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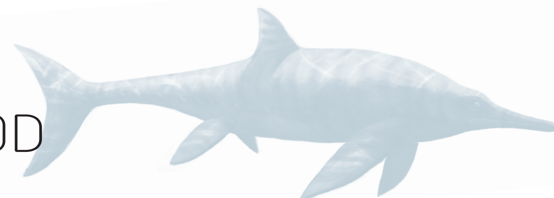
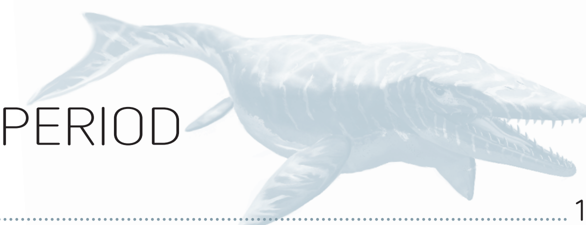


CHAPTER 6

THE CRETACEOUS PERIOD



CHAPTER 7

THE CENOZOIC ERA

Mary Anning, One of the First Palaeontologists

◄ Fig. 2.17. Mary Anning and her dog Tray, at some point prior to 1842, to the east of Lyme Regis.

From the end of the seventeenth century on, several fossilized vertebrae, which we now know belonged to ichthyosaurs and plesiosaurs, started attracting the attention of naturalists but were thought to belong to "fish," a term which then included a number of marine animals, including cetaceans. While for a long time naturalists, thinkers, and even artists (like Leonardo da Vinci) had been asking themselves about various such petrified objects (called "osteoliths"), which had been found since antiquity, no serious hypothesis had been formulated to explain their true nature, their often truly ancient age, and the reason for their presence in rocks. According to the religious precepts that were prevalent at the time, Earth was estimated to be on the order of six thousand years old, so fossils were most often interpreted as being the remains of animals that had drowned in the biblical Flood. However, in the first decades of the nineteenth century, there arose two new scientific disciplines: geology (thanks to the Scotsmen James Hutton and Charles Lyell) and paleontology (thanks to the Frenchmen Jean Baptiste de Lamarck and, above all, Georges Cuvier—see p. 95). Developments in these fields would lead to considerable advances in our knowledge and interpretation of fossils.

Like Maastricht in the Netherlands (see p. 95), Lyme Regis, a small seaside resort in Dorset, on the southern coast of England, is a major destination for paleontologists, especially those specializing in marine reptiles of the Mesozoic. This small town is also the location John Fowles chose for his novel about the love between Sarah Woodruff and paleontologist Charles Smithson in *The French Lieutenant's Woman*, made famous following its 1981 movie adaptation of the same title, directed by Karel Reisz. Lyme Regis is also the center of the action in Tracy Chevalier's novel *Remarkable Creatures* (2009), adapted for the screen by Francis Lee as *Ammonite* (2020). Why this location for these love stories? What is the common bond that ties them together? The answer is fossils—numerous, spectacular fossils, of historical interest.

Lyme Regis's fossils would not mean much if behind them there were not a woman, Mary Anning (1799–1847), who remained in the shadows for over a century and a half but has recently found her place in the limelight. She lived to be only forty-eight, in an England in which little consideration was given to women who were born poor. She nevertheless left an indelible mark on the development and the influence of paleontology, especially on the exciting history of the discovery of marine reptiles from the Mesozoic.

The history of this woman is a singular one, starting with a twist of fate when, at the age of 15 months, she was the only survivor in a group of people hit by lightning. Her father was a carpenter, and the family had difficulty making ends meet. To round out their income, he explored the imposing coastal cliffs of black marl that border Lyme Regis to the east and the west (fig. 2.18), looking for fossils. From a very early age, Mary and her brother Joseph would accompany their father, while their mother sold their findings to tourists. Fossils of invertebrates are abundant in the thick marly series of the local Blue Lias formation, deposited in the early Early Jurassic (roughly 200–190 Ma), but the remains of vertebrates (such as vertebrae and teeth) are found here as well.

