft) TL, 30 kg (60 lb)**

FOSSIL REMAINS Skull and skeleton severely flattened top to bottom.
ANATOMICAL CHARACTERISTICS Head long, snout fairly slender.
AGE Late Jurassic; middle or late Tithonian.
DISTRIBUTION AND FORMATIONS Western Argentina; middle Vaca Muerta.
HABITAT Continental shelf.
NOTES Shared its habitat with *Arthropterygius*? *thalassonotus*, *Dakosaurus andiniensis*?, unnamed genus and species?

### *Grendelius mordax*

**5.5 m (18 ft) TL, 800 kg (1,700 lb)**

FOSSIL REMAINS Skull, skeletal remains.
ANATOMICAL CHARACTERISTICS Snout very long, robust, teeth fairly large, stout.
AGE Late Jurassic; late Kimmeridgian and/or early Tithonian.



*Grendelius mordax*

**DISTRIBUTION AND FORMATIONS** Southern England; middle Kimmeridge Clay.
**HABITAT** Island archipelago shallows.
**NOTES** Some researchers consider this to be same as poorly preserved *Brachypterygius extremus*. Shared its habitat with *Pliosaurus westburyensis*, *Nannopterygius enthekiodon*.

### *Grendelius? alekseevi*

**4 m (13 ft) TL, 300 kg (650 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; early Tithonian.
**DISTRIBUTION AND FORMATIONS** Western Russia; unnamed.
**NOTES** Placement in *Grendelius* not certain.

### *Grendelius? zhuravlevi*

**3.5 m (11 ft) TL, 200 kg (450 lb)**

**FOSSIL REMAINS** Partial skull and skeletons.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; early Tithonian.
**DISTRIBUTION AND FORMATIONS** Southwestern Russia; unnamed.
**NOTES** Placement in *Grendelius* not certain.

### *Undorosaurus gorodischensis*

**4 m (13 ft) TL, 300 kg (650 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; middle Tithonian.
**DISTRIBUTION AND FORMATIONS** Southern Russia; unnamed.
**HABITAT** Continental shelf.

### *Maiaspondylus lindoei*

**Adult size uncertain**

**FOSSIL REMAINS** Partial skull and skeleton, other remains including juvenile.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; early Albian.
**DISTRIBUTION AND FORMATIONS** Southern Northwest Territories; upper Loon River.
**HABITAT** Continental shelf.

### Unnamed genus *cantabrigiensis*

**Adult size uncertain**

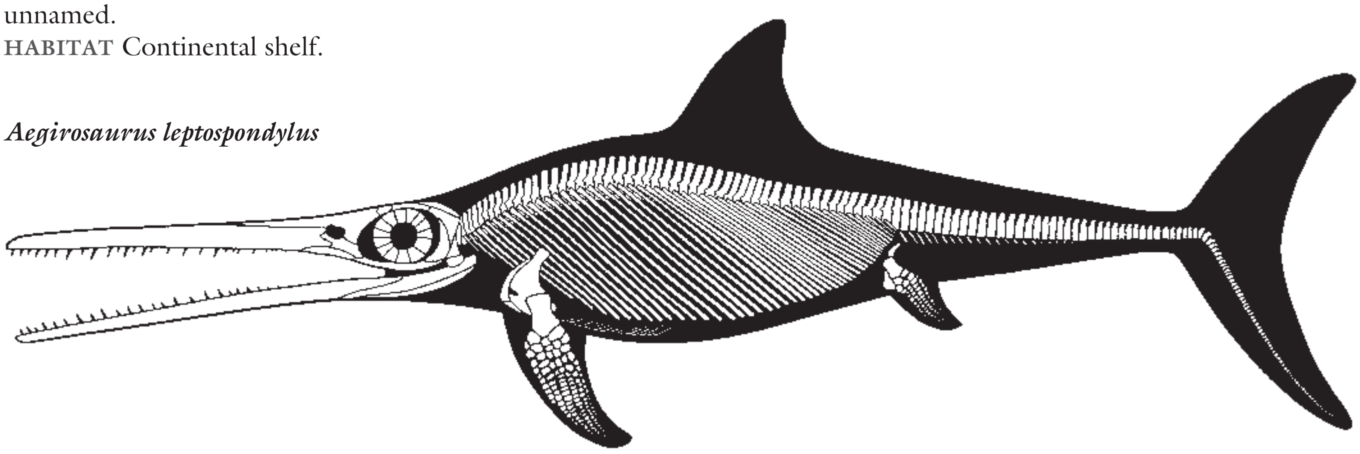
**FOSSIL REMAINS** Minority of skull and skeletons, possibly immature.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; Cenomanian.
**DISTRIBUTION AND FORMATIONS** Eastern England; Greensand.
**HABITAT** Island archipelago shallows.
**NOTES** Assignment of these poorly preserved remains to much earlier and remote *Maiaspondylus*, and of poorly preserved Russian remains to this species, is at best extremely problematic.

### *Aegirosaurus leptospondylus*

**1.6 m (5.2 ft) TL, 15 kg (30 lb)**

**FOSSIL REMAINS** A few skulls and skeletons, some with soft tissues.
**ANATOMICAL CHARACTERISTICS** Head extremely long, snout very long, fairly robust, teeth moderate in number, medium sized. Trunk fairly compact. Lunate fluke large. Foreflipper medium sized.
**AGE** Late Jurassic; early Tithonian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Altmühltal (Solnhofen).
**HABITAT** Island archipelago shallows.

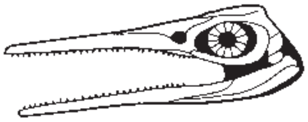
*Aegirosaurus leptospondylus*



### *Sveltonectes insolitus*

**3 m (10 ft) TL, 125 kg (275 lb)**

**FOSSIL REMAINS** Skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Snout fairly robust, teeth fairly numerous, rather small, stout.
**AGE** Early Cretaceous; late Barremian.
**DISTRIBUTION AND FORMATIONS** Western Russia; unnamed.
**HABITAT** Continental shelf.



*Sveltonectes insolitus*

### *Kyhytysuka sachicarum*

**5.5 m (18 ft) TL, 800 kg (1,700 lb)**

**FOSSIL REMAINS** Two skulls and partial of skeleton.
**ANATOMICAL CHARACTERISTICS** Head large, snout very long, fairly robust, teeth numerous, medium sized, range progressing aft from slender piercing to cutting to stouter crushing.
**AGE** Early Cretaceous; latest Barremian and/or early Aptian.
**DISTRIBUTION AND FORMATIONS** Colombia; upper Paja.
**HABITAT** Continental shelf.
**NOTES** Has incorrectly been placed in *Platypterygius*. Shared its habitat with *Monquirasaurus*, *Callawayasaurus*.

*Kyhytysuka sachicarum*

### Unnamed genus *hercynicus*

**7 m (23 ft) TL, 1.5 tonnes**

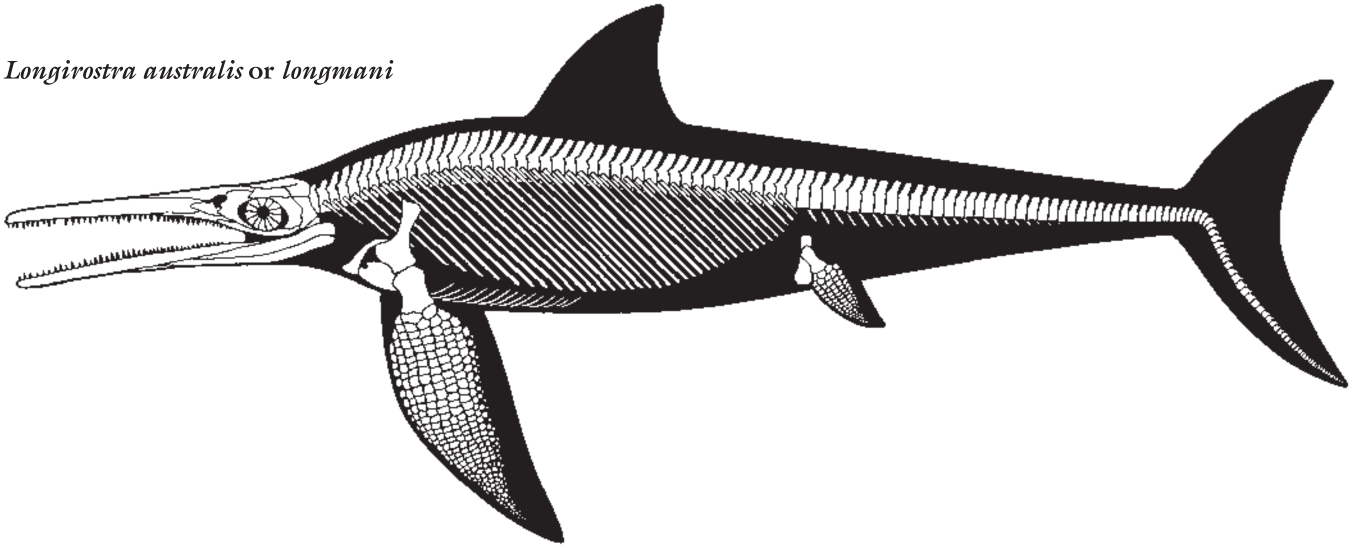
**FOSSIL REMAINS** Two partial skulls and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; Aptian.
**DISTRIBUTION AND FORMATIONS** Northern Germany, northwestern France; unnamed.
**HABITAT** Island archipelago shallows.
**NOTES** Usually placed, as many mid-Cretaceous ichthyosaurs have been, in *Platypterygius*, even though the original specimens of *P. platydactylus* were fragmentary and destroyed by Allied bombardment in World War II.

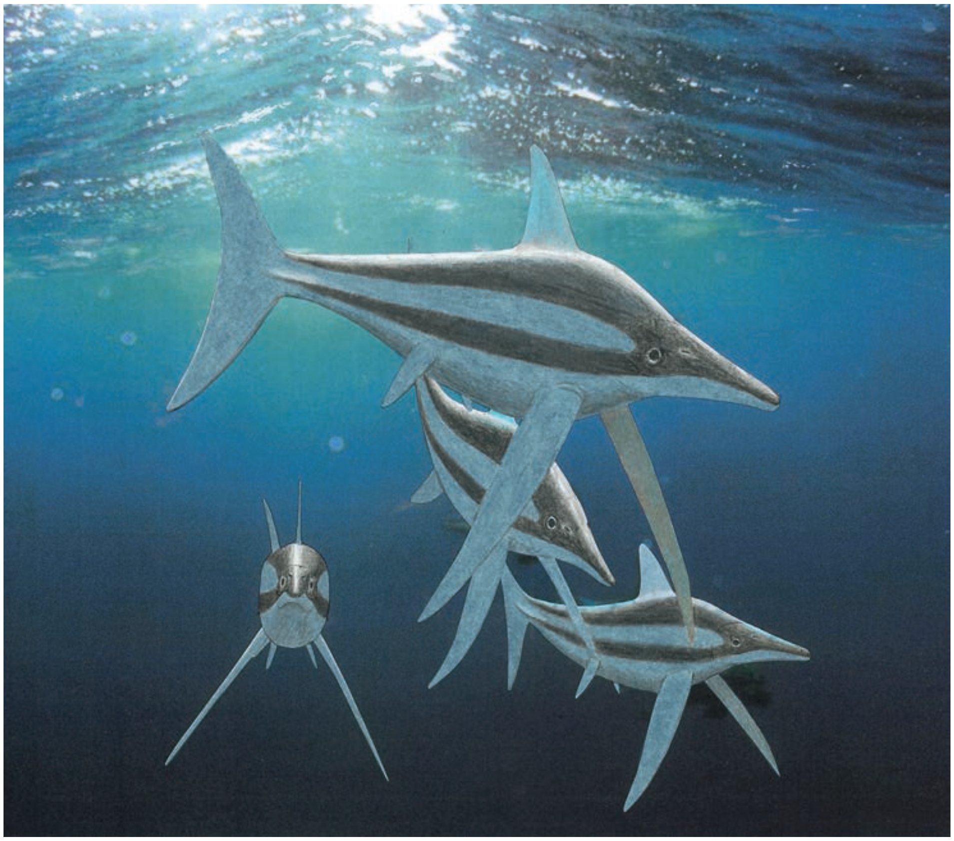
### *Longirostra australis* or *longmani*

**6 m (20 ft) TL, 1 tonne**

**FOSSIL REMAINS** Skull and majority of skeleton, other remains.
**ANATOMICAL CHARACTERISTICS** Head large, snout very long, fairly robust, teeth numerous, medium sized, stout. Foreflipper very large, consists of a pavement of nine rows of elements in which radius and ulna are barely larger than rest.
**AGE** Early Cretaceous; middle to late Albian.
**DISTRIBUTION AND FORMATIONS** Northeastern Australia; Toolebuc, Allaru Mudstone.
**HABITAT** Shallow seaway, temperate.
**HABITS** Combined high speed and maneuverability.
**NOTES** Whether all specimens are one species is not certain, correct species designation also uncertain. Usual placement in *Platypterygius* not correct, so subgeneric name applies. Remains of small enantiornithine coastal bird have been found in gut region of one specimen. Shared its habitat with ?*Kronosaurus*, *Eromangasaurus*, *Cratochelone*, *Notochelone*, *Bouliachelys*.

*Longirostra australis* or *longmani*





***Longirostra australis* or *longmani***

### *Caypullisaurus bonapartei*

**0.9 m (3 ft) TL, 4 kg (8 lb)**

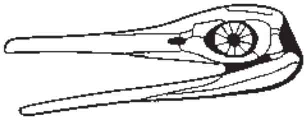
FOSSIL REMAINS Two skulls and partial skeleton.
ANATOMICAL CHARACTERISTICS Snout not particularly elongated and sharp tipped, toothless. Flippers not large.
AGE Early Cretaceous; early Tithonian.
DISTRIBUTION AND FORMATIONS Western Argentina; lower Vaca Muerta.
HABITAT Continental shelf.
NOTES Shared its habitat with *Pliosaurus*? *patagonicus*, *Cricosaurus araucanensis*.

### Unnamed genus and species

**1.2 m (4 ft) TL, 8 kg (18 lb)**

FOSSIL REMAINS Two skulls and partial skeleton.
ANATOMICAL CHARACTERISTICS Snout moderately elongated and fairly robust with blunt tip, toothless.
AGE Late Jurassic; late Tithonian.
DISTRIBUTION AND FORMATIONS Western Argentina; middle Vaca Muerta.
HABITAT Continental shelf.
NOTES Placement in *Caypullisaurus* is problematic, may be the same genus as the next entry. Shared its habitat with *Arthropterygius*? *thalassonotus*, *Dakosaurus andiniensis*, *Sumpalla*?

***Caypullisaurus bonapartei***



**Unnamed genus and species (Tithonian age)**

**Unnamed genus and species (Berriasian age)**

### Unnamed genus and species

**1.5 m (5 ft) TL, 15 kg (30 lb)**

FOSSIL REMAINS Two skulls and partial skeleton.
ANATOMICAL CHARACTERISTICS Snout moderately elongated and more robust, with blunt tip, toothless.
AGE Early Cretaceous; lower Berriasian.
DISTRIBUTION AND FORMATIONS Western Argentina; upper Vaca Muerta.
HABITAT Continental shelf.
NOTES As per previous entry. Shared its habitat with *Cricosaurus puelchorum*, *Purranisaurus potens*.

### *Simbirskiasaurus birjukovi*

**3.5 m (12 ft) TL, 200 kg (450 lb)**

FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Nostrils divided into front and rear opening.
AGE Early Cretaceous; lower Barremian.
DISTRIBUTION AND FORMATIONS Western Russia; unnamed.
HABITAT Continental shelf.

### *Athabascasaurus bitumineus*

**3.5 m (12 ft) TL, 200 kg (450 lb)**

FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Teeth moderate in number and rather small.
AGE Early Cretaceous; earliest Albian.
DISTRIBUTION AND FORMATIONS Alberta; lower Clearwater.
HABITAT Interior seaway, polar.
NOTES Shared its habitat with *Nichollssaura*, *Wapuskanectes*.

### *Pervushovisaurus bannovkensis*

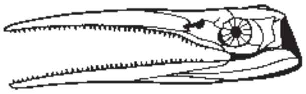
**4 m (13 ft) TL, 300 kg (650 lb)**

FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Snout very long, fairly robust, teeth numerous, rather small, robust, intermeshing.
AGE Late Cretaceous; middle Cenomanian.
DISTRIBUTION AND FORMATIONS Southwestern Russia; unnamed.
HABITAT Continental shelf.

### *Tenuirostria americanus*

**3 m (10 ft) TL, 125 kg (275 lb)**

FOSSIL REMAINS Skull, partial skeletal remains.
ANATOMICAL CHARACTERISTICS Head large, snout very long, fairly robust, teeth numerous, medium sized, stout.
AGE Late Cretaceous; middle Cenomanian.
DISTRIBUTION AND FORMATIONS Wyoming; upper Mowry Shale.
HABITAT Interior seaway.
NOTES Usual placement in much earlier *Platypterygius* not correct, so subgeneric name applies. Last known ichthyosaur.



*Tenuirostria americanus*

# SQUAMATES (LIZARDS AND SNAKES)

SMALL TO GIGANTIC NEODIAPSIDS FROM THE EARLY TRIASSIC TO THE MODERN ERA, GLOBAL

ANATOMICAL CHARACTERISTICS Diverse. Fully terrestrial to fully marine. Usually a flexible transverse joint at top of flat-roofed skull between snout and temporal region, lower temporal bar absent, so skulls usually strongly kinetic, coronoid process prominent. Gastralia absent. Some limbless. Extremely variable. Two temporal openings in the skull, often lost by partial opening or by closure. Ribs usually swept backward.
HABITAT AND HABITS Highly variable, fully aquatic to fully terrestrial to aerial, herbivorous to archpredatory. Lay soft-shelled eggs and give live birth, no parental care.

## LACERTILIANS (LIZARDS)

SMALL TO GIGANTIC SQUAMATES FROM THE LATE TRIASSIC TO THE MODERN ERA, GLOBAL

ANATOMICAL CHARACTERISTICS Trunks not hyperelongated. All have limbs.
HABITAT AND HABITS Very variable, fully aquatic to fully terrestrial to aerial, herbivorous to archpredatory.

### TOXICOFERANS

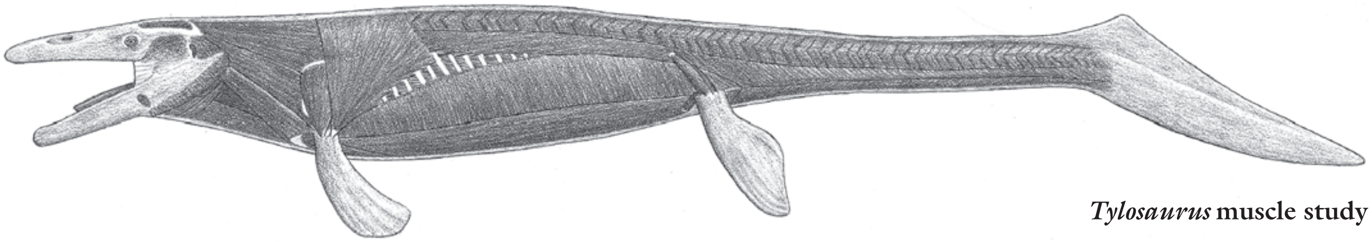
SMALL TO GIGANTIC LACERTILIANS FROM THE EARLY CRETACEOUS TO THE MODERN ERA, GLOBAL

HABITAT Terrestrial to marine.
HABITS Small to big game hunters.
NOTES The existence of this very diverse group is not certain.

### MOSASAUROIDS (SEA LIZARDS)

SMALL TO GIGANTIC TOXICOFERANS FROM THE LATE CRETACEOUS, GLOBAL

ANATOMICAL CHARACTERISTICS Fairly uniform. Highly aquatic. Heads fairly to quite large, generally subtriangular, neither very narrow nor very broad, snout at least nearly half head length, quadrate modified into



*Tylosaurus* **muscle study**

subcircular auditory depression, teeth modest in number, never very small, with bulbous roots, some on mouth roof. Aft tail flattened. Small bony scapula blade greatly expanded by large cartilage fan, clavicles reduced or absent. Limbs modified at least into stiff-jointed partial hydrofoils. Hydrodynamically streamlined, primarily axial undulators of anguilliform to transitional anguilliform-carangiform grade, flippers primarily for stability and maneuvering.
**HABITAT** Freshwaters to oceans, although dependence on periodic access to freshwater may preclude dwelling in deep oceans in most or all cases.
**HABITS** Swimming performance good to high. Ambush and/or pursuit fishers and hunters of small to large game.
**NOTES** Relationships to other lizards and snakes uncertain.

## AIGIALOSAURIDS

### SMALL MOSASAUROIDS FROM THE LATE CRETACEOUS OF NORTH AMERICA AND EUROPE

**ANATOMICAL CHARACTERISTICS** Aft tail straight. Limbs short, modified into stiffened paddles, fingers and toes present but not highly elongated, presumably webbed. Primarily axial undulators of anguilliform grade, limbs primarily for stability and maneuvering, pressed tight to body when hydrocruising.
**HABITAT** Coastal and brackish shorelines, lagoons, reefs, estuaries.
**HABITS** Swimming performance good. Shallow-water ambush and pursuit fishers of small to medium-sized game. Possibly bred and nested on beaches.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

### *Aigialosaurus dalmaticus*

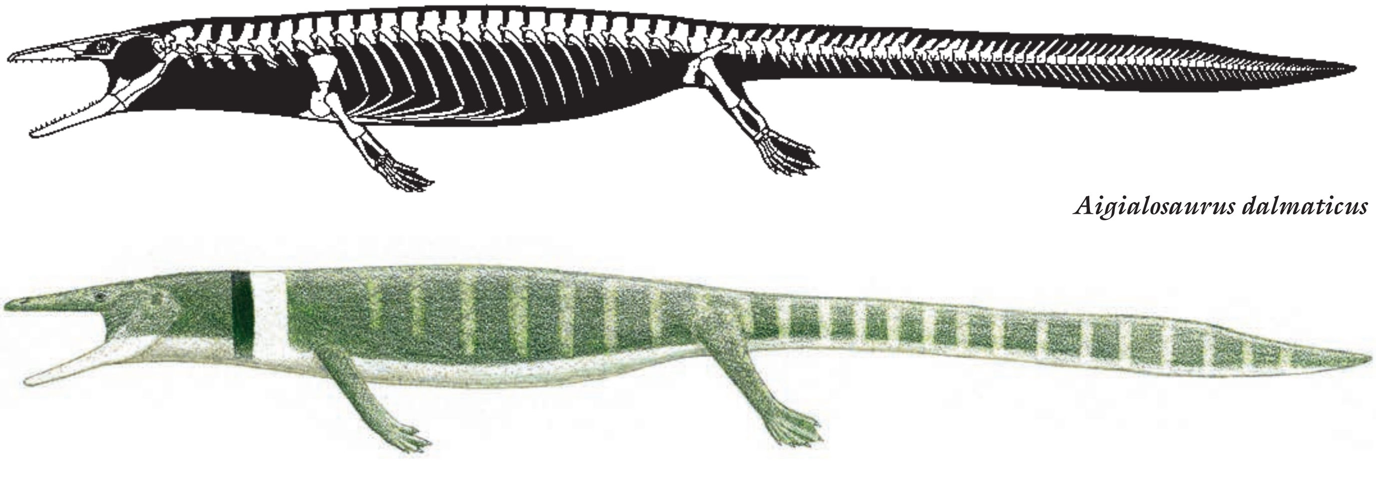
**1.15 m (3.8 ft) TL, 3 kg (6.5 lb)**

**FOSSIL REMAINS** Majority of two skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Teeth rather small and widely spaced. Arm and leg similar in size.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Croatia; unnamed.
**HABITAT** Island archipelago shallows.
**NOTES** *Opetiosaurus bucchichi* may be the same species. May have shared its habitat with *Pontosaurus lesinensis.*

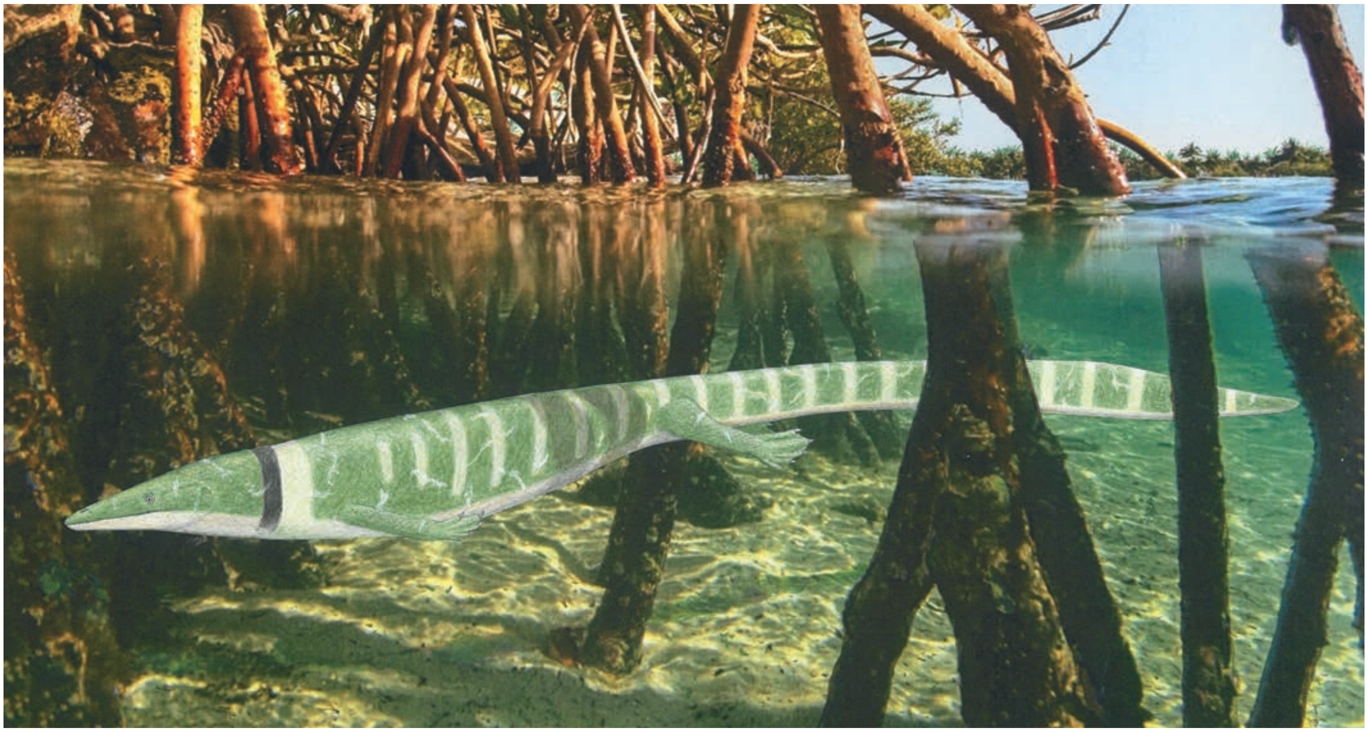
### *Komensaurus carrolli*

**1 m (3.3 ft) TL, 2 kg (4.5 lb)**

**FOSSIL REMAINS** Minority of skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Slovenia; upper Povir.
**HABITAT** Island archipelago shallows.