Around 1810 Joseph found a complete skull, 1.2 meters long, of an animal that was unknown at the time. Several months later, thanks to a landslide at the same location, Mary (who was 12 years old) and her brother found the torso corresponding to the skull. The animal must have been almost 5 meters long. It was the first mostly complete skeleton of an ichthyosaur ever found. But for the time being, no one was aware of it, and for a good reason: this emblematic group of marine reptiles from the Mesozoic would not be identified as such until several years later. For the moment, scientists attributed the skeleton to an unknown "fish."

This discovery was the beginning of a long career for Mary, who would establish her reputation as a "fossil searcher" throughout Europe. The many skeletons she uncovered allowed for the description of the first ichthyosaurs and plesiosaurs, by English geologists William Conybeare and Henry de la Beche, between 1821 and 1824. These authors described at least three species of ichthyosaurs from Lyme Regis: *Ichthyosaurus communis* (3 meters), *I. tenuirostris* (today *Leptonectes*, 4 meters) and *I. platydon* (today *Temnodontosaurus*, 9 meters), a mega-predator from the Lower Jurassic (see chapter 5, pp. 146–47). The first specimen Mary and her brother had found was an *I. platydon*.

When in 1823 Mary was the first to discover a plesiosaur, *Plesiosaurus dolichodeirus* (see "*Plesiosaurus*," p. 55), the creature's form seemed so improbable that even important scientists such as Cuvier surmised the specimen was a fake, assembled by Mary from fossils of different origins. But after other skeletons exhibiting the same characteristics were found, Cuvier had to surrender to the evidence and admit his mistake. Mary also discovered several thalattosuchian crocodiles; was the first to find a pterosaur outside Germany; discovered several remarkable actinopterygians; found fossils of several previously unknown cephalopods, some with their ink sac preserved; and was the first to find fossilized excrements, called coprolites.

But Mary Anning was not only a fossil "hunter." Although she had received only a minimal education, she nonetheless acquired, thanks to an insatiable curiosity and by consulting the works available at the time, a deep knowledge of the fossils she unearthed and the terrain she found them in. She also knew how to draw and interpret them. The extent of her knowledge

▼ Fig. 2.18. The Blue Lias cliffs, east of Lyme Regis, county Dorset (England), where Mary Anning found her Lower Jurassic fossils. These cliffs are part of the Jurassic Coast, Britain's only World Heritage Site.

◄ Fig. 2.19. Henry de la Beche, *Duria Antiquior*, 1830. National Museum Cardiff.
This is the first reconstruction of a complete paleoecosystem, based on the discoveries made by Mary Anning in the Lias of Lyme Regis.

rivaled that of established researchers, and her understanding of the terrain had few equals: many learned men came to consult her and to look for fossils with her. Swiss American paleontologist Louis Agassiz, impressed by his meeting with Mary, would name two species of fossil fish in her honor (*Acrodus anningiae* and *Belenostomus anningiae*).

Although her exceptional discoveries were the basis for the careers of many scientists of the period, she was never quoted in their articles, and almost no one, with the exception of Louis Agassiz, made reference to her discoveries. She never published an article under her name alone, except for a letter she sent to the *Magazine of Natural History* in 1839 to point out that she had discovered the newly named fossil shark *Hybodus* long before its naming, by Louis Agassiz, in 1837. For her, *Hybodus* was therefore not “new,” as the magazine described it. The letter did perhaps betray some naivete on her part, in that in paleontology (and biology) a species does not officially exist until after it has been named and described.

As a woman born into the working class, Mary had only very restricted educational opportunities, and access to the scientific circles of the period, such as the Geological Society of London, was forbidden to her. Nevertheless, the academic world showed its gratitude because, thanks to the kindness of her friend, paleontologist William Buckland, in 1820 the British Society for the Advancement of Science granted her an annual pension. Likewise, when in 1847 she fell gravely ill, the Geological Society of London organized a subscription to help pay her expenses. She remained poor nonetheless, even after the sales she made of her many finds. The time when important fossils would sell for millions of dollars at auction houses had, unfortunately for her, not yet arrived. Many of her longtime friends came to her financial aid several times during her life. In 1820, Colonel Thomas Birch sold fossils that he had bought previously from her at an auction organized in London and donated the proceeds to her; Georges Cuvier was present at this sale and acquired several specimens of ichthyosaurs and plesiosaurs for the museum in Paris. In 1830 Henry De la Beche completed the first reconstruction of the history of an ecosystem (named *Duria Antiquior* [fig. 2.19], which means “A More Ancient Dorset”), based on the fossils found by Mary Anning; the profit from the sales of the copies he had made of it were intended to help her. After her death, the members of the Geological Society paid tribute to her and had some stained glass created in her memory placed in the church of Saint Michael in Lyme Regis, where it can be seen today. Nevertheless, as time went by her name was slowly forgotten, but in the last several decades she has been remembered and rightly given consideration as an important figure in paleontology. In 2010 members of the Royal Society named her among the ten women in British history who have had the greatest influence on science.

Mary Anning’s exceptional discoveries had a major impact on the development of paleontology as a science and stimulated the learned men of the time in all respects. The often complete and well-preserved skeletons she found allowed researchers, from the 1820s on, to form a precise idea of what ichthyosaurs and plesiosaurs must have looked like, to understand their reptilian nature, and to realize they had no equivalent in the nature of the period. Thanks to these new fossils, Cuvier’s theory—according to which, worlds inhabited by creatures very different from today’s must have existed and then disappeared—became increasingly convincing.