*Aigialosaurus dalmaticus*



***Aigialosaurus dalmaticus***

**NOTES** Shared its habitat with *Adriosaurus suessi*, *A.? skrbinensis*, *A.? microbrachis*, *Acteosaurus*, *Eidolosaurus*, *Mesoleptos*, *Carsosaurus.*

### *Carsosaurus marchesetti*

**1.5 m (5 ft) TL, 6 kg (13 lb)**

**FOSSIL REMAINS** Majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Slovenia; upper Povir.
**HABITAT** Island archipelago shallows.

### *Vallecillosaurus donrobertoi*

**1.3 m (4.3 ft) TL, 4.5 kg (10 lb)**

**FOSSIL REMAINS** Partial skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; early Turonian.
**DISTRIBUTION AND FORMATIONS** Northern Mexico; Agua Nueva.
**HABITAT** Continental nearshore.
**NOTES** Phylogenetic position not certain.

### *Portunatasaurus krambergeri*

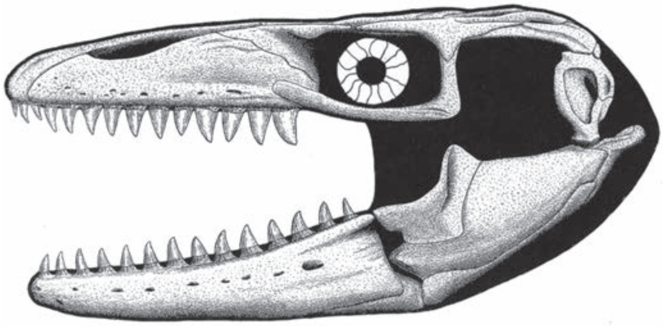
**1 m (3.3 ft) TL, 2 kg (4.5 lb)**

**FOSSIL REMAINS** Skull and majority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Fingers elongated into protoflipper.
**AGE** Late Cretaceous; Cenomanian or Turonian.
**DISTRIBUTION AND FORMATIONS** Croatia; unnamed.
**HABITAT** Island archipelago shallows.
**NOTES** Phylogenetic position not certain.

## MOSASAURIDS

**MEDIUM-SIZED TO GIGANTIC MOSASAUROIDS FROM THE LATE CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Tongues probably stout. Ribcage deep only at chest, short-ribbed lumbar



***Prognathodon***
**(Mosasaurids)**

region aft. Vertebrae at downward flexure of aft tail supported an upper tail fin. Limbs clawless full flippers with increased number of distal elements, outer finger and toe divergent from others. Hydrodynamically well-streamlined, anguilliform to transitional anguilliform-carangiform swimmers. Skin scales small, well ordered, diamond shaped, subtly keeled fore and aft on top of body, smooth on underside.
**HABITAT** Freshwaters to deep oceans.
**HABITS** Swimming performance very good to high. Fishers and hunters of small to big game, including large shelled ammonoids. Probably gave live birth.

### *Goronyosaurus nigeriensis*
**5 m (16 ft) TL, 300 kg (650 lb)**

**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Snout long, robust, subrectangular, lower jaw same, teeth large.
**AGE** Late Cretaceous; middle Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Nigeria; Dukamaje.
**HABITAT** Continental coastal.

## RUSSELLOSAURANS

**MEDIUM-SIZED TO GIGANTIC MOSASAURIDS FROM THE LATE CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Anguilliform to transitional anguilliform-carangiform swimmers.

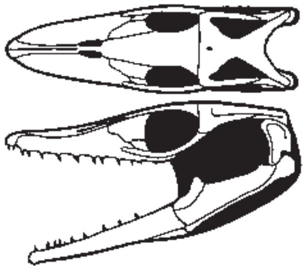
## TETHYSAURINES

**MEDIUM-SIZED TO LARGE RUSSELLOSAURANS FROM THE LATE CRETACEOUS OF EUROPE AND AFRICA**

**ANATOMICAL CHARACTERISTICS** Tail vertebrae at modest downward flexure supported a modest upper tail fin. Anguilliform swimmers.
**HABITAT** Freshwaters to continental coastal.
**HABITS** Swimming performance very good. Ambush and pursuit fishers and hunters of small to big game.

### *Tethysaurus nopscai*
**3 m (10 ft) TL, 70 kg (150 lb)**

**FOSSIL REMAINS** Skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Head fairly narrow, snout somewhat delicate, teeth medium sized.
**AGE** Late Cretaceous; early Turonian.
**DISTRIBUTION AND FORMATIONS** Morocco; unnamed.
**HABITAT** Continental shallows.



*Tethysaurus nopscai*

### *Pannoniasaurus inexceptatus*
**6 m (20 ft) TL, 550 kg (1,200 kg)**

**FOSSIL REMAINS** Partial specimens.
**ANATOMICAL CHARACTERISTICS** Head somewhat shallow.
**AGE** Late Cretaceous; Santonian.
**DISTRIBUTION AND FORMATIONS** Hungary; upper Csehbanya.
**HABITAT** Rivers and lakes.
**HABITS** Flattened head and river habitat suggest crocodile-like aquatic lifestyle, may have snatched land animals when available.
**NOTES** Indicates that some mosasaurs inhabited freshwaters.

## YAGUARASAURINES

**MEDIUM-SIZED RUSSELLOSAURANS FROM THE LATE CRETACEOUS OF THE AMERICAS**

**ANATOMICAL CHARACTERISTICS** Tail vertebrae at modest downward flexure supported a modest upper tail fin. Anguilliform swimmers.
**HABITAT** Coastal.
**HABITS** Swimming performance very good. Ambush and pursuit fishers and hunters of small to big game.

### *Yaguarasaurus columbianus*
**5 m (16.5 ft) TL, 300 kg (650 lb)**

**FOSSIL REMAINS** Skull and minority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Late Cretaceous; late Turonian.
**DISTRIBUTION AND FORMATIONS** Colombia; Hondita or La Frontera.
**HABITAT** Continental coastal.

### *Russellosaurus coheni*
**3 m (10 ft) TL, 70 kg (150 lb)**

**FOSSIL REMAINS** Majority of skull.
**ANATOMICAL CHARACTERISTICS** Head somewhat shallow, teeth large.
**AGE** Late Cretaceous; middle Turonian.

*Russellosaurus coheni*

**DISTRIBUTION AND FORMATIONS** Northeastern Texas; lower Arcadia Park.
**HABITAT** Interior seaway, coastal.
**NOTES** Shared its habitat with *Dallasaurus.*

## TYLOSAURINES

### LARGE TO GIGANTIC RUSSELLOSAURANS FROM THE LATE CRETACEOUS, GLOBAL

**ANATOMICAL CHARACTERISTICS** Heads large, somewhat shallow, snouts long, jaw tips somewhat squared off and without front teeth. Fore and aft flippers similar in size. Tail vertebrae at modest downward flexure supported a modest upper tail fin. Anguilliform swimmers.
**HABITAT** Coastal.
**HABITS** Swimming performance very good. Ambush and pursuit fishers and hunters of small to big game.

### *Tylosaurus nepaeolicus*

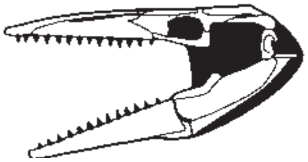
**8.5 m (28 ft) TL, 1.8 tonnes**

**FOSSIL REMAINS** Two skulls, adult partial, minority of skeleton, some soft tissues.
**ANATOMICAL CHARACTERISTICS** Snout shallow, teeth medium sized, intermeshing. Coloration appears to have been dark overall.
**AGE** Late Cretaceous; late Coniacian to late Santonian?
**DISTRIBUTION AND FORMATIONS** Kansas; lower to upper Niobrara?
**HABITAT** Interior seaway was shifting from maximum to less broad and deep.
**NOTES** *T. kansasensis* is probably a juvenile of this species. Some of the later specimens assigned to this species are probably unnamed species. May be the direct ancestor of *T. proriger.*

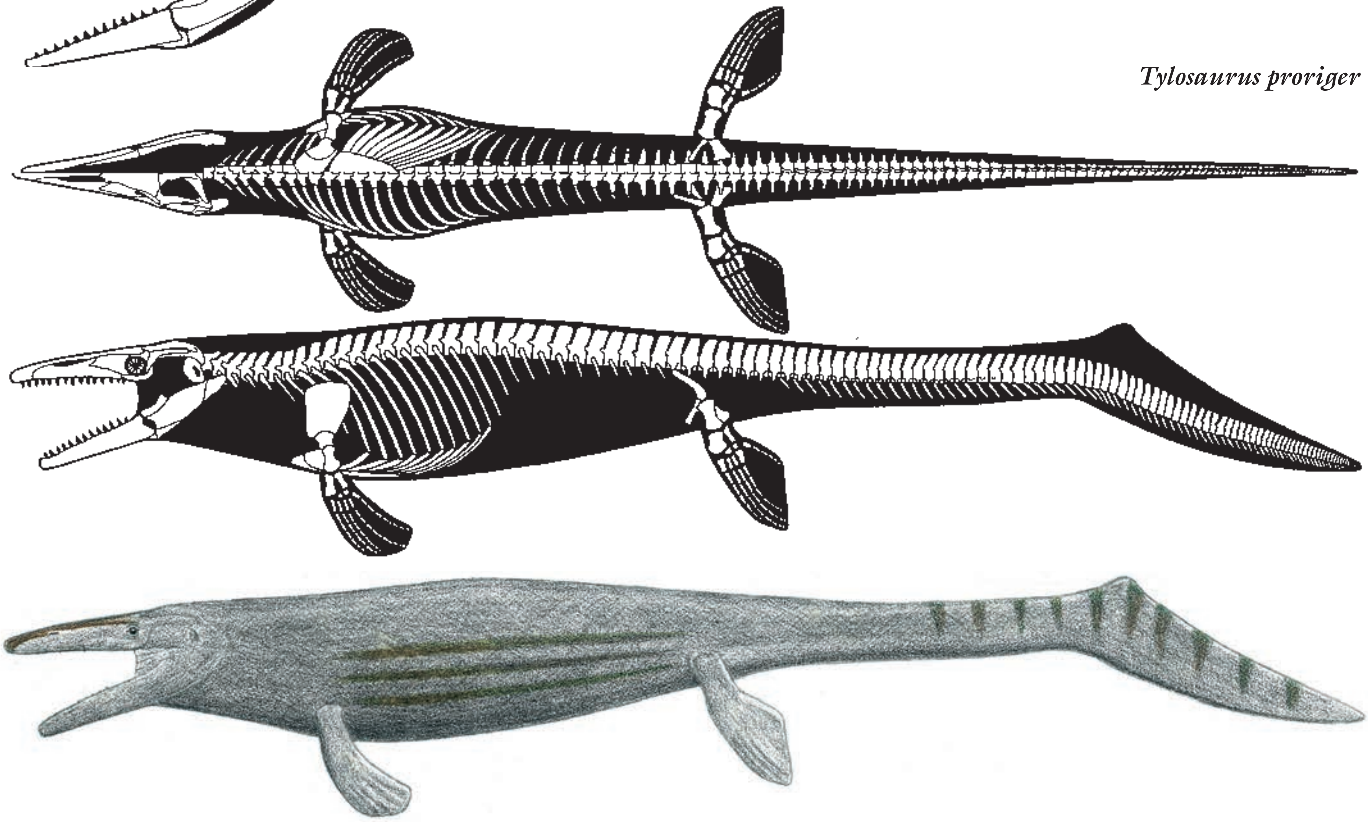
### *Tylosaurus proriger*

**13 m (43 ft) TL, 6.7 tonnes**

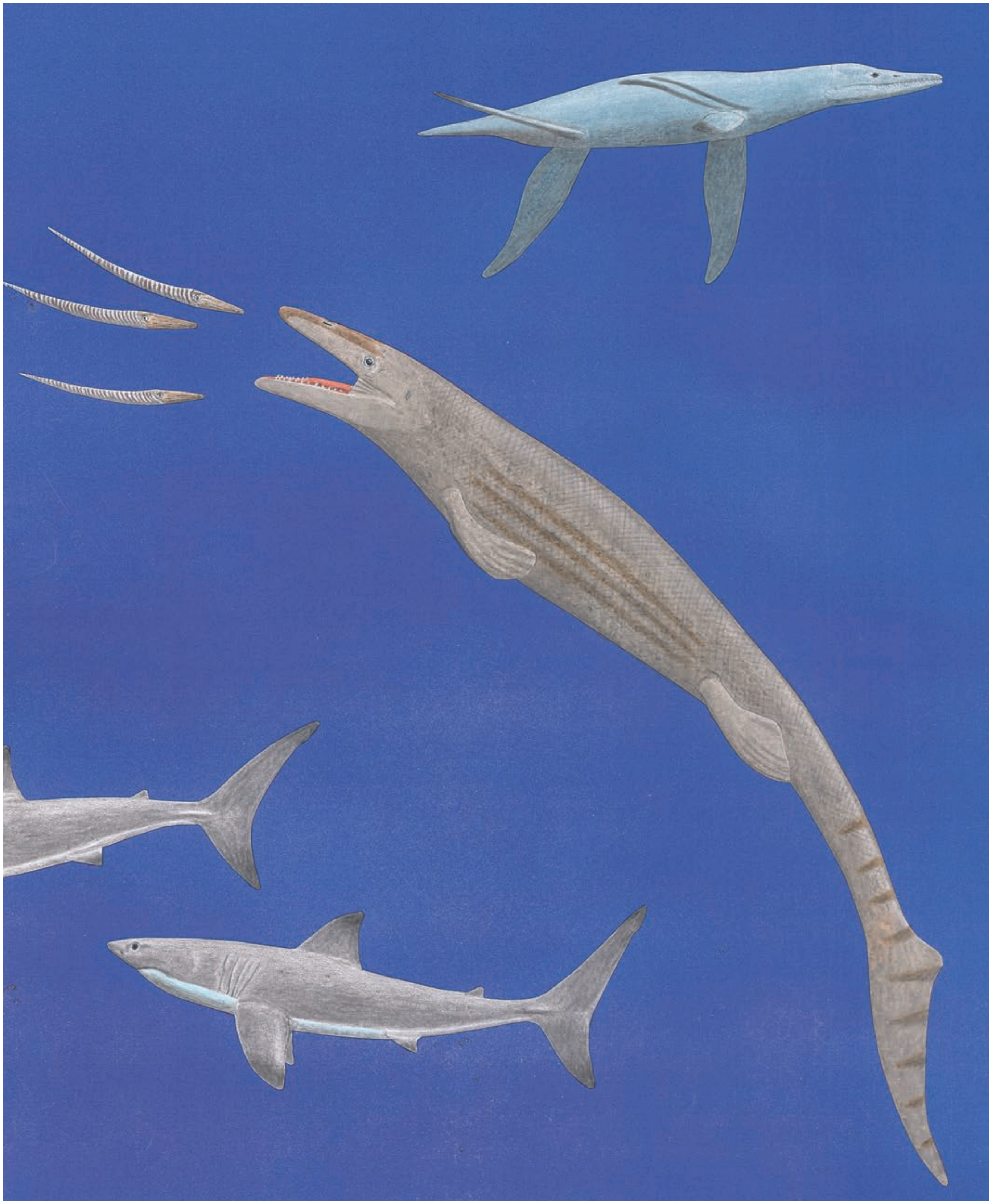
**FOSSIL REMAINS** Several skulls and skeletons of varying completeness.
**ANATOMICAL CHARACTERISTICS** Snout robust, teeth large.
**AGE** Late Cretaceous; middle Santonian to early Campanian.
**DISTRIBUTION AND FORMATIONS** Kansas, Manitoba; upper Niobrara, lower Pierre Shale.



*Tylosaurus nepaeolicus*



*Tylosaurus proriger*



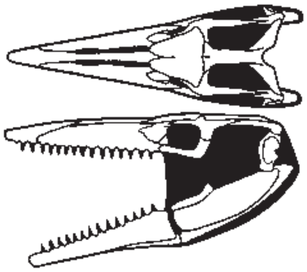
*Tylosaurus proriger* and *Dolichorhynchops bonneri*

**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** Shared its habitat with *Styxosaurus browni*, *Elasmosaurus*, *Dolichorhynchops bonneri*, *Latoplatecarpus*, *Globidens*? *dakotensis*, *Toxochelys latiremus*. May be the direct ancestor of *Tylosaurus pembinensis*.

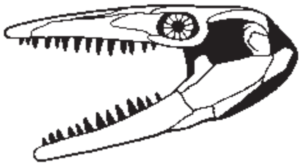
### *Tylosaurus pembinensis*

**12 m (40 ft) TL, 5 tonnes**

**FOSSIL REMAINS** Majority of skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth medium sized, tightly intermeshing.
**AGE** Late Cretaceous; middle Campanian.
**DISTRIBUTION AND FORMATIONS** Manitoba; middle Pierre Shale.
**HABITAT** Interior seaway was becoming much narrower.
**NOTES** Shared its habitat with *Plioplatecarpus*? *primaevus*. May be the direct ancestor of *T. saskatchewanensis*.



*Tylosaurus pembinensis*



*Tylosaurus saskatchewanensis*

### *Tylosaurus saskatchewanensis*

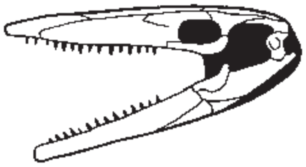
**9 m (30 ft) TL, 2 tonnes**

**FOSSIL REMAINS** Skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth quite large.
**AGE** Late Cretaceous; late Campanian.
**DISTRIBUTION AND FORMATIONS** Saskatchewan; upper Bearpaw Shale.
**HABITAT** Interior seaway was becoming very narrow.
**NOTES** Shared its habitat with *Nakonanectes*, *Terminonatator*, *Plioplatecarpus*? *primaevus*. May be the direct ancestor of *T. bernardi*.

### *Tylosaurus* or *Hainosaurus bernardi*

**12 m (40 ft) TL, 5 tonnes**

**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Snout deep, teeth rather small.
**AGE** Late Cretaceous; early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Belgium; Ciply Phosphatic Chalk.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Prognathodon solvayi*, *Phosphorosaurus*, *Mosasaurus lemonnieri*.



*Tylosaurus* or *Hainosaurus bernardi*

### *Taniwhasaurus oweni*

**7 m (23 ft) TL, 3 tonnes**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; earliest Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Southern New Zealand; lower Conway.
**HABITAT** Island coastal.

### *Taniwhasaurus* (or *Lakumasaurus*) *antarcticus*

**Adult size uncertain**

**FOSSIL REMAINS** Majority of skull and minority of skeleton, possibly juvenile.
**ANATOMICAL CHARACTERISTICS** Teeth large.
**AGE** Late Cretaceous; late Campanian.
**DISTRIBUTION AND FORMATIONS** Antarctic Peninsula; Santa Marta.
**HABITAT** Continental coastal, polar.

### *Kaikaifilu hervei*

**10 m (33 ft) TL, 3 tonnes**

**FOSSIL REMAINS** Partial skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Antarctic Peninsula; Lopez de Bertodano.
**HABITAT** Continental coastal, polar.
**NOTES** Shared its habitat with *Morturneria*.

## PLIOPLATECARPINES

**MEDIUM-SIZED RUSSELLOSAURANS FROM THE LATE CRETACEOUS OF NORTH AMERICA AND AFRICA**

**ANATOMICAL CHARACTERISTICS** Heads medium sized, teeth medium sized. Tail vertebrae at strong downward flexure supported a fairly large upper tail fin. Transitional anguilliform-carangiform swimmers.
**HABITAT** Coastal to deep oceans.
**HABITS** Swimming performance very good to high. Ambush and especially pursuit fishers and hunters of small to big game.
**NOTES** Absence from at least some other seas probably reflects lack of sufficient sampling. This group appears to have evolved high-speed swimming independently from Mosasaurinians.

### *Angolasaurus bocagei*

**4 m (13 ft) TL, 200 kg (450 lb)**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; middle or late Turonian.
**DISTRIBUTION AND FORMATIONS** Angola; Tadi.
**HABITAT** Continental shelf.

### *Selmasaurus? johnsoni*

**Adult size uncertain**

**FOSSIL REMAINS** Partial skull and skeleton, possibly immature.
**ANATOMICAL CHARACTERISTICS** Teeth large, long spikes.
**AGE** Late Cretaceous; early Santonian.
**DISTRIBUTION AND FORMATIONS** Kansas; lower Niobrara.
**HABITAT** Interior seaway was at maximum breadth and depth.
**NOTES** Placement in the much later genus *Selmasaurus* is uncertain. Shared its habitat with *Ectenosaurus*, *Plesioplatecarpus*, *Chelosphargis.*

### *Selmasaurus russelli*

**Adult size uncertain**

**FOSSIL REMAINS** Minority of skull and skeleton, possibly immature.
**ANATOMICAL CHARACTERISTICS** Skull appears to have been akinetic.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** Alabama; lower Mooreville Chalk.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Polycotylus latipinnis*, *Protostega*.

### *Gavialimimus almaghribensis*

**5 m (16 ft) TL, 350 kg (750 lb)**

**FOSSIL REMAINS** Majority of skull, badly crushed.
**ANATOMICAL CHARACTERISTICS** Head elongated, snout long and narrow, teeth large, stout, widely spaced, not numerous.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Morocco; upper Couche III.
**HABITAT** Continental shelf.

### *Ectenosaurus clidastoides*

**6 m (20 ft) TL, 600 kg (1,300 lb)**

**FOSSIL REMAINS** Complete skull with partial skeleton, severely flattened, skin, internal fibers.
**ANATOMICAL CHARACTERISTICS** Head large, fairly narrow, snout long, teeth medium sized. Scales small, 2 × 3 mm.
**AGE** Late Cretaceous; early Santonian.
**DISTRIBUTION AND FORMATIONS** Kansas, Texas; lower Niobrara.
**HABITAT** Interior seaway was at maximum breadth and depth.
**NOTES** Original specimen in a German museum lost during World War II. Shared its habitat with *Selmasaurus? johnsoni*, *Plesioplatecarpus*, *Chelosphargis.*

### *Plesioplatecarpus planifrons*

**5 m (16 ft) TL, 350 kg (750 lb)**

**FOSSIL REMAINS** A number of skulls and skeletons of varying completeness, often severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Snout rather short, head broad.
**AGE** Late Cretaceous; middle Coniacian to early Santonian.
**DISTRIBUTION AND FORMATIONS** Kansas, Alabama; lower Niobrara, upper Eutaw.
**HABITAT** Interior seaway was at maximum breadth and depth, continental shelf.
**NOTES** Shared its habitat with *Selmasaurus? johnsoni*, *Ectenosaurus*, *Chelosphargis.*

### *Latoplatecarpus nichollsae*

**Adult size uncertain**

**FOSSIL REMAINS** Two skulls complete and partial, severely crushed, two partial skeletons, possibly immature.
**ANATOMICAL CHARACTERISTICS** Quadrate and tympanic circle large, teeth large.
**AGE** Late Cretaceous; early Campanian.