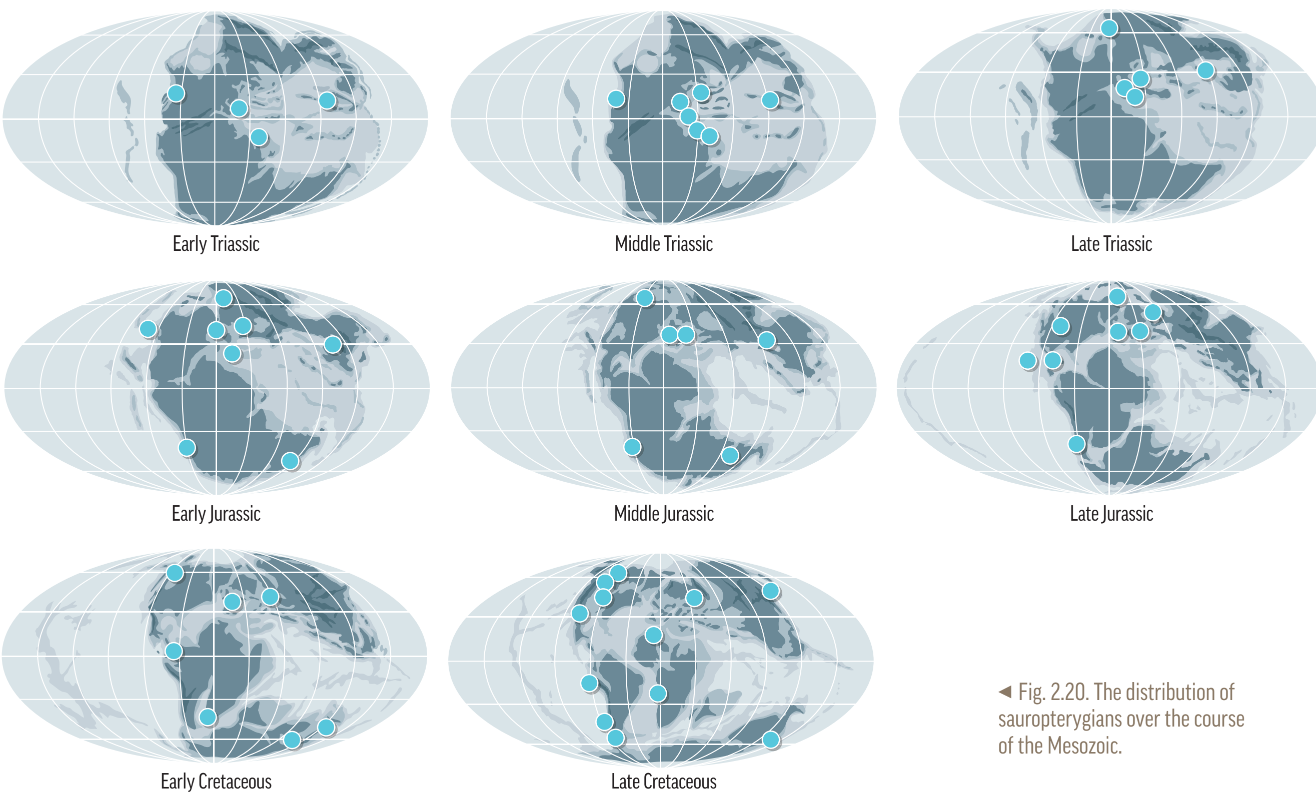
VI

The Sauropterygians: Loch Ness Monster & Co.

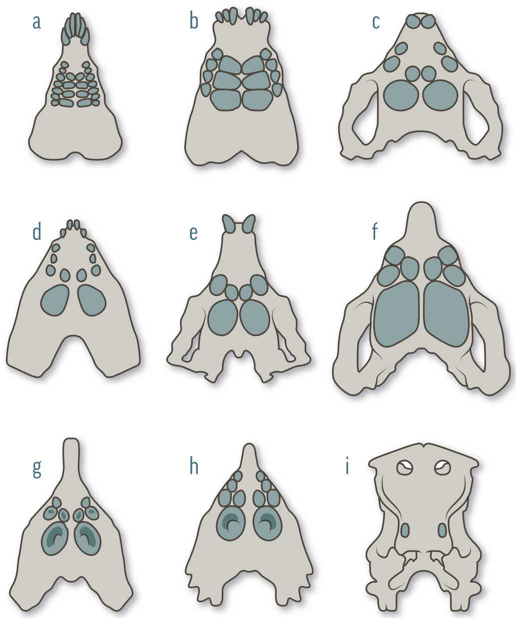
The name "sauropterygian" (from the Greek *sauros*, "lizard," and *pterux*, "wing," a reference to the anatomy of their swimming paddles) is hardly known to the public, and yet the order Sauropterygia includes one of the Mesozoic's most recognizable groups of marine reptiles: the plesiosaurs. These animals with a long neck and a barrel-shaped body, which some optimists imagine they have glimpsed in the troubled waters of Loch Ness, fascinate people, because their bizarre construction has no modern or past equivalent. Long before the plesiosaurs, however, other sauropterygians swarmed in the seas and oceans of the Triassic, not suspecting that they would someday lose their place to these monstrous-looking relatives.

It was British paleontologist Sir Richard Owen who, in 1860, proposed the name Sauropterygia to describe a group of animals that included, in addition to the plesiosaurs, the nothosaurs and the placodonts. Although our knowledge has grown considerably since then, the label "sauropterygian," after having fallen out of use for a very long time, started to regain favor at the end of the 1990s and is today used by everybody in the field, which proves that Owen's observations were sufficiently accurate for his definition of the group to remain valid.

And yet the kinship relations between Sauropterygia and other groups of reptiles are not yet clearly established. Sauropterygians are most often considered diapsids that lost



◄ Fig. 2.20. The distribution of sauropterygians over the course of the Mesozoic.



► Fig. 2.21. A palatal view of the skulls of various placodonts, showing the large, short, bulbous teeth that are typical of the group as well as their differences in form and arrangement. *Paraplacodus* (a), *Placodus* (b), *Cyamodus* (c), *Sinocyamodus* (d), *Protenodontosaurus* (e), *Macroplacus* (f), *Psephoderma* (g), *Placochelys* (h), *Henodus* (i).

their lower temporal fossae. After appearing at the beginning of the Triassic, they divided into two major lineages: the eosauropterygians, which include the famous plesiosaurs and pliosaurs, and the placodonts, which had very atypical characteristics. The most diverse of all marine reptiles, sauropterygians had spread throughout the world by 180 million years ago (fig. 2.20).

The Placodonts: Have the Armor-Clad Step Forward!

During the Triassic, over the course of about 50 million years (252–201 Ma), the placodonts lived in the epicontinental seas at the edges of the Tethys (see chapter 1, p. 10). Their fossilized remains have been found

Henodus

Henodus, a placodont, comes from the Lower Carnian stage in Germany. Roughly 1 meter long, it was almost equally wide. Its back and its underside were armored by bony plates of various sizes—called osteoderms—and covered with horny scales. Its rectangular, flattened head was significantly different from that of most placodonts. The sharp borders of its snout were lined with tiny denticles. In its actual jaws were only four small