*Latoplatecarpus nichollsae*

**DISTRIBUTION AND FORMATIONS** Manitoba; lower Pierre Shale.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** Probably includes *L. willistoni*. Shared its habitat with *Styxosaurus browni*, *Elasmosaurus*, *Dolichorhynchops bonneri*, *Tylosaurus proriger*, *Globidens? dakotensis*, *Toxochelys latiremus*.

### *Platecarpus tympanicus*

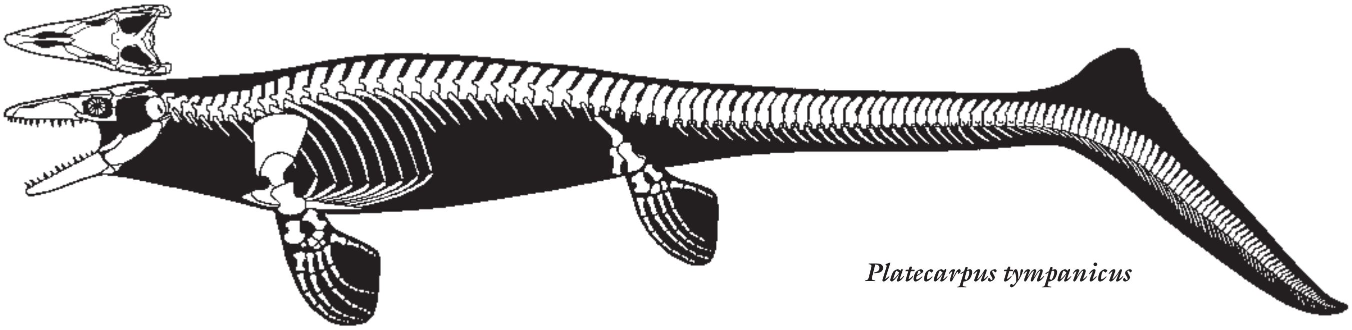
**5.4 m (17.5 ft) TL, 440 kg (1,000 lb)**

**FOSSIL REMAINS** Skull and numerous other remains.
**ANATOMICAL CHARACTERISTICS** Snout not elongated, teeth medium sized. Fore and aft flippers similar in size. Scales fairly large, 3.5 × 4.5 mm.
**AGE** Late Cretaceous; middle Santonian to earliest Campanian.
**DISTRIBUTION AND FORMATIONS** Kansas; middle to uppermost Niobrara.
**HABITAT** Interior seaway was shifting from maximum to less broad and deep.
**NOTES** Shared its habitat with *Styxosaurus snowii*, *Polycotylus latipinnis*, *Dolichorhynchops osborni*, *Eonatator sternbergii*, *Clidastes propython*, *Ctenochelys stenoporus*, *Protostega gigas*. May be the direct ancestor of *Plioplatecarpus? primaevus.*

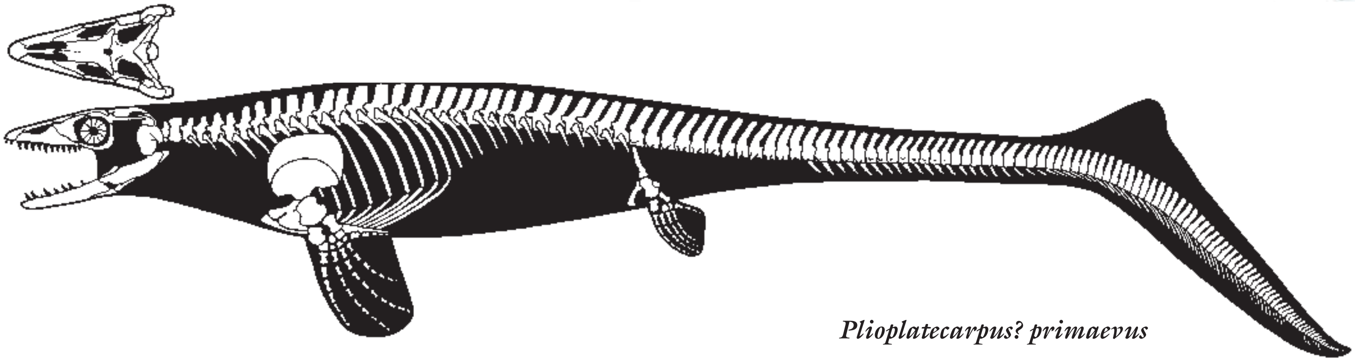
### *Plioplatecarpus? primaevus*

**3.9 m (12.5 ft) TL, 170 kg (375 lb)**

**FOSSIL REMAINS** A number of partial skulls and skeletons, mostly immature.
**ANATOMICAL CHARACTERISTICS** Head short, orbits large. Foreflipper much larger than aft.
**AGE** Late Cretaceous; early to late Campanian or to early Maastrichtian.



*Platecarpus tympanicus*



*Plioplatecarpus? primaevus*

**DISTRIBUTION AND FORMATIONS** Dakotas, Kansas, Saskatchewan; lower to middle Pierre Shale, upper Bearpaw Shale.
**HABITAT** Interior seaway was becoming very narrow.
**HABITS** Deep water if adult orbits large.
**NOTES** May include *P. peckensis*. Shared its habitat with *Nakonanectes*, *Terminonatator*, *Tylosaurus pembinensis*, *T. saskatchewanensis*.

### *Plioplatecarpus? houzeaui*

**Adult size uncertain**

**FOSSIL REMAINS** Crushed skull and partial skeleton, probably immature, possibly other remains.
**ANATOMICAL CHARACTERISTICS** Teeth fairly large.
**AGE** Late Cretaceous; middle Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Belgium; Brown Phosphate Chalk.
**HABITAT** Island archipelago shallows.
**HABITS** Deep water.
**NOTES** May be the direct ancestor of *P. marshi*.

### *Plioplatecarpus marshi*

**5 m (16 ft) TL, 350 kg (750 lb)**

**FOSSIL REMAINS** Partial skull and several partial skeletons.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Belgium; upper Gulpen.
**HABITAT** Island archipelago shallows.
**HABITS** Deep water.
**NOTES** May be the direct descendant of *P. houzeaui*. Whether any other known species belong to this genus is at best uncertain.

## MOSASAURANS

**SMALL TO GIGANTIC MOSASAURIDS FROM THE LATE CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Anguilliform to transitional anguilliform-carangiform swimmers.

## HALISAURINES

**SMALL TO MEDIUM-SIZED MOSASAURANS FROM THE LATE CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Heads not very large. Tail vertebrae at modest downward flexure supported a modest upper tail fin. Anguilliform swimmers.
**HABITAT** Continental coastal.
**HABITS** Swimming performance very good. Ambush and pursuit fishers and hunters of small to big game.

### *Halisaurus platyspondylus*

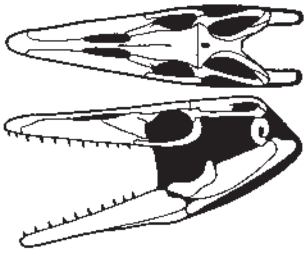
**4 m (13 ft) TL, 200 kg (450 lb)**

**FOSSIL REMAINS** Partial skulls and skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; middle to late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** New Jersey, Maryland; New Egypt, Severn.
**HABITAT** Continental coastal.

### *Halisaurus arambourgi*

**5 m (16 ft) TL, 350 kg (750 lb)**

**FOSSIL REMAINS** Two partial skulls and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Snout not long, teeth widely spaced, medium sized.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Morocco; unnamed.
**HABITAT** Continental coastal.



***Halisaurus arambourgi***

### *Eonatator sternbergii*

**3.5 m (11 ft) TL, 100 kg (220 lb)**

**FOSSIL REMAINS** Partial skull and majority and minority of two skeletons.
**ANATOMICAL CHARACTERISTICS** Head fairly large, fairly narrow, snout elongated. Flippers medium and similar in size.
**AGE** Late Cretaceous; earliest Campanian.
**DISTRIBUTION AND FORMATIONS** Kansas; uppermost Niobrara.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** Shared its habitat with *Styxosaurus snowii*, *Polycotylus latipinnis*, *Dolichorhynchops osborni*, *Platecarpus tympanicus*, *Clidastes propython*, *Ctenochelys stenoporus*, *Protostega gigas*.

### *Eonatator? coellensis*

**2.8 m (9 ft) TL, 50 kg (110 lb)**

**FOSSIL REMAINS** Skull and majority of skeleton with soft tissues.

**ANATOMICAL CHARACTERISTICS** Head fairly large, fairly narrow, snout elongated. Flippers medium and similar in size.
**AGE** Late Cretaceous; Campanian.
**DISTRIBUTION AND FORMATIONS** Colombia; upper Lydite.
**HABITAT** Continental coastal.

### *Phosphorosaurus ponpetelegans*
**Adult size not certain**

**FOSSIL REMAINS** Majority of skull and minority of skeleton, possibly immature.
**ANATOMICAL CHARACTERISTICS** Orbits face somewhat forward and may have had overlapping fields of vision.
**AGE** Late Cretaceous; earliest Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Japan; Hakobuchi.
**HABITAT** Island coastal.

### *Phosphorosaurus ortliebi*
**Adult size not certain**

**FOSSIL REMAINS** Partial skull, possibly immature.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Belgium; Ciply Phosphatic Chalk.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Tylosaurus* or *Hainosaurus bernardi*, *Prognathodon solvayi*, *Mosasaurus lemonnieri*.

## MOSASAURINES

**SMALL TO GIGANTIC MOSASAURANS FROM THE LATE CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Tail vertebrae at modest downward flexure supported a modest upper tail fin. Anguilliform swimmers.
**HABITAT** Coastal.
**HABITS** Swimming performance very good. Ambush and especially pursuit fishers and hunters of small to big game.

## MOSASAURINE MISCELLANEA

### *Dallasaurus turneri*
**1 m (3.3 ft) TL, 2 kg (4.5 lb)**

**FOSSIL REMAINS** Partial skull and two partial skeletons.
**ANATOMICAL CHARACTERISTICS** Flippers not fully developed.
**AGE** Late Cretaceous; middle Turonian.
**DISTRIBUTION AND FORMATIONS** Texas; lower Arcadia Park Shale.
**HABITAT** Interior seaway.
**NOTES** May be a more basal mosasauroid. Shared its habitat with *Russellosaurus*.

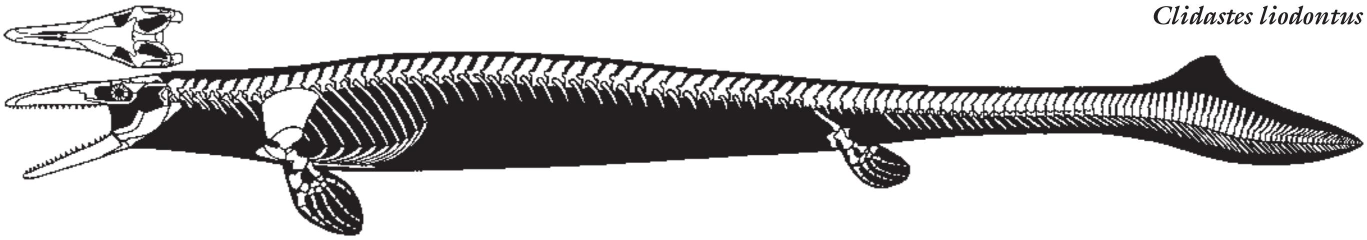
## CLIDASTINIANS

**SMALL TO GIGANTIC MOSASAURANS FROM THE LATE CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Teeth robust. Trunk elongated. Tall tail vertebrae at modest downward flexure supported a modest upper tail fin, tail including aft distal downward-flexed segment rather short. Anguilliform swimmers.
**HABITAT** Coastal.
**HABITS** Swimming performance very good. Ambush and pursuit fishers and hunters of small to big game, some crushers.

### *Clidastes liodontus*
**3 m (10 ft) TL, 55 kg (120 lb)**

**FOSSIL REMAINS** Several specimens.
**ANATOMICAL CHARACTERISTICS** Head medium sized, fairly narrow, teeth medium sized, stout. Flippers small, fore larger than aft.
**AGE** Late Cretaceous; late Coniacian to late Santonian.
**DISTRIBUTION AND FORMATIONS** Kansas, Texas; lower to middle Niobrara.
**HABITAT** Interior seaway was shifting from maximum to less broad and deep.
**NOTES** Assigned time span probably too long for a single species. May be direct ancestor of *C. propython*.

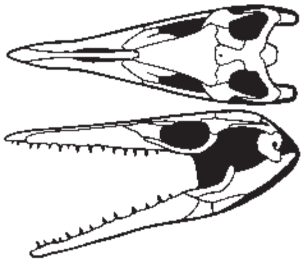

*Clidastes liodontus*

*Clidastes liodontus*

## *Clidastes propython*

**3 m (10 ft) TL, 55 kg (120 lb)**

FOSSIL REMAINS Several specimens.
ANATOMICAL CHARACTERISTICS Head shallow, teeth rather small, stout.
AGE Late Cretaceous; middle Santonian to earliest Campanian.
DISTRIBUTION AND FORMATIONS Kansas, South Dakota, Colorado; middle to uppermost Niobrara.
HABITAT Interior seaway was shifting from maximum to less broad and deep.
NOTES Shared its habitat with *Styxosaurus snowii*, *Polycotylus latipinnis*, *Dolichorhynchops osborni*, *Platecarpus tympanicus*, *Eonatator sternbergii*, *Ctenochelys stenoporus*, *Protostega gigas*.



*Clidastes propython*

## *Prognathodon? overtoni*

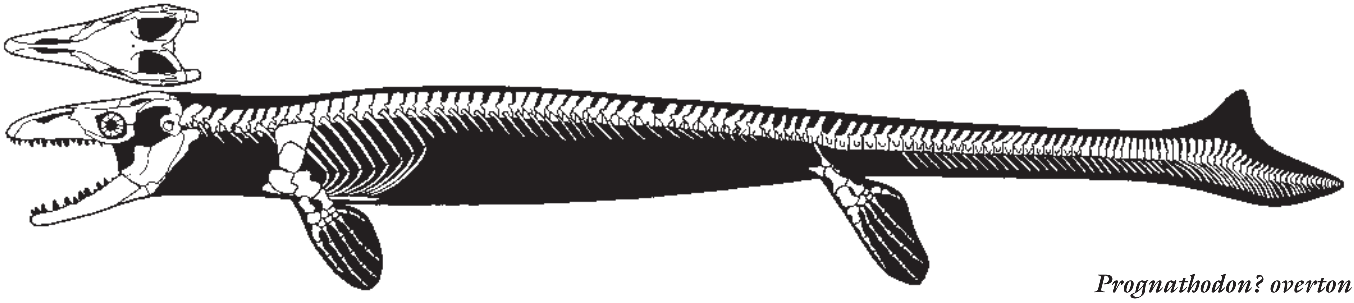
**8 m (25 ft) TL, 1 tonne**

FOSSIL REMAINS Skulls and skeletal remains.
ANATOMICAL CHARACTERISTICS Head large, fairly broad, heavily constructed, snout deep, teeth large, stout and blunted. Flippers medium and similar in size.
AGE Late Cretaceous; late Campanian.
DISTRIBUTION AND FORMATIONS South Dakota, southern Alberta; upper Pierre Shale, lower Bearpaw Shale.
HABITAT Interior seaway was becoming much narrower.
HABITS Specialized for crushing hard-shelled prey.
NOTES Shared its habitat with *Albertonectes*, *Dolichorhynchops herschelensis*, *Mosasaurus? missouriensis*, *Archelon*.

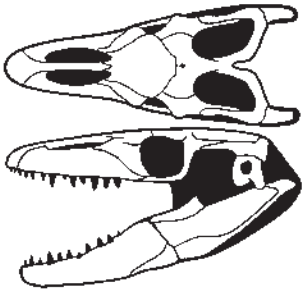
## *Prognathodon? currii*

**11 m (36 ft) TL, 2.8 tonnes**

FOSSIL REMAINS Skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head large, fairly broad, heavily constructed, snout deep, teeth large, stout, and blunted.
AGE Late Cretaceous; late Campanian.
DISTRIBUTION AND FORMATIONS Israel; upper Mishash.



*Prognathodon? overtoni*



*Prognathodon? currii*

**HABITAT** Continental shelf.
**HABITS** Specialized for crushing hard-shelled prey.

### *Prognathodon solvayi*

**Adult size uncertain**

**FOSSIL REMAINS** Adult partial skull, immature skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth large.
**AGE** Late Cretaceous; early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Belgium; Ciply Phosphatic Chalk.
**HABITAT** Island archipelago shallows.
**HABITS** Specialized for crushing hard-shelled prey.
**NOTES** *P. giganteus* may be the adult of this species. The assignment of at least some other species to this genus is uncertain. Shared its habitat with *Tylosaurus* or *Hainosaurus bernardi*, *Phosphorosaurus*, *Mosasaurus lemonnieri*.

### *Tenerasaurus* (or *Prognathodon?*) *hashimi*

Adult size uncertain

**FOSSIL REMAINS** Majority of skeleton, with soft tissues, probably immature.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Jordan; upper Muwaqqar Chalk.
**HABITAT** Continental shelf.
**NOTES** Whether this is a distinct genus or within *Prognathodon* is not certain.

### Unnamed genus and species

**5 m (16 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Majority of skull.
**ANATOMICAL CHARACTERISTICS** Head fairly heavily constructed, snout shallow, teeth medium sized, stout.
**AGE** Late Cretaceous; Campanian or Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Northern New Zealand; Maungataniwha Sandstone.
**HABITAT** Island coastal.
**NOTES** Placement within *Prognathodon overtoni* incorrect.

### *Globidens alabamaensis*

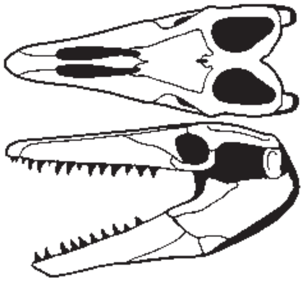
**4.5 m (15 ft) TL, 200 kg (450 lb)**

**FOSSIL REMAINS** Minority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Skull heavily constructed, teeth short, blunt, aft set fairly large knobs.
**AGE** Late Cretaceous; middle Campanian.
**DISTRIBUTION AND FORMATIONS** Alabama; upper Mooreville Chalk.
**HABITAT** Continental shelf.
**HABITS** Highly specialized for crushing hard-shelled prey.
**NOTES** Shared its habitat with *Toxochelys moorevillensis*, *Corsochelys*, *Ctenochelys acris*, *Prionochelys.*

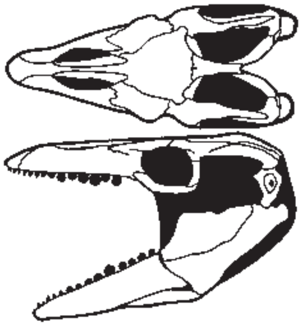
### *Globidens? dakotensis*

**6 m (20 ft) TL, 450 kg (1,000 lb)**

**FOSSIL REMAINS** Majority of skull.
**ANATOMICAL CHARACTERISTICS** Head fairly broad, heavily constructed, especially lower jaw, snout rather short, teeth short, blunt, aft set fairly large knobs.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** South Dakota; lower Pierre Shale.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**HABITS** Highly specialized for crushing hard-shelled prey.
**NOTES** Whether this is the same genus as incomplete *G. alabamaensis* is not certain. Additional specimens from other locations may or may not represent the species. Shared its habitat with *Styxosaurus browni*, *Elasmosaurus*, *Dolichorhynchops bonneri*, *Tylosaurus proriger*, *Latoplatecarpus*, *Toxochelys latiremus.*



**Unnamed genus and species (Maungataniwha Sandstone)**



***Globidens? dakotensis***

### *Globidens? simplex*

**5.5 m (18 ft) TL, 350 kg (750 lb)**

**FOSSIL REMAINS** Partial skull, other remains.
**ANATOMICAL CHARACTERISTICS** Skull heavily constructed, teeth short, blunt knobs, especially aft.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Angola; unnamed.
**HABITAT** Continental shelf.
**HABITS** Highly specialized for crushing hard-shelled prey.
**NOTES** That this species belongs to the same genus as the much earlier *Globidens* is problematic.

## MOSASAURINIANS

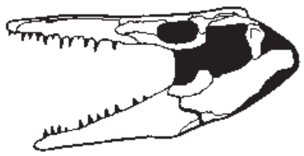
**LARGE TO GIGANTIC MOSASAURANS FROM THE LATE CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Head medium sized, teeth sharp. Tall tail vertebrae at strong downward flexure supported a fairly large upper tail fin. Transitional anguilliform-carangiform swimmers.
**HABITAT** Coastal to deep oceans.
**HABITS** Swimming performance very good to high. Pursuit fishers and hunters of small to big game.
**NOTES** This group appears to have evolved high-speed swimming independently from plioplatecarpines.

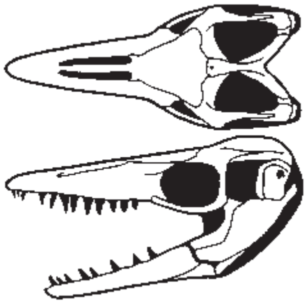
### *Moanasaurus mangahouangae*

**12 m (40 ft) TL, 4 tonnes**

**FOSSIL REMAINS** Majority of skull, minority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth medium sized.
**AGE** Late Cretaceous; Campanian and/or Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Northern New Zealand; unnamed.
**HABITAT** Island coastal and probably deep ocean.
**NOTES** Probably includes *Rikisaurus tehoensis.*



***Moanasaurus mangahouangae* or *Rikisaurus tehoensis***



***Eremiasaurus heterodontus***

### *Eremiasaurus heterodontus*

**5 m (16 ft) TL, 300 kg (650 lb)**

**FOSSIL REMAINS** Majority of two skulls and skeletons, badly damaged.
**ANATOMICAL CHARACTERISTICS** Head fairly broad, snout fairly deep, teeth large, increasingly blunted progressing aft.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Morocco; unnamed.
**HABITS** Continental shelf.

### *Plesiotylosaurus crassidens*

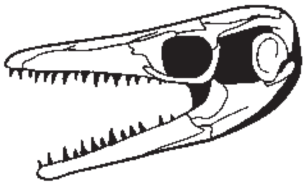
**6.5 m (21 ft) TL, 700 kg (1,500 lb)**

**FOSSIL REMAINS** Skull remains, badly damaged.
**ANATOMICAL CHARACTERISTICS** Skull heavily constructed, teeth small.
**AGE** Late Cretaceous; middle Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Central California; lower Moreno.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Plotosaurus.*

### *Mosasaurus? missouriensis*

**6.5 m (21 ft) TL, 700 kg (1,500 lb)**

**FOSSIL REMAINS** Skull and partial skeleton, other remains.
**ANATOMICAL CHARACTERISTICS** Head somewhat deep, teeth medium sized.
**AGE** Late Cretaceous; late Campanian.
**DISTRIBUTION AND FORMATIONS** South Dakota, Montana, Alberta; upper Pierre Shale, middle Bearpaw Shale.
**HABITAT** Interior seaway was becoming much narrower.
**NOTES** Shared its habitat with *Prognathodon? overtoni*, *Nichollsemys*, *Archelon*.



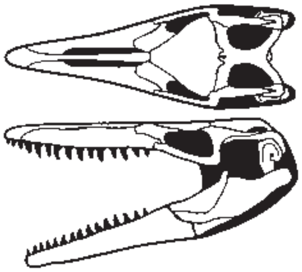
***Mosasaurus? missouriensis***

### *Mosasaurus? conodon*

**7 m (23 ft) TL, 900 kg (2,000 lb)**

**FOSSIL REMAINS** Skull and other partial specimens.
**ANATOMICAL CHARACTERISTICS** Head moderately broad, shallow, teeth fairly large.
**AGE** Late Cretaceous; late Campanian and/or early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** New Jersey, Maryland? Alabama? Arkansas? Montana? Colorado? South Dakota?; Navesink, Severn? Demopolis Chalk?

Marlbrook Chalk? upper Pierre Shale? lower Bearpaw Shale?
**NOTES** Whether this species belongs in *Mosasaurus* is uncertain. It is possible that the species is limited to the original poorly preserved specimen from New Jersey. Shared that habitat with *Cimoliasaurus*.



***Mosasaurus? conodon***

***Mosasaurus lemonnieri***

### *Mosasaurus lemonnieri*

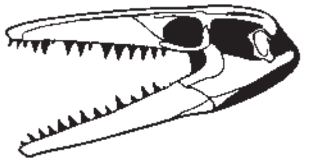
**12 m (40 ft) TL, 4.5 tonnes**

**FOSSIL REMAINS** Skulls and skeletal remains, juvenile to adult.
**ANATOMICAL CHARACTERISTICS** Head not deep, teeth rather small.
**AGE** Late Cretaceous; early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Belgium; Ciply Phosphatic Chalk.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Tylosaurus* or *Hainosaurus bernardi*, *Prognathodon solvayi*, *Phosphorosaurus*. May be the direct ancestor of *M. hoffmanni*.

### *Mosasaurus hoffmanni*

**13 m (43 ft) TL, 5.5 tonnes**

**FOSSIL REMAINS** Skulls and skeletal remains.
**ANATOMICAL CHARACTERISTICS** Head not deep, teeth large.



***Mosasaurus hoffmanni***

**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Netherlands, etc.?; Maastricht, etc.?
**HABITAT** Island archipelago shallows.
**NOTES** A classic mosasaur. Assignment of many specimens from a number of continents to this species and to the genus is uncertain, those not from the late Maastrichtian being especially problematic. May include a Russian lower jaw that may be the largest known specimen of the taxon.

### *Mosasaurus? beaugei*

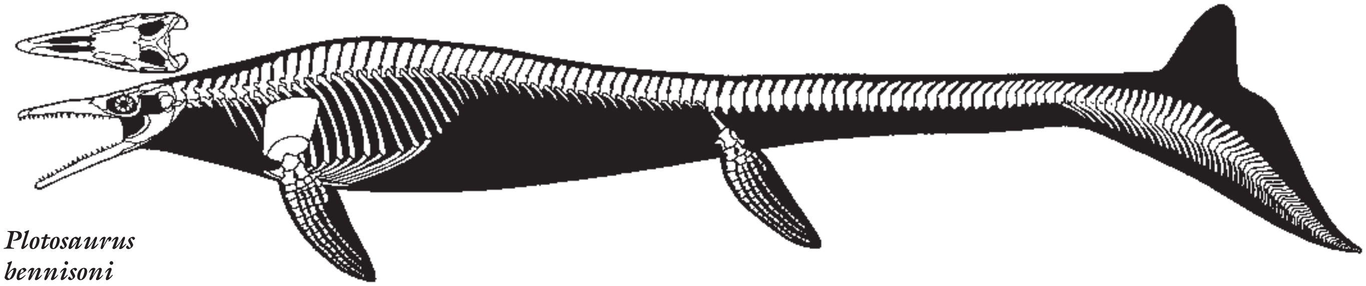
**8.5 m (28 ft) TL, 1.5 tonnes**

**FOSSIL REMAINS** Two partial skulls, other remains.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Morocco; unnamed.
**HABITAT** Continental shelf.
**NOTES** Whether this species belongs in *Mosasaurus* is uncertain.

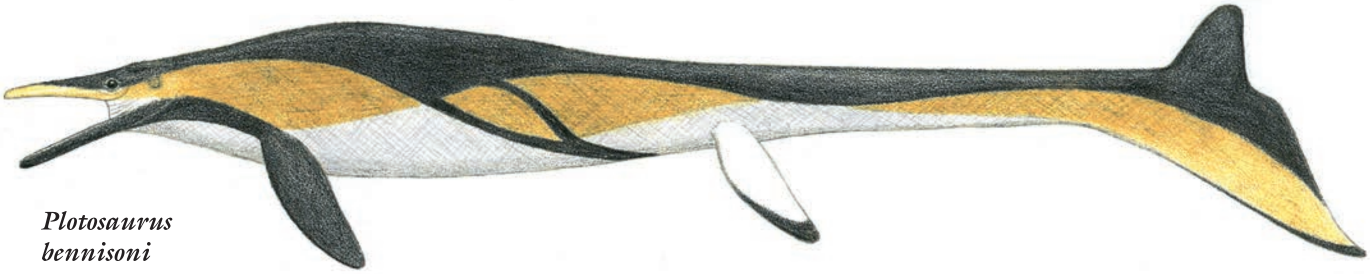
### *Plotosaurus bennisoni*

**13 m (43 ft) TL, 5.9 tonnes**

**FOSSIL REMAINS** Skull and skeletal remains, adult and immature.
**ANATOMICAL CHARACTERISTICS** Head somewhat shallow, moderately broad, teeth fairly numerous, medium sized. Chest fairly deep. Fins fairly long, narrow, similar in size fore and aft.
**AGE** Late Cretaceous; middle Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Central California; lower Moreno.
**HABITAT** Continental shelf and possibly deep ocean.
**HABITS** High-speed pursuit predator.
**NOTES** *P. tuckeri* may be adult of this species. Shared its habitat with *Plesiotylosaurus*. The fastest-swimming known mosasaur.



***Plotosaurus bennisoni***



*Plotosaurus bennisoni*

## OPHIDIOMORPHS

### SMALL TOXICOFERANS FROM THE LATE CRETACEOUS TO THE MODERN ERA, GLOBAL

**ANATOMICAL CHARACTERISTICS** Fairly diverse. Heads neither large nor heavily constructed. Vertebral series elongated and made extraflexible via a high number of vertebrae (140 or more) and extra articulations between them. Aft tails straight. Limbs at least somewhat reduced, not full flippers. Hydrodynamically streamlined, anguilliform swimmers.
**HABITAT** Coastal and brackish shorelines, lagoons, reefs, estuaries, probably accessed freshwater frequently, including rainwater atop salt water.
**HABITS** Swimming performance good. Shallow-water ambush and pursuit fishers of small to medium-sized game. Possibly bred and nested on beaches.

## DOLICHOSAURIDS

### SMALL OPHIDIOMORPHS FROM THE LATE CRETACEOUS OF EUROPE AND THE MIDDLE EAST

**ANATOMICAL CHARACTERISTICS** Uniform. Heads moderate in size, subtriangular, teeth stout, subconical, gently recurved. Trunks and tails very elongated and tails especially slender. Ribs heavily constructed. Fingers and toes usually present.
**HABITAT** Coastal and brackish shorelines, lagoons, reefs, estuaries.
**HABITS** Swimming performance good. Shallow-water ambush and pursuit fishers of small game. Possibly bred and nested on beaches.
**NOTES** Absence from at least some other seas probably reflects lack of sufficient sampling. May be the lizards closest to snakes, which may have had an aquatic origin; this is uncertain because snakes may have evolved from burrowing lizards.

### *Dolichosaurus longicollis*

**1.5 m (5 ft) TL, 3.5 kg (8 lb)**

**FOSSIL REMAINS** Several partial skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head moderate in size, neck elongated.
**AGE** Late Cretaceous; early Cenomanian.
**DISTRIBUTION AND FORMATIONS** Southeastern England; Chalk Marl.
**HABITAT** Island nearshore.
**NOTES** May have shared its habitat with *Coniasaurus.*

### *Coniasaurus cressidus*

**0.5 m (1.6 ft) TL, 0.15 kg (0.35 lb)**

**FOSSIL REMAINS** A few partial specimens.
**ANATOMICAL CHARACTERISTICS** Teeth large and robust, blunt tipped, especially aft.
**AGE** Late Cretaceous; early or middle Cenomanian.
**DISTRIBUTION AND FORMATIONS** Southeastern England; Chalk Marl.
**HABITAT** Island nearshore.

### *Aphanizocnemus libanensis*

**0.3 m (1 ft) TL, 0.28 kg (0.6 lb)**

**FOSSIL REMAINS** Skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Snout rather small, coronoid process moderate in height. Neck moderately long. Arms and legs fairly well developed, lower leg bones very short and broadened.
**AGE** Late Cretaceous; middle Cenomanian.

*Aphanizocnemus libanensis*

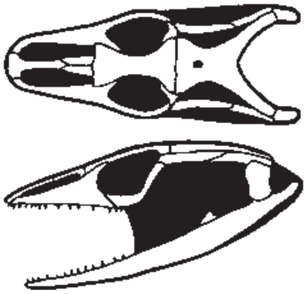
*Aphanizocnemus libanensis*

**DISTRIBUTION AND FORMATIONS** Lebanon; Hakel or Sannine.
**HABITAT** Continental nearshore.

### *Pontosaurus kornhuberi*

**1 m (3.3 ft) TL, 1.1 kg (2.5 lb)**

**FOSSIL REMAINS** Skull and skeleton, latter severely flattened top to bottom, with soft tissues.
**ANATOMICAL CHARACTERISTICS** Snout pointed and rather small, teeth small. Neck moderately long. Arms and legs fairly well developed.



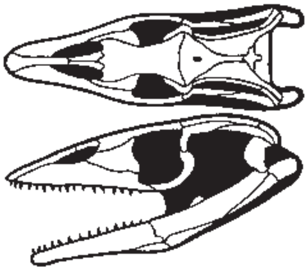
*Pontosaurus kornhuberi*

**AGE** Late Cretaceous; middle Cenomanian.
**DISTRIBUTION AND FORMATIONS** Lebanon; Sannine.
**HABITAT** Continental nearshore.
**NOTES** Some lizard-type scales are preserved on skull and body. Shared its habitat with *Eupodophis*, possibly with *Aphanizocnemus*.

### *Pontosaurus lesinensis*

**1.2 m (4 ft) TL, 2 kg (4.5 lb)**

**FOSSIL REMAINS** Skull and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Snout pointed, coronoid process short, teeth small. Neck moderately long. Arms fairly well developed.



*Pontosaurus lesinensis*

**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Croatia; unnamed.
**HABITAT** Island nearshore.
**NOTES** May have shared its habitat with *Aigialosaurus.*

### *Adriosaurus suessi*

**0.3 m (1 ft) TL, 0.28 kg (0.6 lb)**

**FOSSIL REMAINS** Majority of skull and skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Snout moderate in size. Arms and legs small.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Slovenia; upper Povir.
**HABITAT** Island nearshore.
**NOTES** It is not certain whether the members of this genus are variations of one species, or different genera. Shared its habitat with *A.? skrbinensis*, *A.? microbrachis*, *Acteosaurus*, *Eidolosaurus*, *Mesoleptos*, *Komensaurus*, *Carsosaurus.*

### Unnamed genus or *Adriosaurus skrbinensis*

**0.4 m (1.3 ft) TL, 0.7 kg (0.15 lb)**

**FOSSIL REMAINS** Partial skull and majority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Arms much shorter than legs.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Slovenia; upper Povir.
**HABITAT** Island nearshore.
**NOTES** Not certain belongs in larger-limbed genus *Adriosaurus.*

### Unnamed genus or *Adriosaurus microbrachis*

**0.5 m (1.6 ft) TL, 0.15 kg (0.35 lb)**

**FOSSIL REMAINS** Majority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Arms reduced to humerus splinter, legs strongly reduced.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Slovenia; upper Povir.
**HABITAT** Continental nearshore.
**NOTES** Not certain belongs in much larger-limbed genus *Adriosaurus.*

### *Acteosaurus tommasinii*

**0.5 m (1.6 ft) TL, 0.15 kg (0.35 lb)**

**FOSSIL REMAINS** Majority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Arms much shorter than legs.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Slovenia; upper Povir.
**HABITAT** Continental nearshore.

### *Eidolosaurus trauthi*

**Size uncertain**

**FOSSIL REMAINS** Partial remains.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Slovenia; upper Povir.
**HABITAT** Island nearshore.

### *Mesoleptos zendrinii*

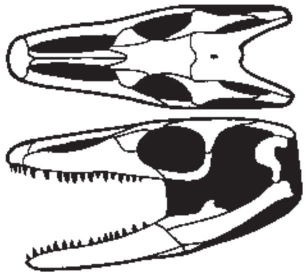
**1 m (3.3 ft) TL, 1 kg (2 lb)**

**FOSSIL REMAINS** Two partial skeletons.
**ANATOMICAL CHARACTERISTICS** Neck rather long.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Slovenia; upper Povir.
**HABITAT** Island nearshore.
**NOTES** A specimen from Palestine referred to this species may be a different taxon.

### *Judeasaurus tchernovi*

**1 m (3.3 ft) TL, 1.1 kg (2.5 lb)**

**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Snout large, coronoid process tall, teeth fairly large.
**AGE** Late Cretaceous; late Cenomanian or early Turonian.
**DISTRIBUTION AND FORMATIONS** Israel or West Bank; upper Kefar Sha'ul or Bina.
**HABITAT** Continental nearshore.



*Judeasaurus tchernovi*

## OPHIDIANS (SNAKES)

**SMALL OPHIDIOMORPHS FROM THE LATE CRETACEOUS TO THE MODERN ERA, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Fairly uniform. Heads small, subrectangular in side view, lightly constructed, upper temporal bar incomplete, very akinetic, snout not large, teeth bladed, recurved with an S-curved, very sharp tip. Neck moderately long, trunk extremely elongated, slender, and hyperflexible, tail moderate in length or short, total vertebrae over 160. Limbs if present vestigial and not functional in locomotion, which is entirely serpentine. Highly hydrodynamically streamlined, entirely anguilliform swimmers.
**HABITAT** Nearshore reefs, reefs, mangroves, lagoons.
**HABITS** Swimming performance good. Ambush and crevice fishers of small game. Deposit eggs ashore or give live birth in the water.

## SIMOLIOPHIIDS (SEA SNAKES)

**SMALL OPHIDIANS FROM THE LATE CRETACEOUS OF EUROPE AND THE MIDDLE EAST**

**ANATOMICAL CHARACTERISTICS** Uniform. Highly aquatic. Arms absent, if legs present they are very reduced. Nonvenomous.
**NOTES** Absence from at least some other seas probably reflects lack of sufficient sampling. May be basal snakes that evolved from marine, dolichosaur-type lizards, or snakes that evolved from land ancestors and invaded the seas.

### *Eupodophis descouensi*

**0.9 m (3 ft) TL, 0.7 kg (1.5 lb)**

**FOSSIL REMAINS** Skull and skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Skull subtriangular in top view. Tail very short. Foot present but very reduced.
**AGE** Late Cretaceous; middle Cenomanian.
**DISTRIBUTION AND FORMATIONS** Lebanon; Sannine.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with *Pontosaurus kornhuberi*, possibly with *Aphanizocnemus.*

### *Haasiophis terrasanctus*

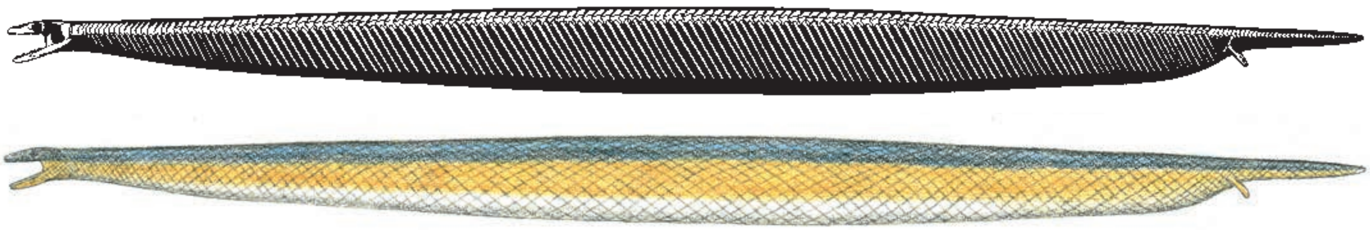
**Adult size uncertain**

**FOSSIL REMAINS** Skull and skeleton, probably juvenile, severely flattened top to bottom.

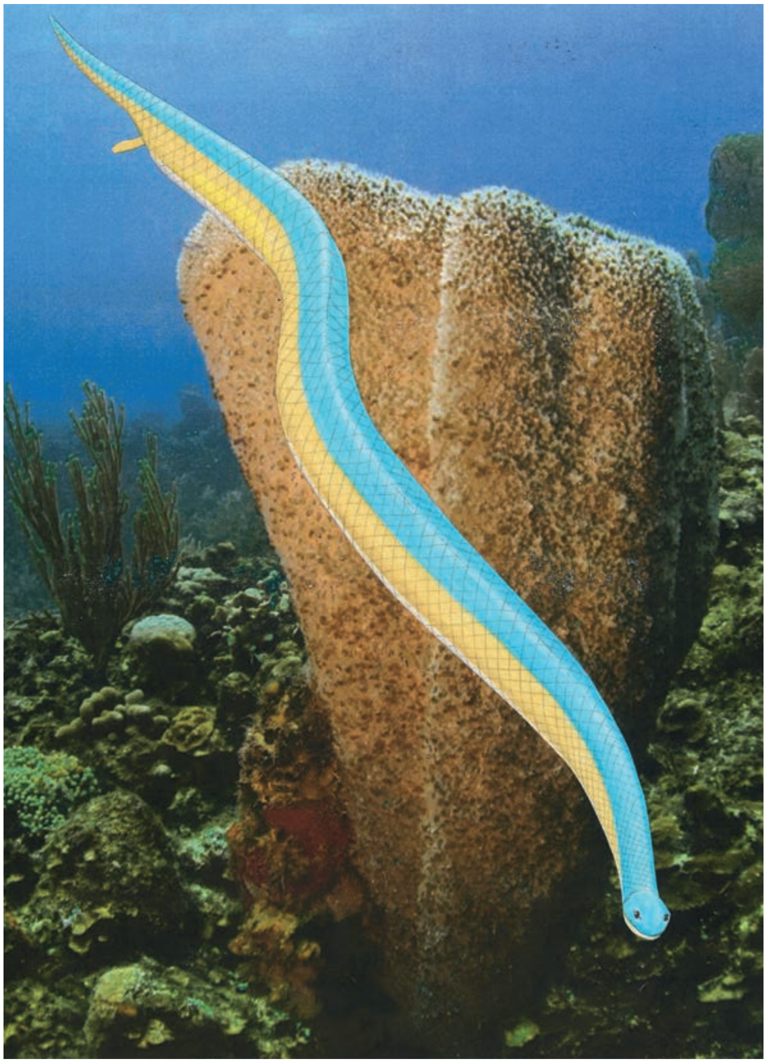
**ANATOMICAL CHARACTERISTICS** Head subrectangular in top view, coronoid process short. Tail fairly long. Foot present but very reduced.
**AGE** Late Cretaceous; early or middle Cenomanian.
**DISTRIBUTION AND FORMATIONS** West Bank; Amminadav or Bet-Meir.
**HABITAT** Continental nearshore.
**NOTES** Shared its habitat with or may be a juvenile of *Pachyrhachis*.

### *Pachyrhachis problematicus*
**1.9 m (6 ft) TL, 7 kg (15 lb)**

**FOSSIL REMAINS** Skull and majority of two skeletons.
**ANATOMICAL CHARACTERISTICS** Skull subrectangular in top view, coronoid process tall. Tail probably not long. Foot absent.
**AGE** Late Cretaceous; early Cenomanian.
**DISTRIBUTION AND FORMATIONS** West Bank; Bet-Meir.
**HABITAT** Continental nearshore.



*Pachyrhachis problematicus*



*Pachyrhachis problematicus*

***Pachyophis woodwardi***
**0.6 m (2 ft) TL, 0.2 kg (0.5 lb)**

FOSSIL REMAINS Minority of skull and complete skeleton, two partial skeletons, severely flattened top to bottom.
ANATOMICAL CHARACTERISTICS Skeleton thick boned. Legs absent.
AGE Late Cretaceous; late Cenomanian.
DISTRIBUTION AND FORMATIONS Bosnia and Herzegovina; unnamed.
HABITAT Island nearshore.
NOTES Shared its habitat with or may be the adult of *Mesophis*.

***Mesophis nopscai***
**0.3 m (1 ft) TL, 0.025 kg (0.06 lb)**

FOSSIL REMAINS Majority of skeleton, severely flattened top to bottom, possibly juvenile.
ANATOMICAL CHARACTERISTICS Skeleton not heavily built. Legs absent.
AGE Late Cretaceous; late Cenomanian.
DISTRIBUTION AND FORMATIONS Bosnia and Herzegovina; unnamed.
HABITAT Island nearshore.

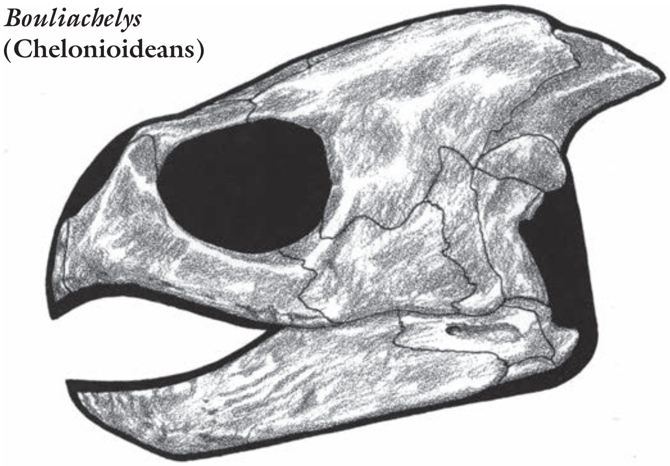
# TESTUDINES (TURTLES)

SMALL TO GIGANTIC NEODIAPSIDS FROM THE EARLY JURASSIC TO THE MODERN ERA, GLOBAL

ANATOMICAL CHARACTERISTICS Diverse. Fully terrestrial to fully marine. Skulls akinetic, unsplit nostrils usually at front of snout, snout usually very short and orbits placed well forward, temporal openings closed, parietal eye absent, deep paired embayments on rear of skull separated by long midline plate, beaked and toothless. Necks short. Trunk enclosed in a carapace, most ribs not swept backward. Tail short. Shoulder girdle within carapace, limbs sprawl out to sides.
HABITAT Fully terrestrial to marine.
HABITS Herbivorous to omnivorous.
NOTES Relationships to other reptiles uncertain.

## CHELONIOIDEANS (SEA TURTLES)

SMALL TO GIGANTIC TESTUDINES FROM THE EARLY CRETACEOUS TO THE MODERN ERA, GLOBAL

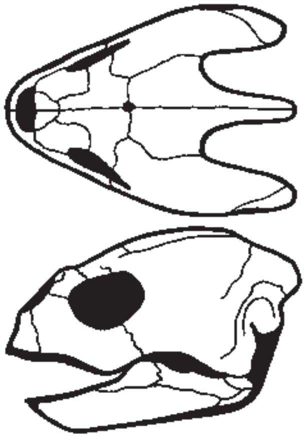

***Bouliachelys***
**(Chelonioideans)**

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads at least fairly broad, subtriangular in top view. Necks nonretractable. Trunk enclosed in a very broad, shallow carapace that is flatter on bottom than on more-domed top, never fully plated, dorsal midline row of plates are paralleled by a solid row of side plates, outer struts are separated by lateral spaces inside outer rim of plates, four irregular interlocking plates cover part of ventral carapace. Tails nonretractable. Limbs nonretractable full flippers, leading two fingers and sometimes first toe clawed, humerus points forward and rest of arm arcs out sideways, foreflippers always large and markedly longer and more hydrofoil shaped than aft flippers. Moderately hydrodynamically streamlined, propulsion provided entirely by foreflippers, aft flippers for stability and maneuvering.
HABITAT Coastal to deep oceans.
HABITS Swimming performance good. Herbivorous to omnivorous with small game fishing, prey often including jellyfish. Move onto beaches and use clawed foreflippers to dig nests for their soft-shelled eggs, no parental care.
NOTES Differing phylogenetic studies do not allow further subdivision into families at this time.

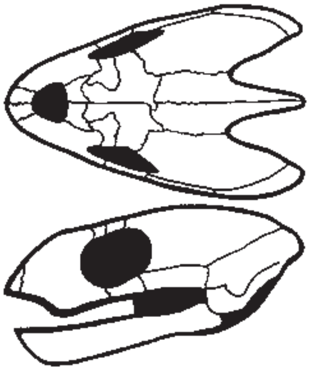
***Desmatochelys? padillai***
**2 m (6.5 ft) TL, 400 kg (900 lb)**

FOSSIL REMAINS Four skulls, majority of skeleton, two partial skeletons.
ANATOMICAL CHARACTERISTICS Head deep, snout short. Lateral dorsal spaces large, separated by thin struts, carapace rim plates narrow. Foreflippers large.

**AGE** Early Cretaceous; late Barremian and/or lower Aptian.
**DISTRIBUTION AND FORMATIONS** Colombia; upper Paja.
**HABITAT** Continental shelf.
**NOTES** That this species is in the much later and distinctive genus *Desmatochelys* is problematic.



***Desmatochelys? padillai***



***Desmatochelys lowi***

### *Desmatochelys lowi*

**1.9 m (6 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head not deep, snout medium sized. Carapace heart shaped, lateral dorsal spaces large, separated by thin struts, carapace rim plates narrow. Foreflippers large.
**AGE** Late Cretaceous; late Cenomanian.
**DISTRIBUTION AND FORMATIONS** Nebraska; middle Greenhorn Limestone.
**HABITS** Interior seaway approaching its greatest maximum.