teeth, two on the top and two on the bottom (fig. 2.21i). The shape of its jaws, and its notable lack of teeth, suggest that the power of its bite and its crushing capability were considerably less than those of other placodonts. *Henodus* may in fact have been a suspensivore (filter feeder).

► Fig. 2.22. *Henodus*, a placodont from the Upper Triassic in Germany.

mainly in Europe and China. The name "placodont," which means "flat tooth," derives from the fact that most of these animals were equipped with large teeth arranged like cobblestones on the palate and the lower jaw, which suggest durophage eating habits (fig. 2.21).

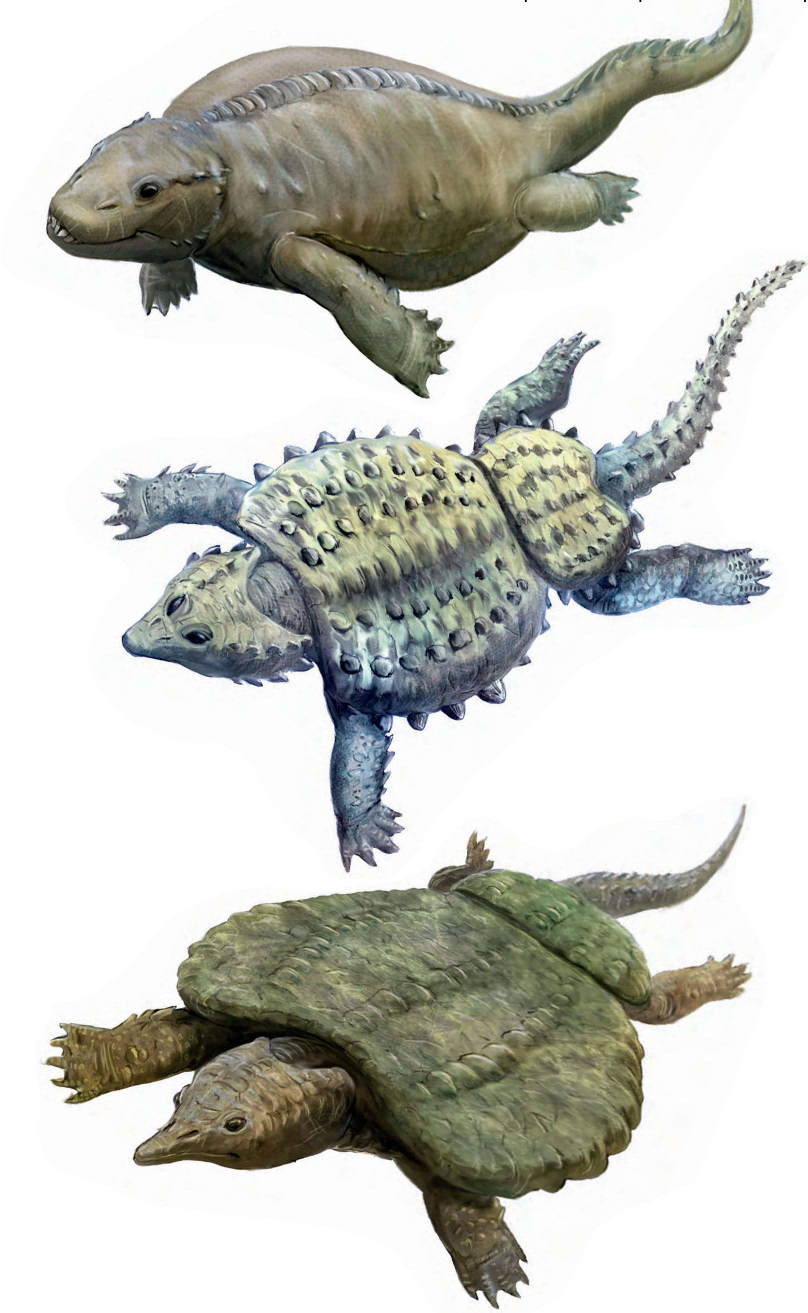
To supplement this cobblestone dentition, some placodonts, such as *Placodus* and *Palatodonta* (from the Netherlands), were endowed with front teeth that were cone-shaped or with incisors, which they probably used to grab their food. Traditionally it is thought that placodonts fed on hard-shelled mollusks and crustaceans. So *Placodus*'s massive skull (fig. 2.23), which in certain places exhibits signs of pachyostosis (see "The Secrets of Bone," p. 129), and its robust mandible must have been meant to efficiently resist the strong pressures experienced while crushing tough prey. Certain placodonts, however, such as *Henodus* (fig. 2.22), had very few teeth, which leads paleontologists to suppose they sucked up their prey instead of catching it in their teeth.