### *Toxochelys latiremis*

**2 m (6.5 ft) TL, 400 kg (900 lb)**

**FOSSIL REMAINS** Skulls, majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Carapace heart shaped, lateral dorsal spaces medium sized.
**AGE** Late Cretaceous; late Coniacian? to early Campanian.
**DISTRIBUTION AND FORMATIONS** Nebraska, South Dakota, Kansas; lower to upper Niobrara?, lower Pierre Shale.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** Assigned time span probably too long for this single species, which could be limited to late Santonian and/or early Campanian. Shared its habitat with *Styxosaurus browni*, *Elasmosaurus*, *Dolichorhynchops bonneri*, *Tylosaurus proriger*, *Latoplatecarpus*, *Globidens*? *dakotensis.*

### *Toxochelys moorevillensis*

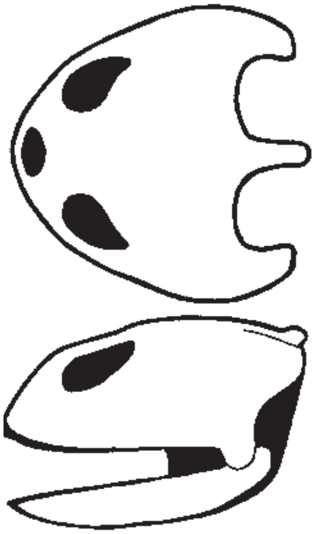
**2 m (6.5 ft) TL, 400 kg (900 lb)**

**FOSSIL REMAINS** Majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Carapace nearly circular, lateral dorsal spaces very small.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** Alabama; upper Mooreville Chalk.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Globidens alabamaensis*, *Ctenochelys acris*, *Corsochelys*, *Prionochelys.*

### *Mexichelys coahuilaensis*

**0.6 m (2 ft) TL, 12 kg (25 lb)**

**FOSSIL REMAINS** Several skulls and partial skeletons.
**ANATOMICAL CHARACTERISTICS** Head very broad, snout short, lower jaw shallow.
**AGE** Late Cretaceous; late Campanian.
**DISTRIBUTION AND FORMATIONS** Northeastern Mexico; Cerro del Pueblo.
**HABITAT** Continental shelf.



***Mexichelys coahuilaensis***

### *Nichollsemys baieri*

**Adult size uncertain**

**FOSSIL REMAINS** Four complete and partial skulls, possibly immature.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Cretaceous; late Campanian.
**DISTRIBUTION AND FORMATIONS** Montana; middle Bearpaw Shale.
**HABITAT** Interior seaway was becoming much narrower.
**NOTES** Shared its habitat with *Prognathodon*? *overtoni*.

### *Ctenochelys stenoporus*

**1.3 m (4.3 ft) TL, 65 kg (150 lb)**

**FOSSIL REMAINS** Partial skulls, majority of skeletons.
**ANATOMICAL CHARACTERISTICS** Carapace oval, lateral dorsal spaces large, separated by thin struts, carapace rim plates small.
**AGE** Late Cretaceous; earliest Campanian.
**DISTRIBUTION AND FORMATIONS** Kansas; uppermost Niobrara.
**HABITAT** Interior seaway was continuing to become less broad and deep.
**NOTES** Shared its habitat with *Styxosaurus snowii*, *Polycotylus latipinnis*, *Dolichorhynchops osborni*, *Platecarpus tympanicus*, *Eonatator sternbergii*, *Clidastes propython*, *Protostega gigas*.

### *Ctenochelys acris*

**1 m (3.3 ft) TL, 35 kg (80 lb)**

**FOSSIL REMAINS** Partial skulls and skeletons, some juvenile.
**ANATOMICAL CHARACTERISTICS** Head broad, snout very short. Carapace heart shaped, carapace rim plates medium sized.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** Alabama; upper Mooreville Chalk.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Globidens alabamaensis*, *Toxochelys moorevillensis*, *Prionochelys*, *Corsochelys*.

### *Corsochelys halinches*

**1.5 m (5 ft) TL, 120 kg (250 lb)**

**FOSSIL REMAINS** Minority of skull and majority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head small. Carapace heart shaped, lateral spaces large and separated by narrow struts, carapace rim plates narrow.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** Alabama; upper Mooreville Chalk.
**HABITAT** Continental shelf.

### *Prionochelys matutina*

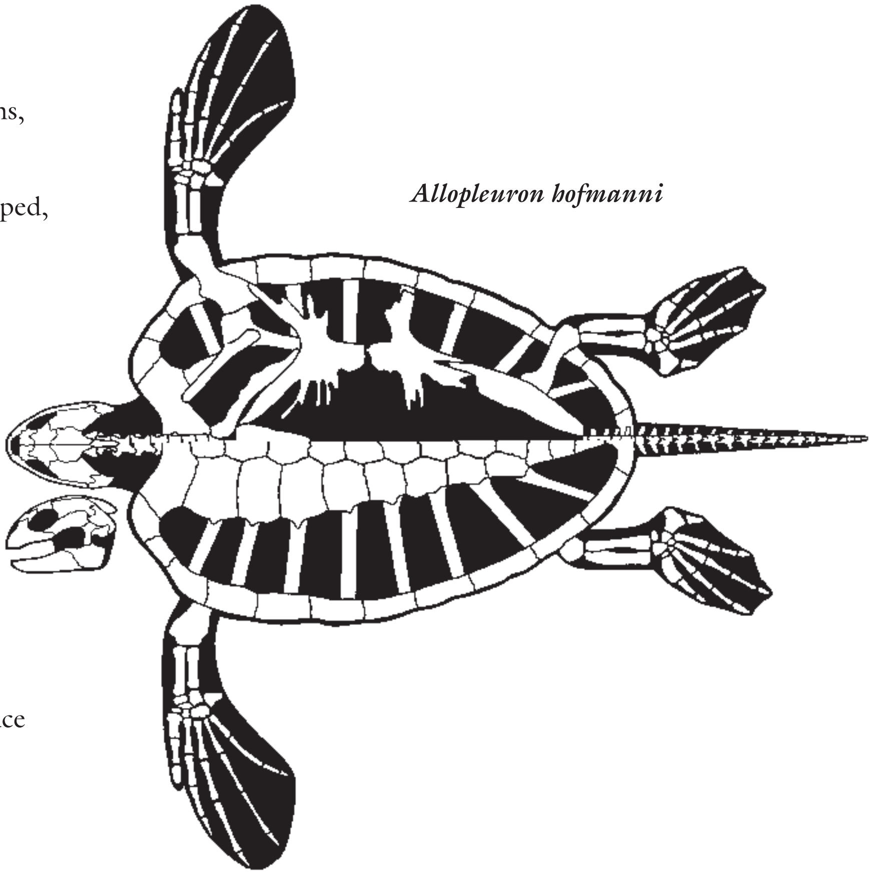
**0.7 m (2.3 ft) TL, 15 kg (30 lb)**

**FOSSIL REMAINS** Minority of skull and skeletal remains, some juvenile.
**ANATOMICAL CHARACTERISTICS** Carapace heart shaped, lateral dorsal openings large, separated by thin struts.
**AGE** Late Cretaceous; early Campanian.
**DISTRIBUTION AND FORMATIONS** Alabama; upper Mooreville Chalk.
**HABITAT** Continental shelf.

### *Allopleuron hofmanni*

**2.3 m (7.5 ft) TL, 700 kg (1,500 lb)**

**FOSSIL REMAINS** Skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Head rather small, moderately broad. Carapace heart shaped, lateral dorsal openings large, separated by thin struts, carapace rim plates medium sized, bottom plates reduced. Aft foot permanently flexed sideways, aftmost toe short and divergent.
**AGE** Late Cretaceous; late Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Belgium; Maastricht.



*Allopleuron hofmanni*

**HABITAT** Island archipelago shallows.
**NOTES** The presence of later members of this genus in the Cenozoic shows that this species survived the K/Pg extinction.

### *Euclastes wielandi*

**Adult size uncertain**

**FOSSIL REMAINS** Skulls, complete and partial, possibly juvenile.
**ANATOMICAL CHARACTERISTICS** Head broad. Carapace oval, lateral dorsal spaces small.
**AGE** Late Cretaceous; latest Maastrichtian and early Paleocene.
**DISTRIBUTION AND FORMATIONS** New Jersey, Maryland; Hornerstown, Brightseat.
**HABITAT** Continental shelf.
**NOTES** This species appears to have survived the K/Pg extinction; other species of this genus were present in the Cenozoic.

### *Alienochelys selloumi*

**2.5 m (8 ft) TL, 800 kg (1,800 lb)**

**FOSSIL REMAINS** Complete skull.
**ANATOMICAL CHARACTERISTICS** Snout very broad and squared off so head is subrectangular in top view, nostrils between orbits, temporal region fairly long, lower jaw fairly deep.
**AGE** Late Cretaceous; latest Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Morocco; unnamed.
**HABITAT** Continental shelf.

### *Mesodermochelys undulatus*

**2 m (6.5 lb) TL, 400 kg (900 lb)**

**FOSSIL REMAINS** Minority of skull and over a dozen partial skeletons.
**ANATOMICAL CHARACTERISTICS** Carapace oval, lateral dorsal spaces rather small, carapace rim plates large.
**AGE** Late Cretaceous; early Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Northern Japan; Hakobuchi.
**HABITAT** Island coastal.
**NOTES** Later specimens probably do not belong to this taxon.

### *Cratochelone berneyi*

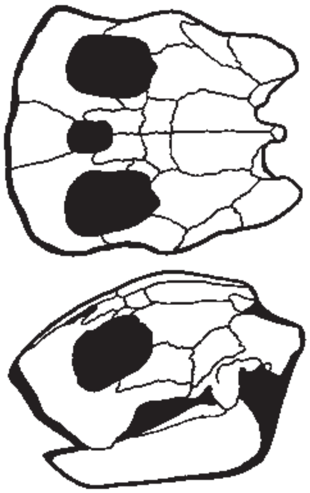
**4? m (13? ft) TL, 3? tonnes**

**FOSSIL REMAINS** Minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Early Cretaceous; middle Albian.
**DISTRIBUTION AND FORMATIONS** Northeastern Australia; Toolebuc.
**HABITAT** Interior seaway.
**NOTES** Although fragmentary remains make it hard to be certain, may rival later *Archelon* as largest known marine turtle. Shared its habitat with ?*Kronosaurus*, *Eromangasaurus*, *Longirostra*, *Bouliachelys*, and the much more common *Notochelone.*

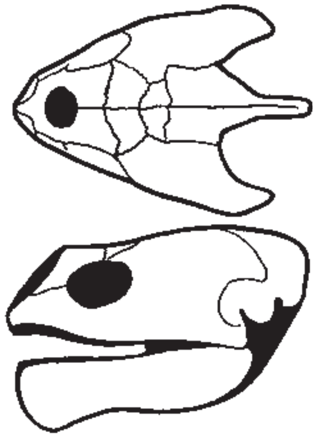
### *Notochelone costata*

**2 m (6.5 ft) TL, 400 kg (900 lb)**

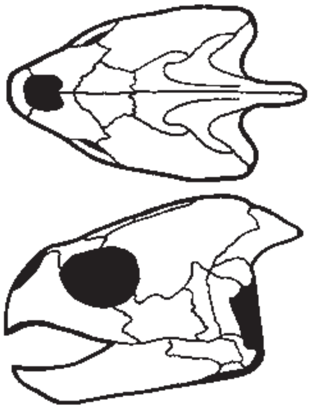
**FOSSIL REMAINS** Skull and partial skeletons.
**ANATOMICAL CHARACTERISTICS** Snout short, temporal region fairly long, head not deep, moderately broad. Lateral dorsal spaces moderately large.
**AGE** Early Cretaceous; middle Albian.
**DISTRIBUTION AND FORMATIONS** Northeastern Australia; Toolebuc.
**HABITAT** Interior seaway.



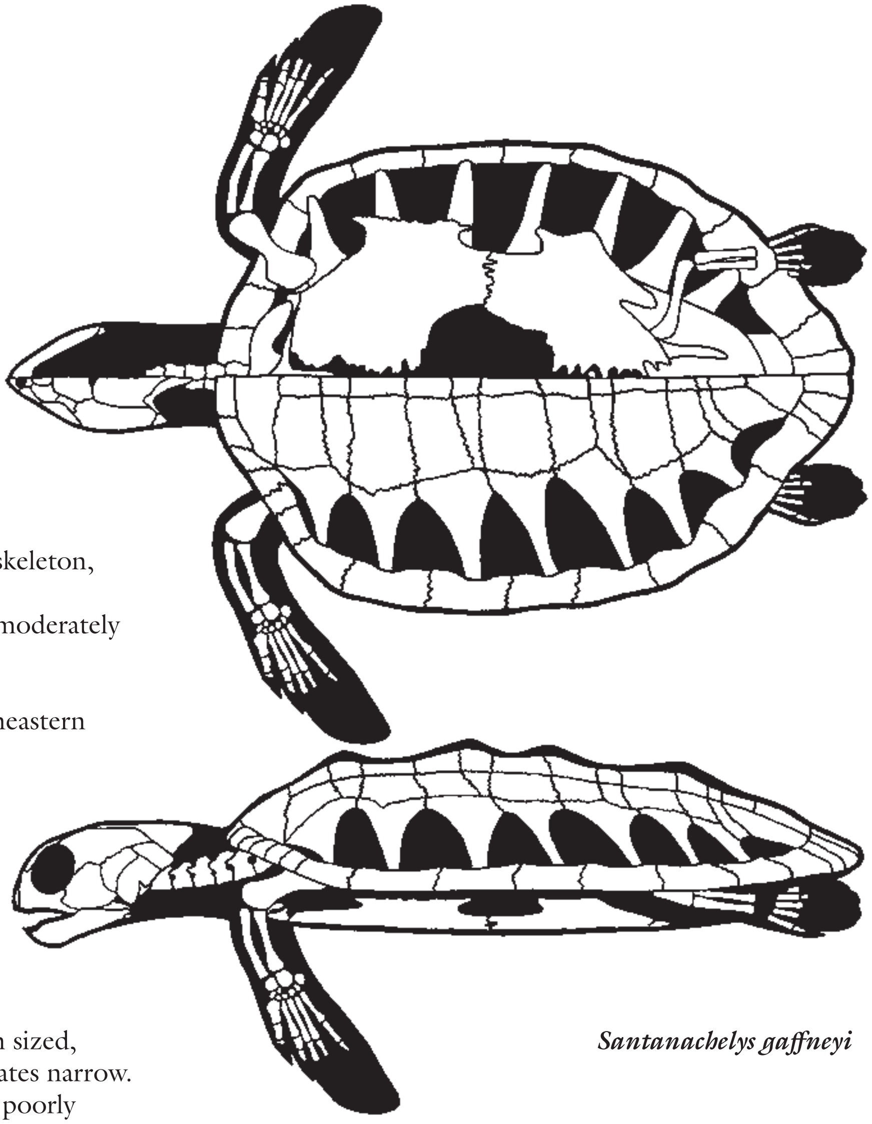
*Alienochelys selloumi*



*Notochelone costata*



*Bouliachelys suteri*



*Santanachelys gaffneyi*

### *Bouliachelys suteri*

**0.5 m (1.5 ft) TL, 5 kg (10 lb)**

**FOSSIL REMAINS** Four skulls, majority of skeleton, two partial skeletons.
**ANATOMICAL CHARACTERISTICS** Head moderately deep and broad.
**AGE** Early Cretaceous; middle Albian.
**DISTRIBUTION AND FORMATIONS** Northeastern Australia; Toolebuc.
**HABITAT** Interior seaway.

### *Santanachelys gaffneyi*

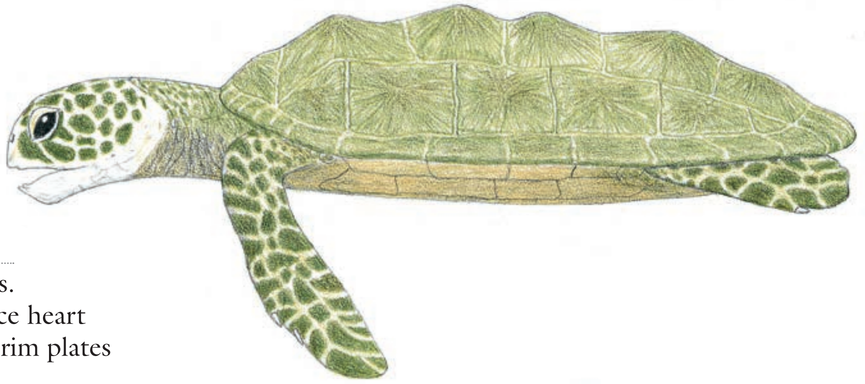
**0.2 m (0.6 ft) TL, 0.4 kg (0.9 lb)**

**FOSSIL REMAINS** Skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head rather small, snout very short and temporal region elongated. Carapace oval, lateral dorsal spaces medium sized, separated by narrow struts, carapace rim plates narrow. Foreflipper medium sized, fingers and toes poorly ossified, no clawed toe present.
**AGE** Early Cretaceous; late Aptian and/or early Albian.
**DISTRIBUTION AND FORMATIONS** Northeastern Brazil; Romualdo.
**HABITAT** Continental shelf.

### *Chelosphargis advena*

**0.6 m (2 ft) TL, 6 kg (13 lb)**

**FOSSIL REMAINS** Partial skull and skeletons.
**ANATOMICAL CHARACTERISTICS** Carapace heart shaped, lateral dorsal spaces small, carapace rim plates large.
**AGE** Late Cretaceous; late Coniacian.
**DISTRIBUTION AND FORMATIONS** Kansas; lower Niobrara.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Selmasaurus? johnsoni*, *Ectenosaurus*, *Plesioplatecarpus.*

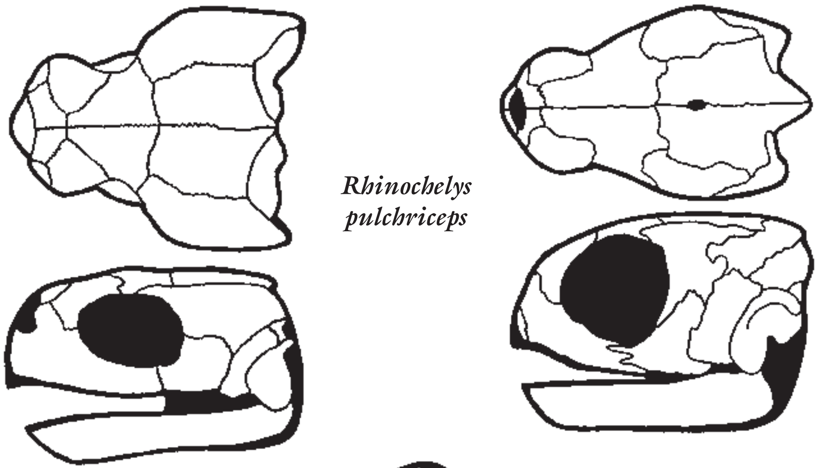


### *Rhinochelys amaberti*

**Adult size not certain**

**FOSSIL REMAINS** Skulls, possibly juvenile.
**ANATOMICAL CHARACTERISTICS** Head deep, quite broad, snout fairly broad.

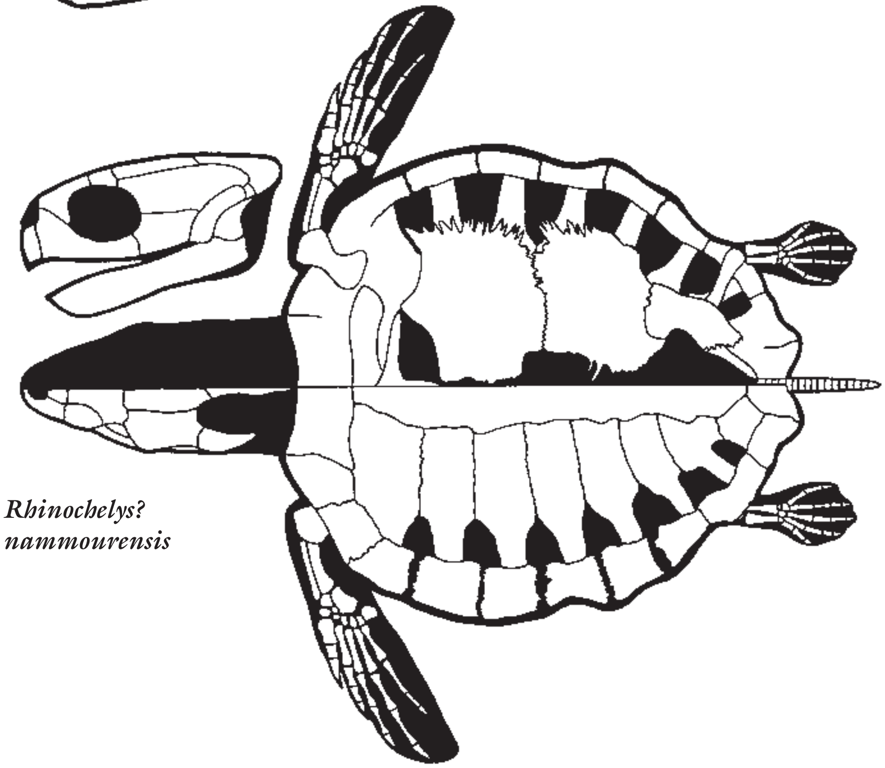
**AGE** Early Cretaceous; late Albian.
**DISTRIBUTION AND FORMATIONS** Eastern France; unnamed.
**HABITAT** Island archipelago shallows.


*Rhinochelys pulchriceps*

### *Rhinochelys pulchriceps*

**0.4 m (1.3 ft) TL, 3.5 kg (8 lb)**

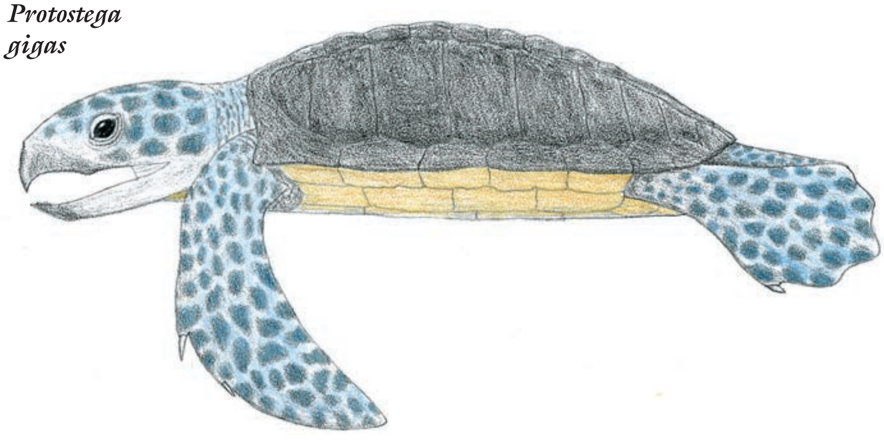
**FOSSIL REMAINS** A few skulls.
**ANATOMICAL CHARACTERISTICS** Head very deep, snout quite broad and very short.
**AGE** Late Cretaceous; early Cenomanian.
**DISTRIBUTION AND FORMATIONS** Eastern England; lower West Melbury Marly Chalk.
**HABITAT** Island archipelago shallows.


*Rhinochelys? nammourensis*

### *Rhinochelys? nammourensis*

**0.85 m (2.75 ft) TL, 35 kg (80 lb)**

**FOSSIL REMAINS** Majority of skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head very large, snout not broad, quite short, and temporal region long. Carapace heart shaped, lateral dorsal spaces small, separated by short robust struts, carapace rim plates large. Foreflipper medium sized, aft flipper small, no clawed toe present.
**AGE** Late Cretaceous; middle Cenomanian.
**DISTRIBUTION AND FORMATIONS** Lebanon; unnamed.
**HABITAT** Continental shelf.

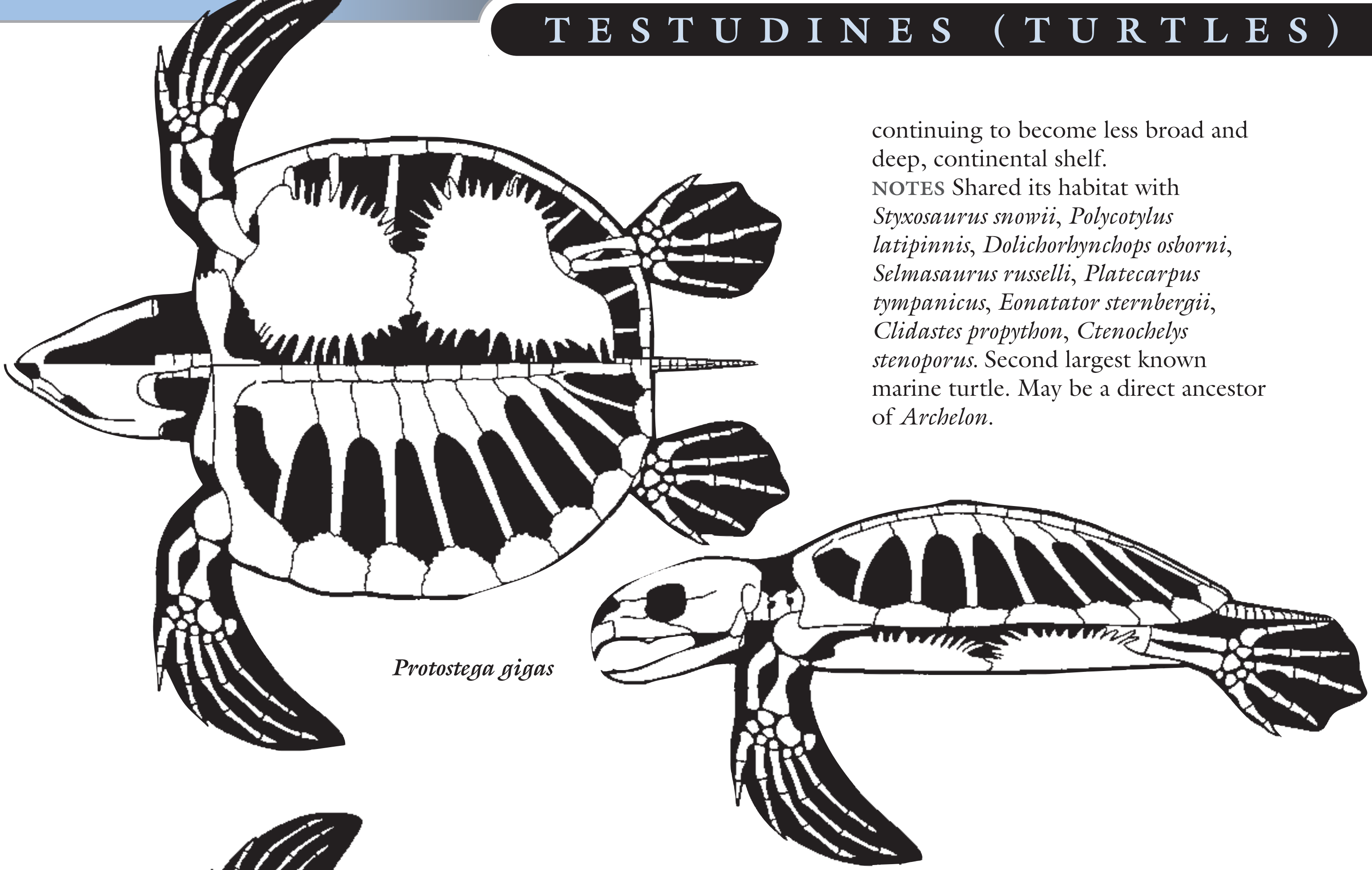

*Protostega gigas*

### *Protostega gigas*

**2.2 m (7.2 ft) TL, 650 kg (1,400 lb)**

**FOSSIL REMAINS** A number of skulls and skeletons of varying completeness.
**ANATOMICAL CHARACTERISTICS** Head very large, beak parrot-like. Carapace roundish, lateral dorsal spaces large, separated by long narrow struts, carapace rim plates large. Foreflipper large, aft flipper fairly large.
**AGE** Late Cretaceous; earliest Campanian.
**DISTRIBUTION AND FORMATIONS** Kansas, Alabama; uppermost Niobrara, lower Mooreville Chalk.
**HABITAT** Interior seaway was

continuing to become less broad and deep, continental shelf.
**NOTES** Shared its habitat with *Styxosaurus snowii*, *Polycotylus latipinnis*, *Dolichorhynchops osborni*, *Selmasaurus russelli*, *Platecarpus tympanicus*, *Eonatator sternbergii*, *Clidastes propython*, *Ctenochelys stenoporus*. Second largest known marine turtle. May be a direct ancestor of *Archelon*.

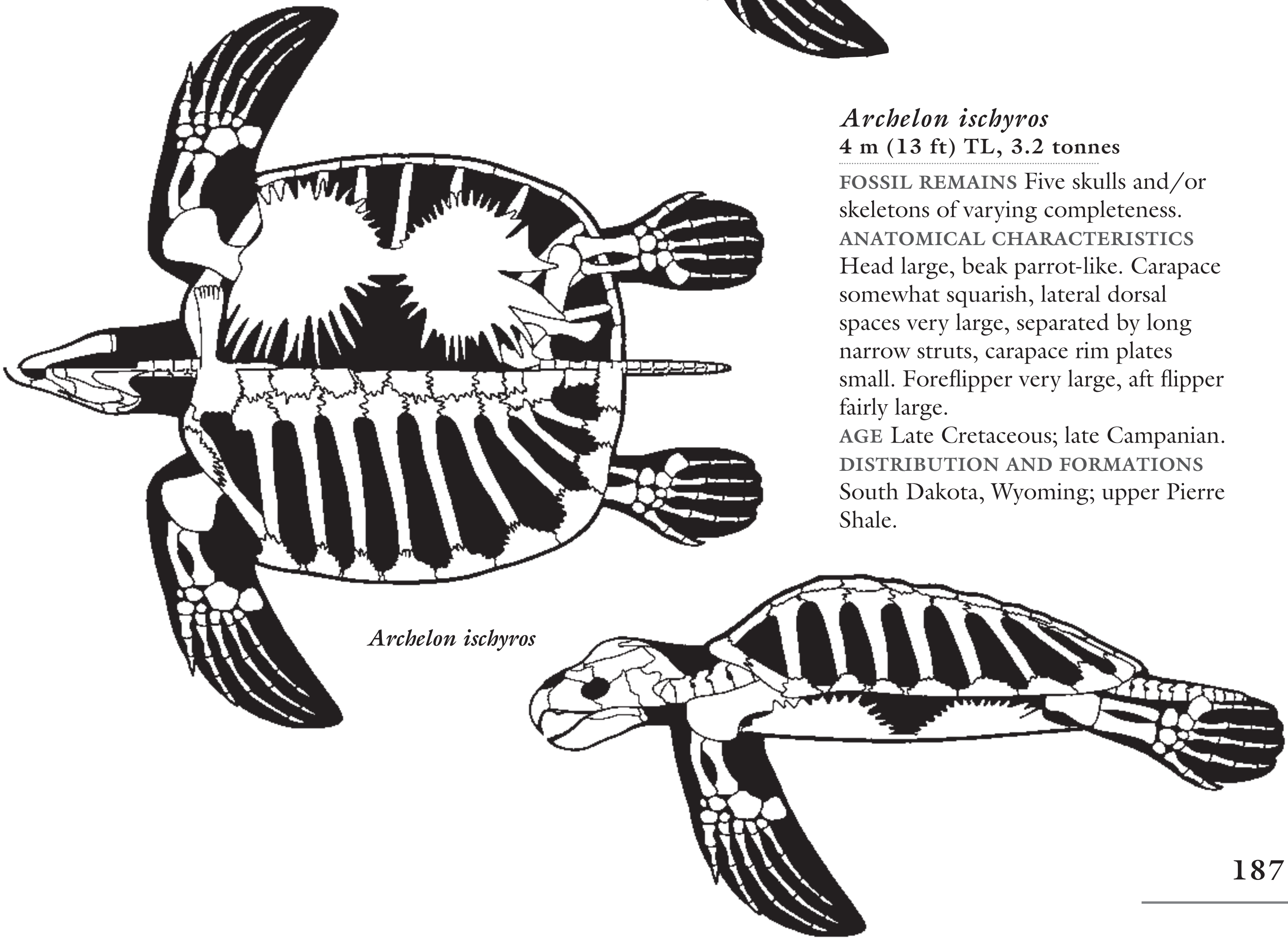


*Protostega gigas*

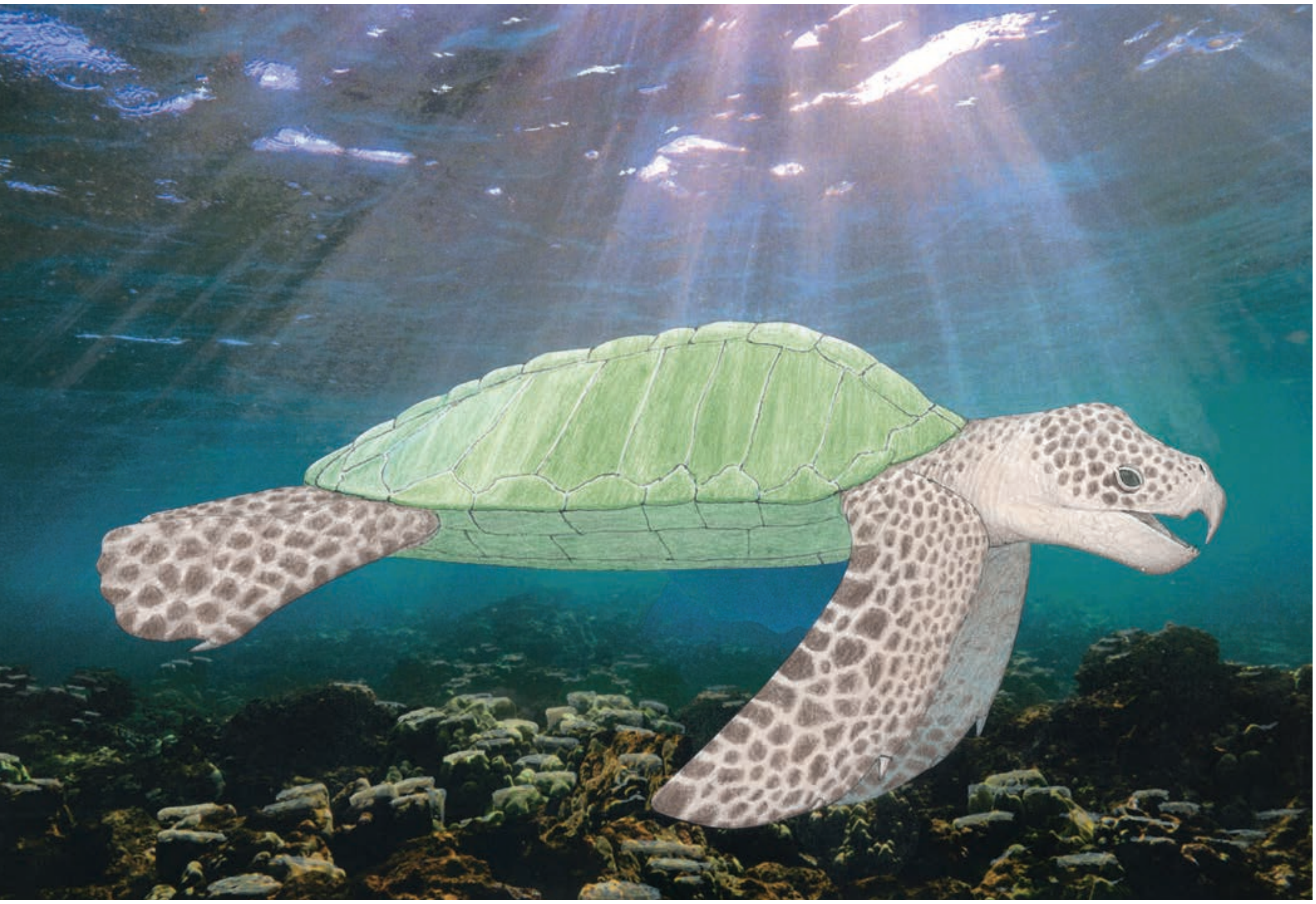
### *Archelon ischyros*

**4 m (13 ft) TL, 3.2 tonnes**

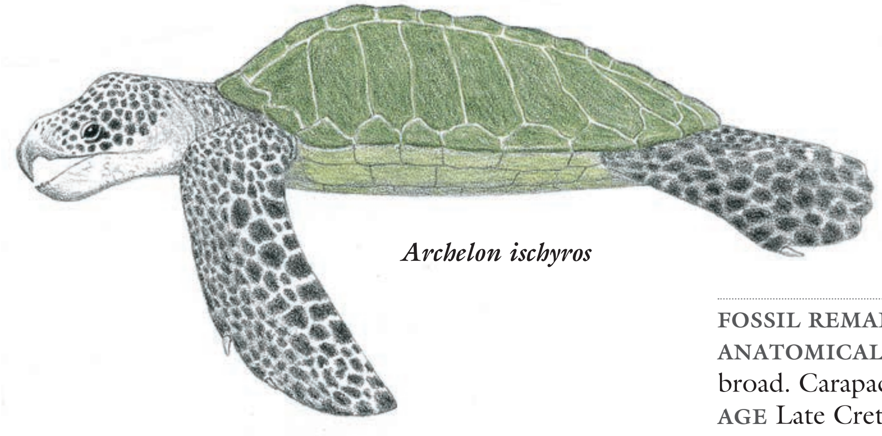
**FOSSIL REMAINS** Five skulls and/or skeletons of varying completeness.
**ANATOMICAL CHARACTERISTICS** Head large, beak parrot-like. Carapace somewhat squarish, lateral dorsal spaces very large, separated by long narrow struts, carapace rim plates small. Foreflipper very large, aft flipper fairly large.
**AGE** Late Cretaceous; late Campanian.
**DISTRIBUTION AND FORMATIONS** South Dakota, Wyoming; upper Pierre Shale.



*Archelon ischyros*



*Archelon ischyros*



*Archelon ischyros*

**HABITAT** Interior seaway was becoming much narrower.
**HABITS** Large size indicates may have preferred deeper waters, but shallowing seaway indicates opposite. Strongly hooked beak may have been used for predation, grubbing on seabeds, intraspecific combat, scavenging, defense against predators.
**NOTES** Shared its habitat with *Prognathodon*? *overtoni*, *Mosasaurus*? *missouriensis*. The classic Mesozoic marine turtle. Largest known sea turtle, although may be matched by earlier, less well-preserved *Cratochelone berneyi*, second largest of all known turtles.

### *Terlinguachelys fischbecki*

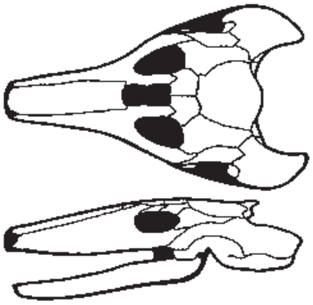
**2.5 m (8 ft) TL, 450 kg (1,000 lb)**

**FOSSIL REMAINS** Partial skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head moderately broad. Carapace somewhat elongated.
**AGE** Late Cretaceous; middle Campanian.
**DISTRIBUTION AND FORMATIONS** Texas; middle Aguja.
**HABITAT** Interior seaway.

### *Ocepechelon bouyai*

**3.5 m (11 ft) TL, 2 tonnes**

**FOSSIL REMAINS** Majority of skull.
**ANATOMICAL CHARACTERISTICS** Head shallow, very broad aft, tip of snout tubular, snout elongated, nostrils well back between orbits that face strongly upward, temporal region expanded well aft of jaw joint.



*Ocepechelon bouyai*

**AGE** Late Cretaceous; latest Maastrichtian.
**DISTRIBUTION AND FORMATIONS** Morocco; unnamed.
**HABITAT** Continental shallows.
**HABITS** Apparent suction feeder.
**NOTES** Shared its habitat with *Zarafasaura*.

# ARCHOSAUROMORPHS

**SMALL TO GIGANTIC NEODIAPSIDS FROM THE MIDDLE PERMIAN TO THE MODERN ERA, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Extremely diverse. Cervical ribs often overlap one another.
**HABITAT AND HABITS** Extremely variable, marine to fully terrestrial to highly aerial, highly herbivorous to archpredatory.
**NOTES** Includes modern crocodilians and birds, which are living dinosaurs.

## TANYSTROPHEIDS

**SMALL TO MEDIUM-SIZED NEODIAPSIDS FROM THE TRIASSIC OF THE NORTHERN HEMISPHERE**

**ANATOMICAL CHARACTERISTICS** Diverse. Fully terrestrial to aquatic. Skulls akinetic, orbits face strongly upward, scleral rings present, teeth conical, some on mouth roof. Necks at least somewhat elongated, slender cervical rib aft rods elongated and overlapping. Trunks fairly elongated. Digits poorly streamlined, aquatic propulsion mainly from limbs.
**HABITAT** Terrestrial and/or freshwaters to coastal nearshore.
**HABITS** Swimming performance poor to mediocre. At least some probably gave live birth.
**NOTES** Aquatic nature of other members of this group, including hyperlong-necked *Tanystropheus*, is uncertain. May have been only archosaurs to bear live young aside from metriorhynchid crocs.

### *Dinocephalosaurus orientalis*
**3 m (11 ft) TL**

**FOSSIL REMAINS** Skull and two partial skeletons, fetus, severely flattened from top to bottom.
**ANATOMICAL CHARACTERISTICS** Head somewhat elongated and subrectangular in top view because squared-off snout tip is fairly broad, large nostrils set a little aft of snout tip, orbits set well aft and temporal region not large, lower jaws shallow, a few upper and lower teeth large. Neck extremely long primarily because of elongation of vertebrae.
**AGE** Middle Triassic; middle Anisian.
**DISTRIBUTION AND FORMATIONS** Southern China; middle Guanling.
**HABITAT** Continental nearshore.
**HABITS** Ambush fisher of small game.
**NOTES** Not sufficiently well known to estimate mass. Shared its habitat with *Atopodentatus*, *Dianopachysaurus*.

## ARCHOSAURIFORMES

**SMALL TO GIGANTIC ARCHOSAUROMORPHS FROM THE LATE PERMIAN TO THE MODERN ERA, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Extremely diverse. Preorbital opening in front of orbits and opening in middle of lower jaws, one or both sometimes closed off, parietal eye very reduced or absent, teeth when present set in sockets.
**HABITAT AND HABITS** Extremely variable, marine to fully terrestrial to highly aerial, highly herbivorous to archpredatory.

### CRUROTARSI OR PSEUDOSUCHIANS

**SMALL TO GIGANTIC ARCHOSAURIFORMES FROM THE EARLY TRIASSIC TO THE MODERN ERA, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Diverse. Skulls akinetic, parietal eye absent. Necks including cervical ribs short. Trunks fairly long, not broad, gastralia slender. Tails moderately long. Ankle a complex joint with a large calcaneal heel tuber. Usually armored to some degree.
**HABITAT** Fully terrestrial to highly marine.
**HABITS** Herbivorous to archpredatory.

## CROCODYLIFORMES

**SMALL TO GIGANTIC PSEUDOSUCHIANS FROM THE LATE TRIASSIC TO THE MODERN ERA, GLOBAL**

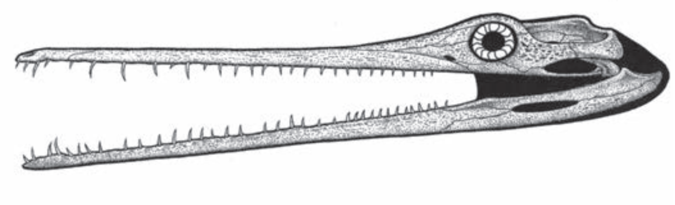
**ANATOMICAL CHARACTERISTICS** Diverse. Heads heavily constructed, akinetic, often shallow with roof flattened, nostrils at tip of snout, preorbital opening reduced or closed off, temporal openings often reduced or closed off, squamosal at upper rear corner of skull massive, teeth usually have bulbous roots, no teeth on mouth roof. Cervical rib overlap modest when present. Gastralia limited to aft portion of abdomen, rib-free lumbar region present. Clavicles absent, coracoid elongated. A pair of carpals elongated. Liver pump respiratory system partially present.
**HABITAT** Fully terrestrial to highly marine.
**HABITS** Herbivorous to archpredatory.

## MESOEUCROCODYLIANS

**SMALL TO GIGANTIC CROCODYLIFORMES FROM THE EARLY JURASSIC TO THE MODERN ERA, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Fairly diverse. Partial secondary mouth roof present. Pelvis at least somewhat reduced, mobile pubis part of the liver-pump respiratory system. Toes increasingly long progressing outward.
**HABITAT** Fully terrestrial to highly marine.
**HABITS** Herbivorous to archpredatory.
**NOTES** Includes modern crocodilians.

***Pelagosaurus* (Thalattosuchians)**



## THALATTOSUCHIANS

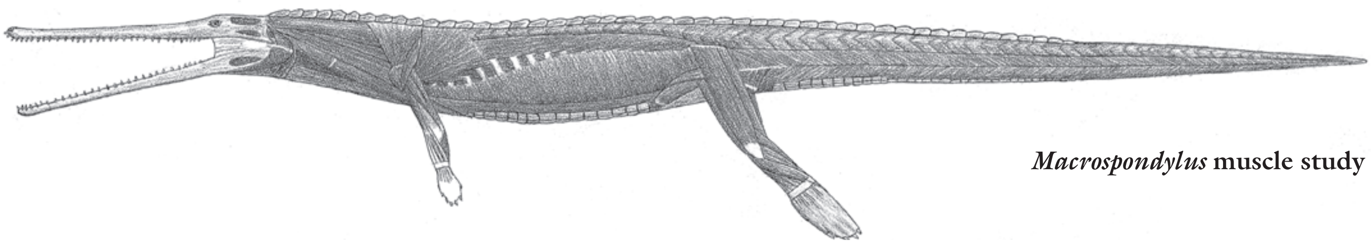
**SMALL TO LARGE MESOEUCROCODYLIANS FROM THE EARLY JURASSIC TO EARLY CRETACEOUS, GLOBAL**

**ANATOMICAL CHARACTERISTICS** Somewhat diverse. Highly aquatic. Upper temporal openings large. Aft tail flattened. Arms strongly reduced both absolutely and compared to legs, latter are paddles, inner fingers and toes most robust, toes increasingly long progressing outward. Moderately hydrodynamically streamlined, primarily axial undulators of anguilliform grade, limbs primarily for stability and maneuvering, pressed tight to body when hydrocruising.
**HABITAT** Freshwaters to perhaps deep oceans.
**HABITS** Swimming performance fair to very good. Ambush and/or pursuit fishers and hunters of small to big game. Probably able to move onshore and breed on beaches.
**NOTES** Restriction of nostrils to tip of snout may have inhibited evolution of group as marine creatures.

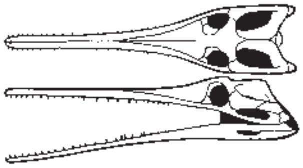
## TELEOSAURIDS

**SMALL TO LARGE THALATTOSUCHIANS FROM THE EARLY TO LATE JURASSIC OF THE EASTERN HEMISPHERE**

**ANATOMICAL CHARACTERISTICS** Uniform. Heads shallow, snouts elongated, tips a little expanded laterally, snouts much narrower than temporal region, preorbital opening closed, lower jaws shallow, teeth numerous, not large, procumbent. Aft tail straight. Hands very small, not hydrodynamic. Parallel single rows of armor atop midline of neck, trunk, and most of tail, multiple rows of armor along midline of aft abdomen and first half of tail.
**HABITAT** Coastal freshwaters to perhaps deep oceans.
**HABITS** Swimming performance fair. Ambush and pursuit fishers and hunters of small to medium-sized game.
**NOTES** The once major multispecies genus *Steneosaurus* has been replaced by a number of new genera.



***Macrospondylus* muscle study**



*Plagiophthalmosuchus gracilirostris*

### *Plagiophthalmosuchus gracilirostris*

**3 m (10) TL, 60 kg (130 lb)**

FOSSIL REMAINS Skull and skeleton severely flattened top to bottom, skull.
ANATOMICAL CHARACTERISTICS Head long, snout very long and very narrow, aft head much shorter, teeth very numerous and slender.
AGE Early Jurassic; early Toarcian.
DISTRIBUTION AND FORMATIONS Northeastern England, Luxembourg; lower Whitby Mudstone, unnamed.
HABITAT Island shallows.
HABITS Preferred small prey.
NOTES Shared its habitat with *Rhomaleosaurus*, *Hauffiosaurus*, *Eurhinosaurus*, *Mystriosaurus*, *Macrospondylus.*

### *Mycterosuchus nasutus*

**5 m (16 ft) TL, 250 kg (550 lb)**

FOSSIL REMAINS Skulls complete and partial, skeleton severely flattened top to bottom.
ANATOMICAL CHARACTERISTICS Snout very long and very narrow, aft head much shorter, teeth very numerous and small.
AGE Early Jurassic; late middle Callovian.
DISTRIBUTION AND FORMATIONS Central England; upper Oxford Clay.
HABITAT Island archipelago shallows.
HABITS Preferred small prey.

### *Aeolodon priscus*

**3.5 m (11 ft) TL, 90 kg (200 lb)**

FOSSIL REMAINS Two complete skulls and skeletons, severely flattened top to bottom.
ANATOMICAL CHARACTERISTICS Head long, snout very long and very narrow, aft head much shorter, teeth very numerous and small.
AGE Late Jurassic; early Tithonian.
DISTRIBUTION AND FORMATIONS Southern Germany, southeastern France; Mörnsheim, unnamed.
HABITAT Island archipelago shallows.
HABITS Preferred small prey.
NOTES Shared its habitat with *Geosaurus giganteus*, *Dakosaurus maximus*, *Cricosaurus elegans*, *Rhacheosaurus.*

### *Bathysuchus megarhinus*

**4 m (13 ft) TL, 140 kg (300 lb)**

FOSSIL REMAINS Minority of two skulls.
ANATOMICAL CHARACTERISTICS Snout very long and narrow, tip laterally expanded.
AGE Late Jurassic; late Kimmeridgian.
DISTRIBUTION AND FORMATIONS Southern England, southwestern France; lower Kimmeridge Clay, Ancholme Group.
HABITAT Island archipelago shallows.
HABITS Preferred small prey.
NOTES Shared its habitat with *Pliosaurus brachydeirus*, *Colymbosaurus megadeirus*, *Torvoneustes*, *Plesiosuchus*, *Neosteneosaurus*, *Lemmysuchus.*

### *Mystriosaurus laurillardi*

**4 m (13 ft) TL, 140 kg (300 lb)**

FOSSIL REMAINS Majority of skull, partial skull.
ANATOMICAL CHARACTERISTICS Snout elongated and narrow, robust, teeth medium sized and fairly stout.
AGE Early Jurassic; early Toarcian.
DISTRIBUTION AND FORMATIONS Southern Germany, northeastern England; Posidonienschiefer, lower Whitby Mudstone.
HABITAT Island archipelago shallows.
NOTES Shared its habitat with *Meyerasaurus*, *Rhomaleosaurus*, *Hauffiosaurus*, *Seeleyosaurus*, *Hydrorion*, *Hauffiopteryx*, unnamed genus *trigonodon*, *Suevoleviathan*, *Eurhinosaurus*, *Stenopterygius*, *Plagiophthalmosuchus*, *Macrospondylus*, *Platysuchus.*

### *Platysuchus multiscrobiculatus*

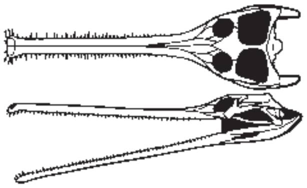
**2.75 m (9 ft) TL, 45 kg (100 lb)**

FOSSIL REMAINS Skull and skeleton, severely flattened top to bottom.
ANATOMICAL CHARACTERISTICS Head long, snout very long and very narrow, aft head much shorter, teeth very numerous and slender.
AGE Early Jurassic; early Toarcian.
DISTRIBUTION AND FORMATIONS Southern Germany; Posidonienschiefer.
HABITAT Island archipelago shallows.
HABITS Preferred small prey.