Placodonts are divided into two groups, according to whether they exhibit body armor or not. The cyamodontoids do. The placodontoids don't or were endowed only with minimally developed bony structures in a line along the spine (fig. 2.24, top). *Placodus*, for example, displays a unique row of bony plates and belongs to the second group. The bony plates of the cyamodontoids were sometimes so developed and contiguous that they covered the entirety of their body and made them resemble turtles, as is the case with *Henodus* and *Plachochelys* (*chelys*

Placodus

Placodus is one of the two genera of the placodontoids. On the upper jaw of its massive skull, it had six front teeth shaped like incisors; it had eight bulbous teeth on the sides; and it had six large and flattened teeth, like cobblestones, on the roof of its mouth (fig. 2.21b). It would dig up the seabed looking for invertebrates, which it grabbed with its front teeth before crushing them with its rear ones. Almost 2 meters long, *Placodus*'s body was not covered by a shell; it was outfitted only with a median range of bony plates that overhung the spine (fig. 2.24).

► Fig. 2.23. *Placodus*, a placodont from the Middle Triassic in Europe and China.



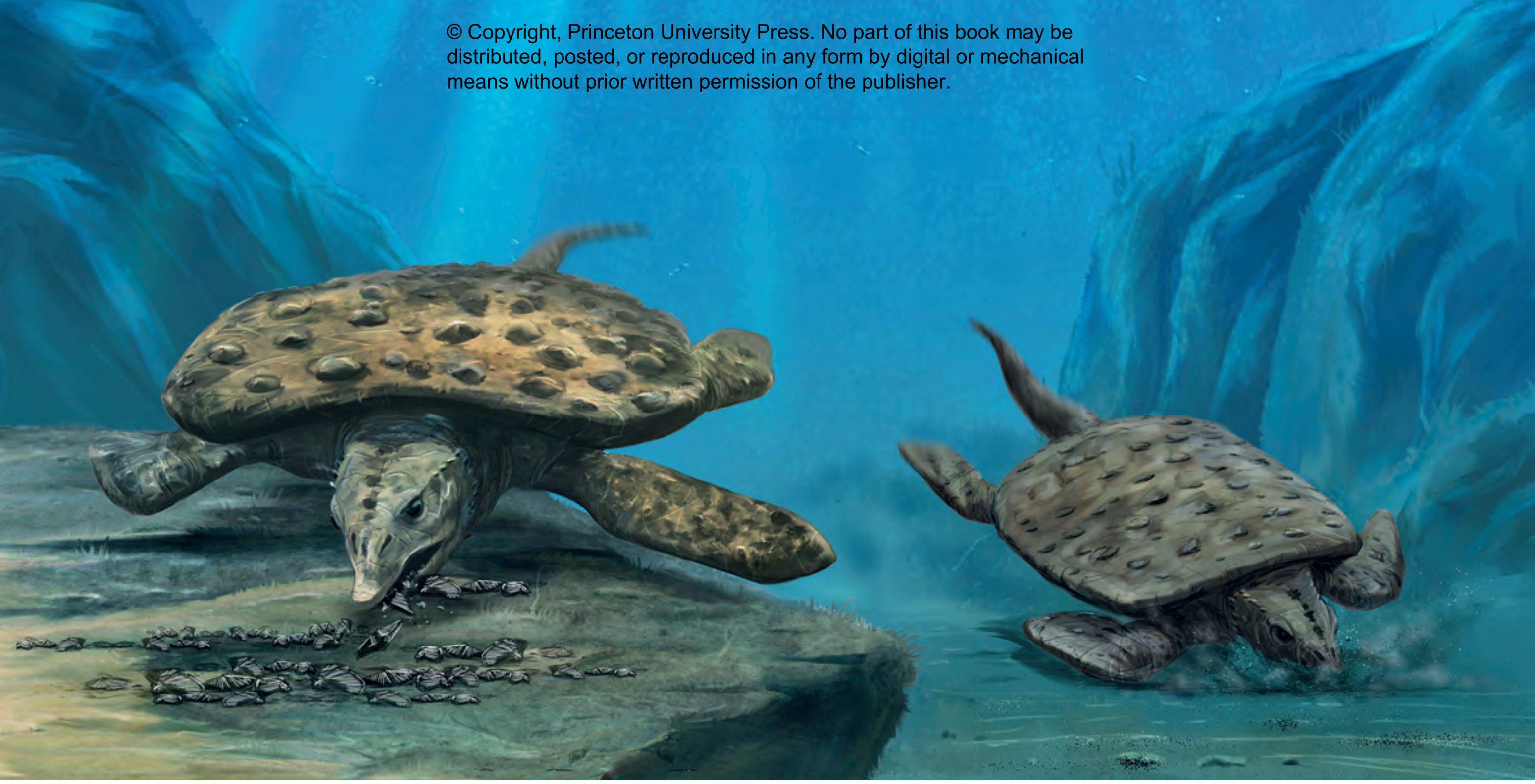
▲ Fig. 2.24. Different types of body armor exhibited by placodonts (*Placodus*, *Cyamodus*, *Psephoderma*), from a simple dorsal row of osteoderms among placodontoids to a strong body armor with diverse and varied ornamentations among the cyamodontoids.

means "turtle" in Greek). In fact, cyamodontoids were once thought to be close relatives of turtles before being considered more properly as sauropterygians.

Cyamodontoids and turtles are the only amniotes ever to have developed armor covering the back, the belly, and the sides. Nevertheless, while all cyamodontoids had a dorsal shield (on the back), the ventral one (on the belly) could be underdeveloped or even absent. The dorsal shield could consist of a single support, as in *Henodus* and *Placochelys*, or be made up of two parts, the larger one situated frontally while the smaller one covered the pelvic area, as in *Cyamodus* (fig. 4.4, pp. 116–17) and *Psephoderma* (fig. 2.24). In addition, while both cyamodontoids and turtles were or are armored, their armatures do not have the same origin at all.