### *Teleosaurus cadomensis*

**3 m (10) TL, 60 kg (130 lb)**

FOSSIL REMAINS Several specimens.
ANATOMICAL CHARACTERISTICS Snout extremely long and very narrow, aft head much shorter, teeth very numerous and slender.
AGE Middle Jurassic; Bathonian.



*Teleosaurus cadomensis*

**DISTRIBUTION AND FORMATIONS** Northern France; unnamed.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred small prey.
**NOTES** Most original remains destroyed by Allied bombardment in World War II. Probably includes *T. geoffroyi*.

### *Indosinosuchus potamosiamensis*
**4 m (13 ft) TL, 140 kg (300 lb)**

**FOSSIL REMAINS** Complete and partial skulls.
**ANATOMICAL CHARACTERISTICS** Snout moderately elongated, aft head about as elongated, teeth moderately numerous, medium sized, fairly stout.
**AGE** Late Jurassic; Tithonian?
**DISTRIBUTION AND FORMATIONS** Thailand; lower Phu Kradung.
**HABITAT** Coastal fresh watercourses.
**NOTES** May include *I. kalasinensis*. Appears to show that at least some marine crocodilians entered freshwater. Age poorly known.

### Unnamed genus and species
**4 m (13 ft) TL, 140 kg (300 lb)**

**FOSSIL REMAINS** Majority of skull, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Snout very long and very narrow, aft head much shorter, teeth very numerous and small.
**AGE** Early Jurassic; Toarcian.
**DISTRIBUTION AND FORMATIONS** Central China; Ziliujing.
**HABITAT** Coastal shallows.
**NOTES** Was previously assigned to poorly preserved and different *Peipehsuchus teleorhinus*. Shared its habitat with *Bishanopliosaurus youngi*.

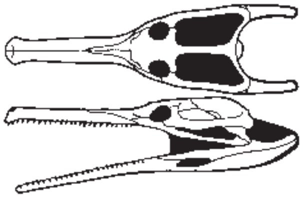
## MACHIMOSAURIDS

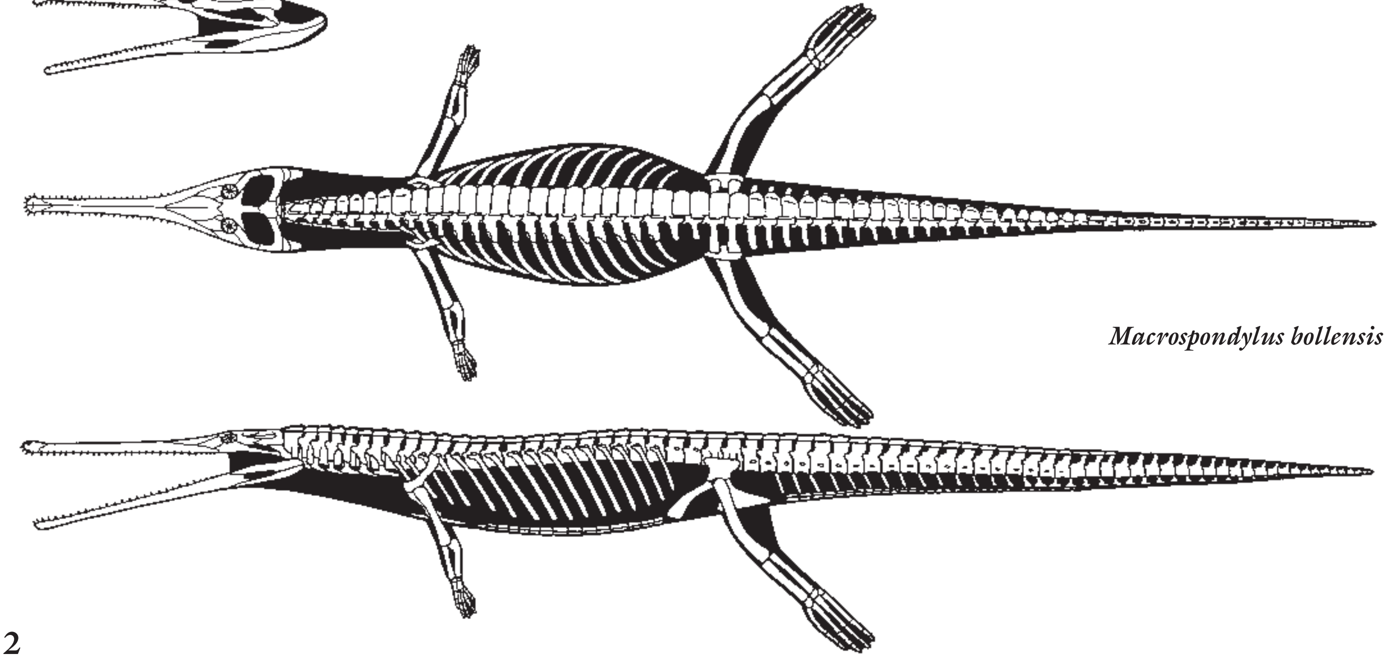
**SMALL TO LARGE THALATTOSUCHIANS FROM THE EARLY JURASSIC TO EARLY CRETACEOUS OF THE EASTERN HEMISPHERE**

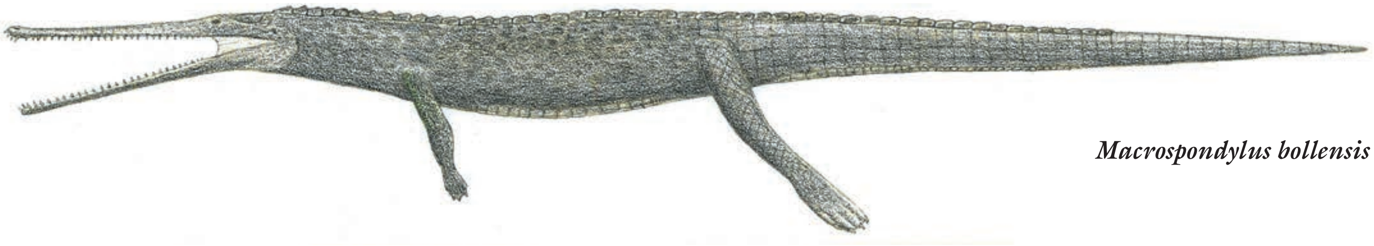
**ANATOMICAL CHARACTERISTICS** Uniform. Heads shallow, snouts elongated, tips a little expanded laterally, snouts much narrower than temporal region, preorbital opening closed, lower jaws shallow, teeth numerous, procumbent. Aft tail straight. Hands very small, not hydrodynamic. Parallel single rows of armor atop midline of neck, trunk, and most of tail, multiple rows of armor along midline of aft abdomen and first half of tail.
**HABITAT** Coastal freshwaters to perhaps deep oceans.
**HABITS** Swimming performance fair. Ambush and pursuit fishers and hunters of small to medium-sized game.
**NOTES** The once major multispecies genus *Steneosaurus* has been replaced by a number of new genera.

### *Macrospondylus bollensis*
**5 m (16.5 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Numerous skulls and skeletons, many complete.
**ANATOMICAL CHARACTERISTICS** Head long, snout very long and very narrow, aft head much shorter, teeth very numerous and rather slender.


***Indosinosuchus potamosiamensis***


***Macrospondylus bollensis***



*Macrospondylus bollensis*

**AGE** Early Jurassic; early Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern Germany, Luxembourg, northeastern England; Posidonienschiefer, lower Whitby Mudstone.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred small prey.
**NOTES** Shared its habitat with *Meyerasaurus*, *Rhomaleosaurus*, *Hauffiosaurus*, *Seeleyosaurus*, *Hydrorion*, *Hauffiopteryx*, unnamed genus *trigonodon*, *Suevoleviathan*, *Eurhinosaurus*, *Stenopterygius*, *Plagiophthalmosuchus*, *Mystriosaurus*, *Platysuchus*. The classic marine crocodilian, long placed within *Steneosaurus*.

### *Clovesuurdameredeor stephani*

**5 m (16.5 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Middle Jurassic; Bathonian.
**DISTRIBUTION AND FORMATIONS** Southern England; Cornbrash.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred small prey.

### *Seldsienean megistorhynchus*

**8 m (26 ft) TL, 1 tonne**

**FOSSIL REMAINS** Partial skulls.
**ANATOMICAL CHARACTERISTICS** Snout very long and narrow, tip laterally expanded.
**AGE** Middle Jurassic; Bathonian.
**DISTRIBUTION AND FORMATIONS** Southern England, France; Cornbrash, unnamed.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred small prey.

### *Deslongchampsina larteti*

**3 m (10) TL, 60 kg (130 lb)**

**FOSSIL REMAINS** Several complete and partial skulls.
**ANATOMICAL CHARACTERISTICS** Snout very long and very narrow, aft head much shorter, teeth moderately numerous, fairly large and slender.
**AGE** Middle Jurassic; late Bathonian.
**DISTRIBUTION AND FORMATIONS** Central England; Cornbrash.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred small prey.
**NOTES** Shared its habitat with *Yvridiosuchus.*

### *Charitomenosuchus leedsi*

**3 m (10) TL, 60 kg (130 lb)**

**FOSSIL REMAINS** A complete and partial skulls, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Snout extremely long and very narrow, aft head much shorter, teeth very numerous and slender.
**AGE** Middle Jurassic; middle Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England, northern France; middle Oxford Clay, Marnes de Dives.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred small prey.
**NOTES** Shared its habitat with *Neosteneosaurus*, *Lemmysuchus*, *Thalattosuchus.*

### *Proexochokefalos heberti*

**5.5 m (18 ft) TL, 600 kg (1,300 lb)**

**FOSSIL REMAINS** Skull.
**ANATOMICAL CHARACTERISTICS** Snout moderately elongated, aft head almost as elongated, teeth limited to front half of jaws, moderately numerous, small, fairly stout.
**AGE** Middle Jurassic; late Callovian.
**DISTRIBUTION AND FORMATIONS** Northwestern France; Marnes de Dives.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Charitomenosuchus.*

*Proexochokefalos heberti*

### *Proexochokefalos bouchardi*

**5 m (16.5 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Majority of skull.
**ANATOMICAL CHARACTERISTICS** Snout moderately elongated, aft head almost as elongated, teeth limited to front half of jaws, moderately numerous, small, fairly stout.

**AGE** Middle Jurassic; Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Northwestern France; Reuchenette.
**HABITAT** Island archipelago shallows.

### *Neosteneosaurus edwardsi*

**5 m (16.5 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Complete and partial remains.
**ANATOMICAL CHARACTERISTICS** Snout elongated and narrow.
**AGE** Middle Jurassic; middle Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England, northern France; middle Oxford Clay, Ancholme Group.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred small prey.
**NOTES** Shared its habitat with *Bathysuchus*, *Lemmysuchus*, *Charitomenosuchus*.

### *Andrianavoay baroni*

**5 m (16.5 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Snout elongated and narrow.
**AGE** Middle Jurassic; Bathonian.
**DISTRIBUTION AND FORMATIONS** Madagascar; uncertain.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred small prey.

### *Lemmysuchus obtusidens*

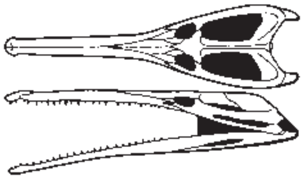
**5 m (16.5 ft) TL, 250 kg (550 lb)**

**FOSSIL REMAINS** Several specimens, complete to partial.
**ANATOMICAL CHARACTERISTICS** Snout moderately elongated, aft head almost as elongated.
**AGE** Middle Jurassic; middle Callovian.
**DISTRIBUTION AND FORMATIONS** Eastern England, northwestern France; middle Oxford Clay, Ancholme Group.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Bathysuchus*, *Neosteneosaurus*, *Charitomenosuchus*.

### *Yvridiosuchus boutilieri*

**4 m (13 ft) TL, 140 kg (300 lb)**

**FOSSIL REMAINS** Two partial skulls.
**ANATOMICAL CHARACTERISTICS** Snout elongated and narrow, robust, aft head almost as elongated, shallow, teeth moderately numerous, medium sized, and fairly stout.
**AGE** Middle Jurassic; late Bathonian.
**DISTRIBUTION AND FORMATIONS** Central England, northern France; Cornbrash, unnamed.
**HABITAT** Island archipelago shallows.



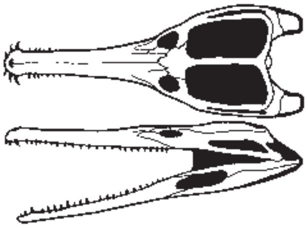
*Yvridiosuchus boutilieri*

**HABITS** Preferred small prey.
**NOTES** Shared its habitat with *Deslongchampsina*.

### Unnamed genus *buffetauti*

**5 m (16.5 ft) TL, 350 kg (800 lb)**

**FOSSIL REMAINS** Two skulls and partial skeleton.
**ANATOMICAL CHARACTERISTICS** Snout elongated, robust, temporal region very large in length and breadth, teeth medium sized.
**AGE** Late Jurassic; early Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern and northern Germany, northern France; Lacunosamergal, Langenberg, Calcaires Coguilliers.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred larger prey.
**NOTES** Placement in *Machimosaurus* very dubious because original genus and species *M. hugii* is based on poorly preserved material.



Unnamed genus *buffetauti*

### Unnamed genus *mosae*

**5 m (16.5 ft) TL, 350 kg (800 lb)**

**FOSSIL REMAINS** Majority of two skulls and skeletons.
**ANATOMICAL CHARACTERISTICS** Snout elongated, robust, temporal region very large in length and breadth, teeth medium sized.
**AGE** Late Jurassic; latest Kimmeridgian and/or lowest Tithonian.
**DISTRIBUTION AND FORMATIONS** Eastern France; unnamed, Argiles de Châtillon.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred larger prey.
**NOTES** Placement in *Machimosaurus* very dubious because original genus and species *M. hugii* is based on poorly preserved material. One specimen was destroyed by Allied bombardment in World War II.

### Unnamed genus *rex*

**7.5 (25 ft) TL, 1 tonne**

**FOSSIL REMAINS** Partial skull and minority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Snout robust, temporal region very large in length and breadth.
**AGE** Early Cretaceous; late Hauterivian and/or early Barremian.
**DISTRIBUTION AND FORMATIONS** Tunisia; lower Douiret.
**HABITAT** Continental shallows.
**HABITS** Preferred larger prey.
**NOTES** Original placement in much earlier *Machimosaurus* highly problematic. Indicates that teleosaurids persisted into Early Cretaceous.

## METRIORHYNCHOIDS

**SMALL TO LARGE THALATTOSUCHIANS FROM THE EARLY JURASSIC TO EARLY CRETACEOUS OF EUROPE AND THE AMERICAS**

**ANATOMICAL CHARACTERISTICS** Orbits face more sideways. Armor at least a little reduced.
**HABITAT** Coastal shallows to perhaps deep oceans.
**HABITS** Swimming performance good to very good. Ambush and/or pursuit fishers and hunters of small to big game.
**NOTES** Absence from at least some other seas probably reflects lack of sufficient sampling.

## PELAGOSAURIDS

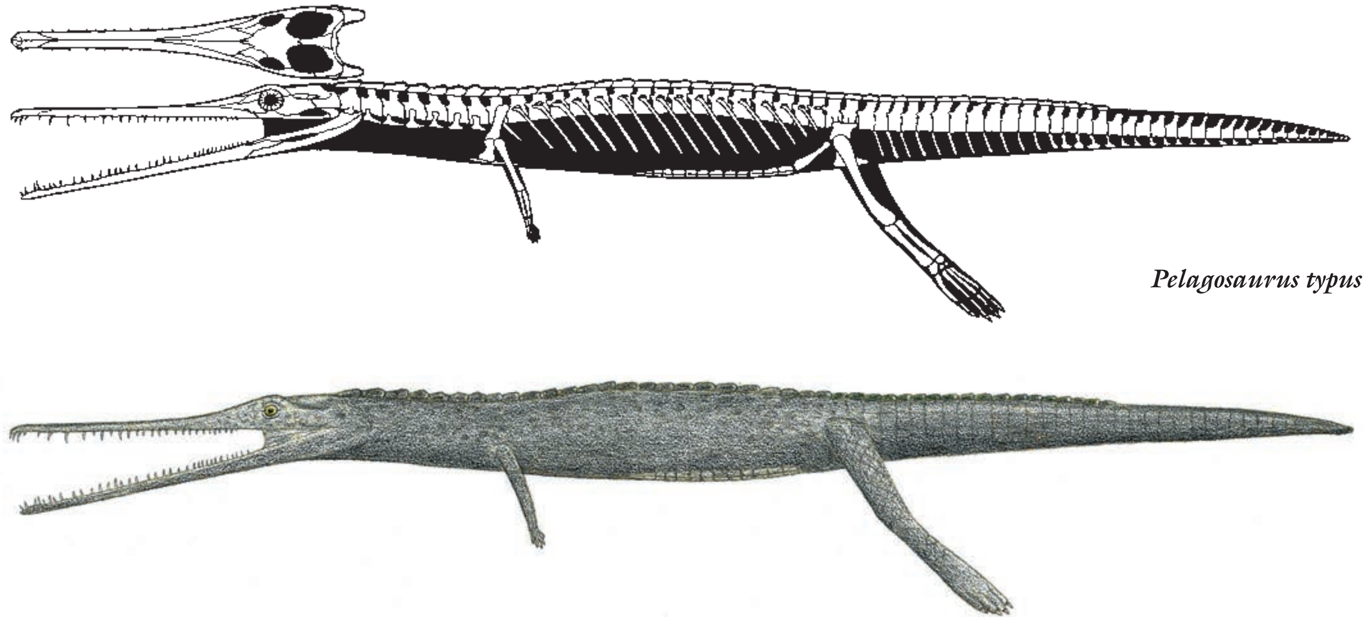
**MEDIUM-SIZED TO LARGE METRIORHYNCHOIDS FROM THE EARLY TO LATE JURASSIC OF EUROPE**

**ANATOMICAL CHARACTERISTICS** Uniform. Heads shallow, snouts elongated, tips a little expanded laterally, snouts much narrower than temporal region, preorbital opening closed, lower jaws shallow, teeth numerous, not large. Aft tail straight. Hands very small, not hydrodynamic. Parallel single rows of armor along midline of neck, trunk, and most of tail, twin rows of armor along midline of aft abdomen and first half of tail.
**HABITAT** Coastal.
**HABITS** Swimming performance good. Ambush and pursuit fishers and hunters of small to medium-sized game.

### *Pelagosaurus typus*

**3 m (10 ft) TL, 60 kg (130 lb)**

**FOSSIL REMAINS** Numerous specimens, some nearly complete.
**ANATOMICAL CHARACTERISTICS** Head very long, snout extremely long and very narrow, aft head much shorter, teeth moderate in number and slender. Tail moderately long.
**AGE** Early Jurassic; Toarcian.
**DISTRIBUTION AND FORMATIONS** Southern England, northern France; lower Upper Lias.
**HABITAT** Island archipelago shallows.
**HABITS** Preferred small prey.



*Pelagosaurus typus*

### *Magyarosuchus fitosi*

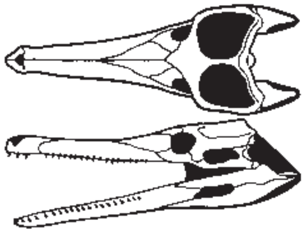
**4.5 m (15 ft) TL, 200 kg (450 lb)**

FOSSIL REMAINS Partial remains.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic; late Tithonian.
DISTRIBUTION AND FORMATIONS Hungary; Kisgerecse Marl.
HABITAT Island archipelago shallows.

### *Teleidosaurus calvadosii*

**3 m (10 ft) TL, 70 kg (150 lb)**

FOSSIL REMAINS Skull, other remains.
ANATOMICAL CHARACTERISTICS Snout moderately elongated, robust, teeth moderate in number, short and stout.
AGE Middle Jurassic; middle Bathonian.
DISTRIBUTION AND FORMATIONS Northern France; Calcaire de Caen.
HABITAT Island archipelago shallows.
NOTES Some remains destroyed by Allied bombardment in World War II.



***Teleidosaurus calvadosii***

### *Eoneustes gaudryi*

**3 m (10 ft) TL, 70 kg (150 lb)**

FOSSIL REMAINS Partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic; late Bajocian to middle Bathonian.
DISTRIBUTION AND FORMATIONS Northern France; Upper Lias.
HABITAT Island archipelago shallows.
NOTES May include *Eoneustes bathonicus.* Some remains destroyed by Allied bombardment in World War II.

### *Zoneait nargorum*

**5 m (16 ft) TL, 350 kg (750 lb)**

FOSSIL REMAINS Several partial skulls and minority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Middle Jurassic; latest Aalenian and/or earliest Bajocian.
DISTRIBUTION AND FORMATIONS Oregon; lower Snowshoe.
HABITAT Island archipelago shallows.

## METRIORHYNCHIDS

**SMALL TO LARGE METRIORHYNCHOIDS FROM THE LATE JURASSIC TO THE EARLY CRETACEOUS, GLOBAL**

ANATOMICAL CHARACTERISTICS Fairly uniform. Orbits face largely sideways. Sharply downward-flexed aft tail vertebrae supported large soft upper fin that was dorsal half of semilunate tail flukes. Forelimbs a small flipper. Pelvis reduced. Unarmored.
HABITAT Coastal shallows to perhaps deep oceans.
HABITS Swimming performance very good. Ambush and especially pursuit fishers and hunters of small to big game.

## GEOSAURINES

**SMALL TO LARGE METRIORHYNCHIDS FROM THE MIDDLE JURASSIC OF EUROPE AND SOUTH AMERICA**

ANATOMICAL CHARACTERISTICS Snouts not extremely elongated, preorbital opening closed.
HABITAT Coastal shallows to perhaps deep oceans.
HABITS Fishers and hunters of small to big game.
NOTES Absence from at least some other seas probably reflects lack of sufficient sampling.

### *Purranisaurus casamiquelai*

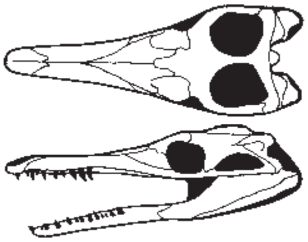
**3 m (10 ft) TL, 80 (180 lb)**

FOSSIL REMAINS Two skulls, complete and partial.
ANATOMICAL CHARACTERISTICS Teeth limited to front portions of jaws, fairly large and robust.
AGE Middle Jurassic; middle Callovian.
DISTRIBUTION AND FORMATIONS Northern Chile; unnamed.
HABITAT Continental shelf.
NOTES Probably includes *P. westermanni.*

### *Purranisaurus potens*

**2.5 m (8 ft) TL, 50 kg (110 lb)**

FOSSIL REMAINS Majority of skull.
ANATOMICAL CHARACTERISTICS Teeth not large.
AGE Late Jurassic and/or Early Cretaceous; late Tithonian and/or early Berriasian.



***Purranisaurus potens***

**DISTRIBUTION AND FORMATIONS** Central Argentina; upper Vaca Muerta.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Cricosaurus puelchorum*.

### *Neptunidraco ammoniticus*

**2.5 m (8 ft) TL, 50 kg (110 lb)**

**FOSSIL REMAINS** Partial skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Middle Jurassic; late Bajocian and/or earliest Bathonian.
**DISTRIBUTION AND FORMATIONS** Northern Italy; lower Rosso Ammonitico Veronese.
**HABITAT** Island archipelago shallows.

### *Torvoneustes carpenteri*

**4.5 m (15 ft) TL, 275 kg (600 lb)**

**FOSSIL REMAINS** Two partial skulls.
**ANATOMICAL CHARACTERISTICS** Snout not elongated, teeth fairly large.
**AGE** Late Jurassic; late Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Kimmeridge Clay.
**HABITAT** Island archipelago shallows.
**NOTES** May include *T. coryphaeus*. Shared its habitat with *Pliosaurus brachydeirus*, *Colymbosaurus megadeirus*, *Bathysuchus*, *Plesiosuchus*.

### *Tyrannoneustes lythrodectikos*

**2.5 m (8 ft) TL, 50 kg (110 lb)**

**FOSSIL REMAINS** Partial skull and skeletal remains.
**ANATOMICAL CHARACTERISTICS** Teeth stout.
**AGE** Middle Jurassic; middle Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Oxford Clay.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Peloneustes*, *Pachycostasaurus*, *Simolestes*, *Liopleurodon*, *Cryptoclidus*, *Muraenosaurus*, *Tricleidus*, *Ophthalmosaurus*, *Suchodus*, *Gracilineustes*.

### *Geosaurus giganteus*

**3 m (10 ft) TL, 80 (180 lb)**

**FOSSIL REMAINS** Four skulls, severely flattened or partial.
**ANATOMICAL CHARACTERISTICS** Snout not elongated, teeth large, intermeshing.
**AGE** Late Jurassic; late early Tithonian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Mörnsheim.
**HABITAT** Island archipelago shallows.
**NOTES** May include *Geosaurus grandis*. Shared its habitat with *Aeolodon*, *Dakosaurus maximus*, *Rhacheosaurus*, *Cricosaurus elegans*.

### *Suchodus brachyrhynchus*

**3 m (10 ft) TL, 80 kg (180 lb)**

**FOSSIL REMAINS** Majority of skull, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Snout not elongated.
**AGE** Middle Jurassic; middle Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Oxford Clay.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Peloneustes*, *Pachycostasaurus*, *Simolestes*, *Liopleurodon*, *Cryptoclidus*, *Muraenosaurus*, *Tricleidus*, *Ophthalmosaurus*, *Tyrannoneustes*, *Gracilineustes*.

### *Plesiosuchus manselii*

**7 m (23 ft) TL, 1 tonne**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Snout not elongated.
**AGE** Late Jurassic; late Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Kimmeridge Clay.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Pliosaurus brachydeirus*, *Colymbosaurus megadeirus*, *Bathysuchus*, *Torvoneustes*.

## DAKOSAURINES

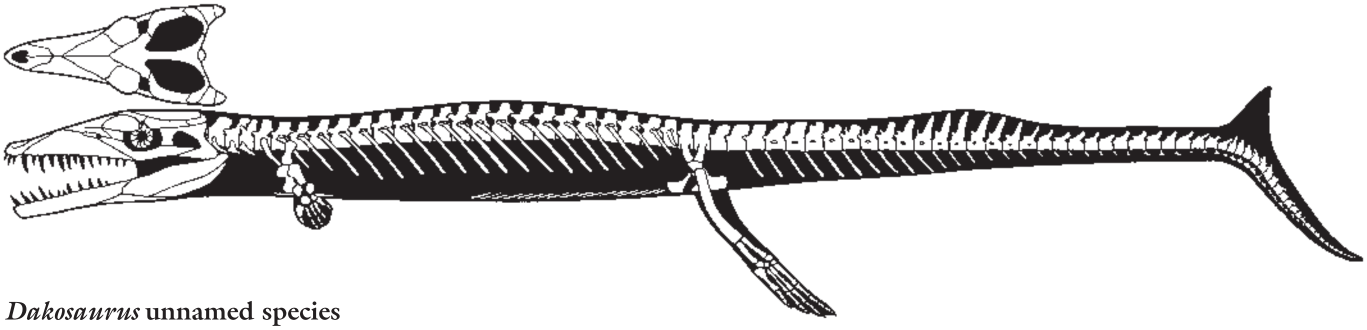
**MEDIUM-SIZED METRIORHYNCHIDS FROM THE MIDDLE TO LATE JURASSIC OF EUROPE AND SOUTH AMERICA**

**ANATOMICAL CHARACTERISTICS** Heads deep along most of their length, moderately broad, preorbital opening small, bar on upper orbital rim shaded eyes, teeth moderate in number and quite large. Trunk shallow. Foreflipper subcircular, clawless.
**HABITAT** Coastal shallows to perhaps deep oceans.
**HABITS** Pursuit fishers and hunters of small to especially big game.
**NOTES** Absence from at least some other seas probably reflects lack of sufficient sampling.

### *Dakosaurus* unnamed species

**4 m (13 ft) TL, 140 kg (300 lb)**

**FOSSIL REMAINS** Complete skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Head very large, subtriangular.
**AGE** Late Jurassic; late Kimmeridgian.



*Dakosaurus* unnamed species

**DISTRIBUTION AND FORMATIONS** Southern Germany; Torleite.
**HABITAT** Island archipelago shallows.
**NOTES** May be direct ancestor of *D. maximus.*

### *Dakosaurus maximus*

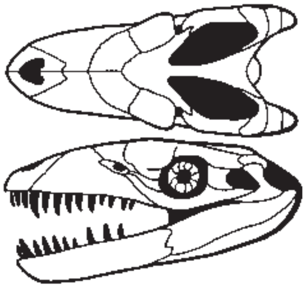
**4.5 m (15 ft) TL, 200 kg (450 lb)**

**FOSSIL REMAINS** Complete and partial skulls and skeleton.
**ANATOMICAL CHARACTERISTICS** Head very large, subtriangular.
**AGE** Late Jurassic; late early Tithonian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Mörnsheim.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Aeolodon*, *Geosaurus giganteus*, *Rhacheosaurus*, *Cricosaurus elegans.*

### *Dakosaurus andiniensis*

**5 m (16.5 ft) TL, 275 kg (600 lb)**

**FOSSIL REMAINS** Complete and partial skulls, minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Head more rectangular in side and top views, teeth more robust, lower jaw deeper.
**AGE** Late Jurassic; late Tithonian.
**DISTRIBUTION AND FORMATIONS** Central Argentina; middle Vaca Muerta.
**HABITAT** Continental shelf.
**NOTES** Shared its habitat with *Arthropterygius*? *thalassonotus*, unnamed genus and species, *Sumpalla*?



*Dakosaurus andiniensis*

## METRIORHYNCHINES

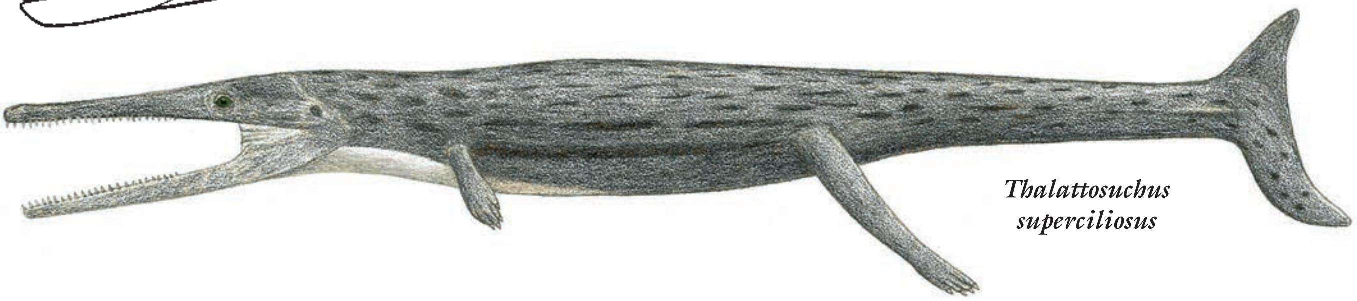
### MEDIUM-SIZED METRIORHYNCHIDS FROM THE MIDDLE TO LATE JURASSIC OF EUROPE

**ANATOMICAL CHARACTERISTICS** Snouts highly elongated, fairly narrow, preorbital opening closed, lower jaws shallow, teeth medium sized, robust. Foreflipper clawed.
**HABITAT** Coastal.
**HABITS** Fishers of small to medium-sized game.
**NOTES** The once major multispecies genus *Metriorhynchus* has been replaced by new genera. Absence from at least some other seas may reflect lack of sufficient sampling.

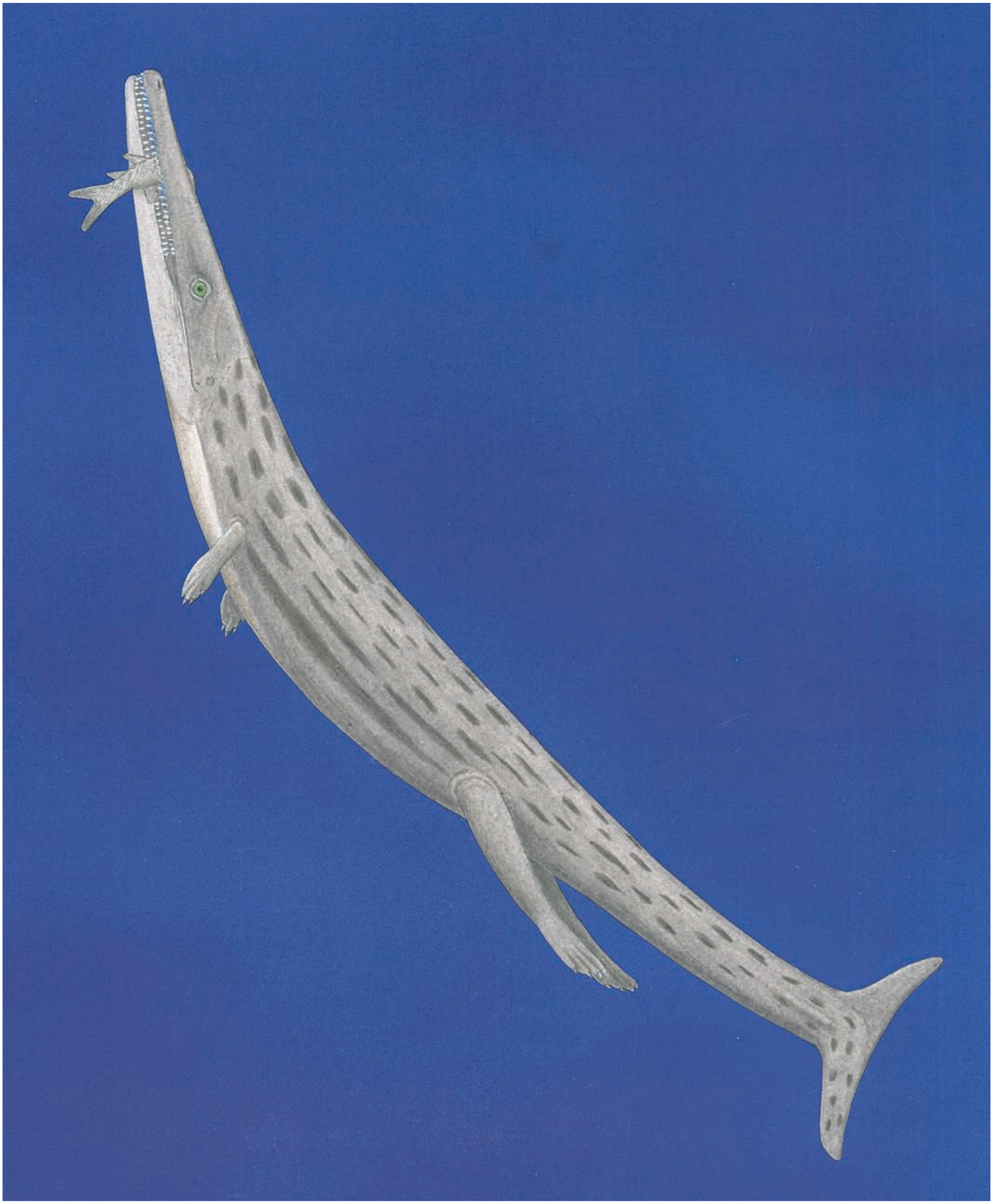
### *Thalattosuchus superciliosus*

**3 m (10 ft) TL, 115 kg (255 lb)**

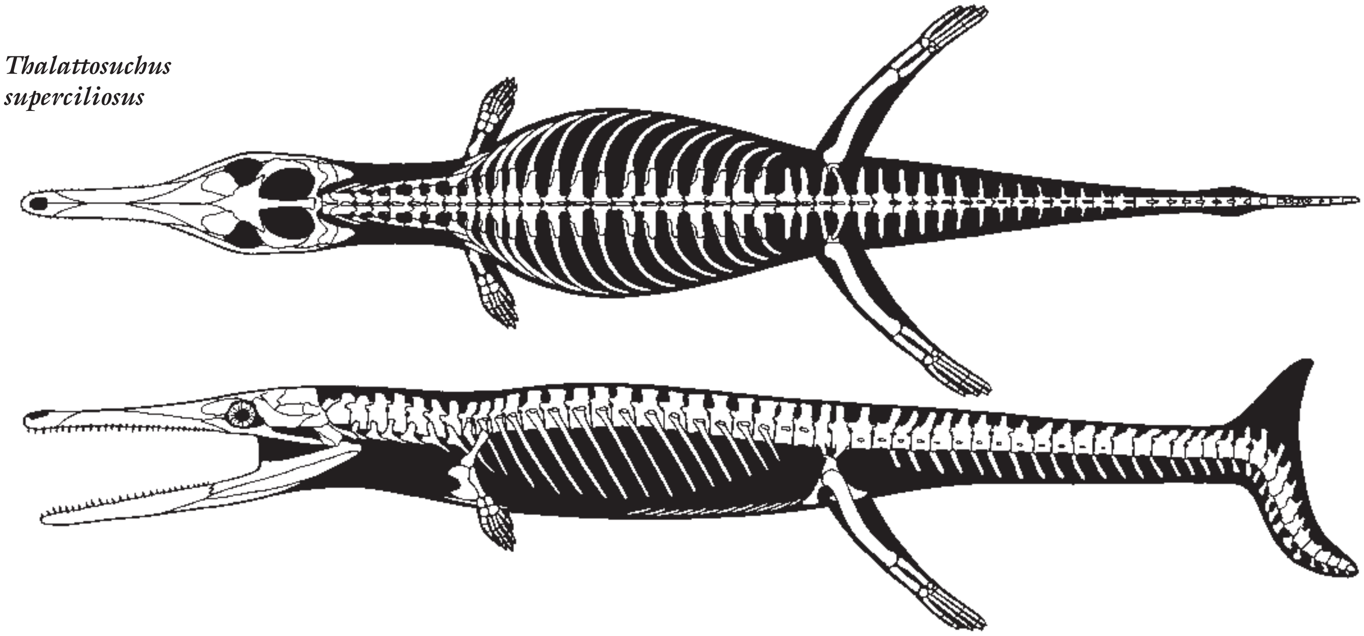
**FOSSIL REMAINS** Skull and skeletal remains.
**ANATOMICAL CHARACTERISTICS** Coronoid process prominent, teeth numerous.
**AGE** Middle Jurassic; late Callovian.
**DISTRIBUTION AND FORMATIONS** Northern France; Marnes de Dives.
**HABITAT** Island archipelago shallows.
**NOTES** May include *Metriorhynchus moreli*. Shared its habitat with *Proexochokefalos.*



*Thalattosuchus superciliosus*



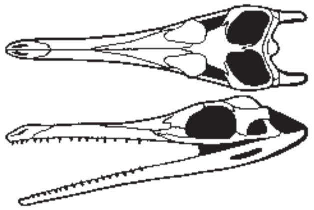
*Thalattosuchus superciliosus*



### *Maledictosuchus riclaensis*

**4 m (13 ft) TL, 275 kg (600 lb)**

**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth not numerous.
**AGE** Middle Jurassic; middle Callovian.
**DISTRIBUTION AND FORMATIONS** Northeastern Spain; Agreda.
**HABITAT** Continental shelf.



*Maledictosuchus riclaensis*

### *Gracilineustes leedsi*

**4 m (13 ft) TL, 140 kg (300 lb)**

**FOSSIL REMAINS** Complete and partial skull, minority of skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Standard for group.
**AGE** Middle Jurassic; middle Callovian.
**DISTRIBUTION AND FORMATIONS** Southern England; lower Oxford Clay.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Peloneustes*, *Pachycostasaurus*, *Simolestes*, *Liopleurodon*, *Cryptoclidus*, *Muraenosaurus*, *Tricleidus*, *Ophthalmosaurus*, *Tyrannoneustes*, *Suchodus.*

## RHACHEOSAURINES

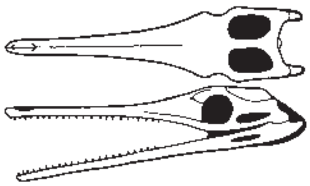
**SMALL TO MEDIUM-SIZED METRIORHYNCHIDS FROM THE MIDDLE TO EARLY CRETACEOUS OF EUROPE AND SOUTH AMERICA**

**ANATOMICAL CHARACTERISTICS** Snouts long and fairly narrow, preorbital opening closed, lower jaws shallow, teeth moderate in number. Foreflipper not clawed.
**HABITAT** Coastal.
**HABITS** Fishers of small to medium-sized game.
**NOTES** Absence from at least some other seas may reflect lack of sufficient sampling.

### *Rhacheosaurus gracilis*

**1.5 m (5 ft) TL, 10 kg (22 lb)**

**FOSSIL REMAINS** A few skulls and skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth rather small.
**AGE** Late Jurassic; late early Tithonian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Mörnsheim.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Aeolodon*, *Geosaurus giganteus*, *Dakosaurus maximus*, *Cricosaurus elegans.*



*Rhacheosaurus gracilis*

### *Cricosaurus bambergensis*

**1.6 m (5.2 ft) TL, 12 kg (25 lb)**

**FOSSIL REMAINS** Skull and skeleton, severely flattened top to bottom.
**ANATOMICAL CHARACTERISTICS** Teeth fairly large.
**AGE** Late Jurassic; early late Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; lower Torleite.
**HABITAT** Island archipelago shallows.
**NOTES** May the direct ancestor of one of the German species below.

### *Cricosaurus albersdoerferi*

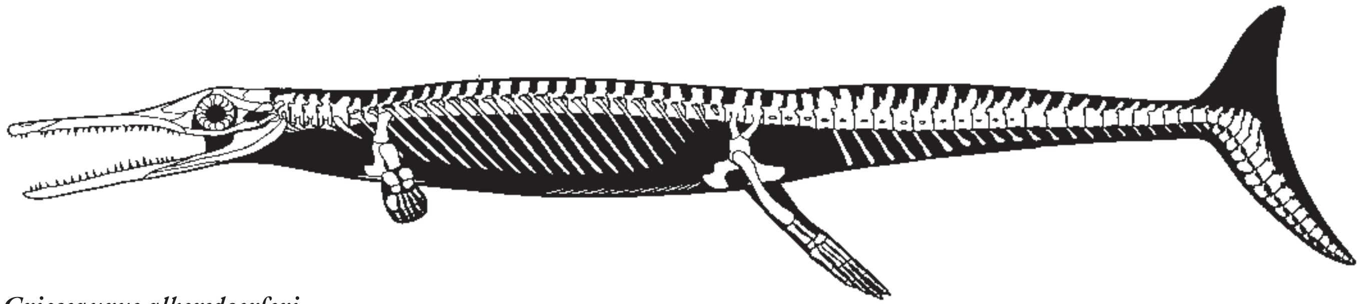
**2.1 m (7 ft) TL, 28 kg (60 lb)**

**FOSSIL REMAINS** Skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth moderate in size. Trunk not as slender. Tail and lower lobe not as long.
**AGE** Late Jurassic; late Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; upper Torleite.
**HABITAT** Island archipelago shallows.
**NOTES** Although this species and *C. suevicus* lived at same time and in same region, they have not been found together in same location.

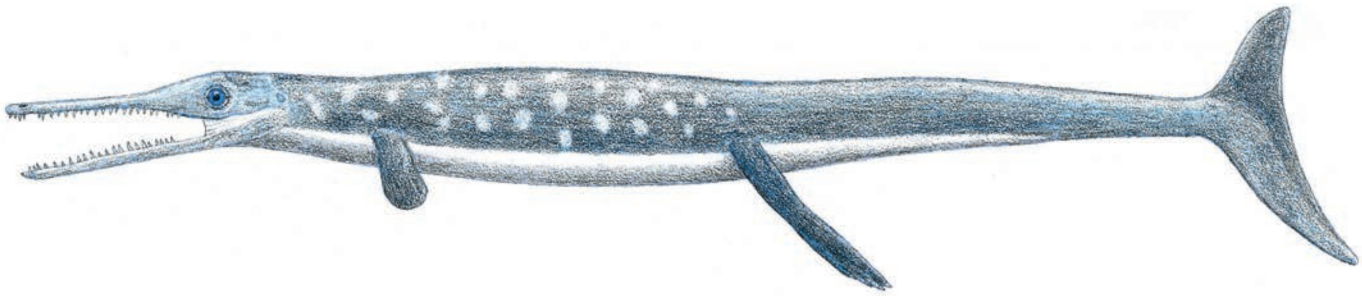
### *Cricosaurus suevicus*

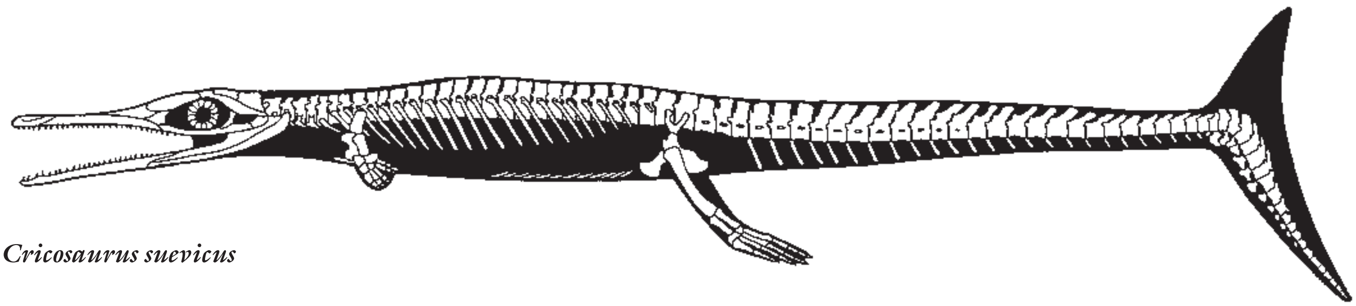
**2 m (6.5 ft) TL, 22 kg (50 lb)**

**FOSSIL REMAINS** Skull and skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth rather small. Trunk slender. Tail and lower tail lobe fairly long.
**AGE** Late Jurassic; late Kimmeridgian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Nusplingen.
**HABITAT** Island archipelago shallows.



*Cricosaurus albersdoerferi*



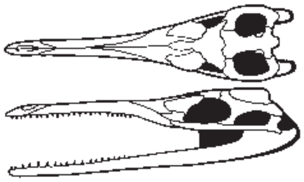


*Cricosaurus suevicus*

### *Cricosaurus elegans*

**3 m (10 ft) TL, 80 kg (180 lb)**

**FOSSIL REMAINS** Majority of skull, partial skull.
**ANATOMICAL CHARACTERISTICS** Teeth fairly large.
**AGE** Late Jurassic; late early Tithonian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Mörnsheim.
**HABITAT** Island archipelago shallows.
**NOTES** *C. rauhuti* may be adult of this species. Shared its habitat with *Aeolodon priscus*, *Geosaurus giganteus*, *Dakosaurus maximus*, *Rhacheosaurus*.



*Cricosaurus araucanensis*

### *Cricosaurus araucanensis*

**3 m (10 ft) TL, 80 kg (180 lb)**

**FOSSIL REMAINS** Skulls and partial skulls and skeleton.
**ANATOMICAL CHARACTERISTICS** Snout elongated, teeth fairly large.
**AGE** Late Jurassic; early Tithonian.
**DISTRIBUTION AND FORMATIONS** Western Argentina; lower Vaca Muerta.
**HABITAT** Continental shallows.
**NOTES** May include *C. lithographicus*. Shared its habitat with *Pliosaurus*? *patagonicus*, *Caypullisaurus*.

### *Cricosaurus vignaudi*

**3 m (10 ft) TL, 80 kg (180 lb)**

**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Insufficient information.
**AGE** Late Jurassic; middle Tithonian.
**DISTRIBUTION AND FORMATIONS** East-central Mexico; upper Pimienta.
**HABITAT** Continental shallows.

### *Cricosaurus? puelchorum*

**1.5 m (5 ft) TL, 10 kg (22 lb)**

**FOSSIL REMAINS** Partial skull.
**ANATOMICAL CHARACTERISTICS** Teeth fairly large.
**AGE** Early Cretaceous; lower Berriasian.
**DISTRIBUTION AND FORMATIONS** Western Argentina; upper Vaca Muerta.
**HABITAT** Continental shelf.
**NOTES** Placement of poorly preserved specimen in earlier *Cricosaurus* is not certain. Shared its habitat with *Purranisaurus potens*.

### *Enaliosuchus schroederi*

**1.5 m (5 ft) TL, 10 kg (22 lb)**

**FOSSIL REMAINS** Majority of skull and minority of skeleton.
**ANATOMICAL CHARACTERISTICS** Teeth fairly large.
**AGE** Early Cretaceous; early Valanginian.
**DISTRIBUTION AND FORMATIONS** Southern Germany; Stadthagen.
**HABITAT** Island archipelago shallows.
**NOTES** Shared its habitat with *Lagenanectes*, *Enaliosuchus*.

# INDEX

## Mesozoic Sea Reptiles Taxa

# FORMATIONS

When a formation is cited more than once on a page, the number of times is indicated in parentheses.