Turtles' shell, made up of a dorsal section called a carapace and a ventral section called a plastron, develops mostly starting from the bony elements of the skeleton: neural spines (bony dorsal projections of the vertebrae) and ribs that are more or less welded together for the carapace; clavicle and ventral ribs for the plastron (see fig. 2.56). Cyamodontoids' armature, by comparison, was generally an assemblage of extra bones that developed in the skin (osteoderms) and formed numerous small plates, either flat or pointed in shape, with a round, polygonal, or hexagonal base. Their armature therefore did not contain any skeletal elements. Because of their dermal origin, these plates were more closely related to those of certain archosaurs, such as the crocodylomorphs (see p. 66) and some dinosaurs (e.g., ankylosaurs and titanosaurs). When cyamodontoids were alive, they must have been covered in keratin. This is the only point they share with turtles, since the plates of turtles' shells are also covered in horny, keratinized scales.

Placodonts' unique set of features has led to many questions regarding their ecology. The placodonts are considered the "sea cows" of the Triassic, or as having engaged in behaviors resembling those of the sirenians (today's dugongs and manatees; see chapter 7, p. 196). And the skeletons of sirenians and those of numerous placodonts do show anatomical and functional **convergences**: they exhibit a marked bone density, called **pachyosteosclerosis** (see "The Secrets of Bone," p. 129), one consequence of which is to make the animals heavier, thus allowing



▲ Fig. 2.25. Placodonts supposedly led a life of digging for food on the seabed.

them to remain submerged near shallow seabeds with minimal muscular exertion and thus minimal use of energy. Among sirenians, this increase in bone mass can be seen especially in the rib area.

In the case of numerous placodonts, the shell or the gastralia are what mostly weighed them down, but this increase in the mass of certain bones did sometimes increase the ballasting effect. Placodonts were therefore probably able to station themselves on the seafloor while searching for food, thanks to their ballasted skeleton (fig. 2.25). Being encumbered with such massive and heavy bodies, they very likely were not fast swimmers.

The Eosauropterygians: Great Travelers

The group Eosauropterygia comprises all sauropterygians other than the placodonts. Eosauropterygians first appeared during the Early Triassic and did not go extinct until the Cretaceous/Paleogene crisis, thus demonstrating an unparalleled longevity among marine reptiles. They occupied all the world's seas and oceans.

Eosauropterygians comprised several lineages: the pachypleurosaurs, the nothosaurs, and the pistosaurs (among which we find the famous plesiosaurs and pliosaurs). Paleontologists often speak of "Triassic sauropterygians" to refer to the sauropterygians other than plesiosaurs and pliosaurs—in other words, those groups that did not continue into the Jurassic. The evolutionary history of Triassic sauropterygians seems tied to fluctuations in sea level: the rise in sea level during the Triassic allowed for the establishment of shallow epicontinental seas, in which these reptiles multiplied and diversified.

The Pachypleurosaurs

The pachypleurosaurs (from the Greek *pachy*, "thick"; *pleuro*, "rib"; and *sauro*, "lizard") are known only from the Middle Triassic and the beginning of the Upper Triassic. Their fossilized remains have been found in western Tethysian provinces (Europe) and eastern ones (China). They were generally small, with the largest of their dozen species barely exceeding a meter in length, although

▲ Fig. 2.26. A cast of *Keichousaurus*, a pachypleurosaur from the Triassic in China. The largest specimens are only 30 centimeters long and must have measured about 5 centimeters at birth.

some, such as *Wumengosaurus*, reached nearly 1.5 meters.

Pachypleurosaurs all exhibit very similar characteristics: a long body, neck, and tail, with a small skull and a short snout. They had large eye sockets and relatively small temporal fossae, the opposite of nothosaurs. Their limbs still resembled those of the terrestrial animals they evolved from, with long zeugopods and five fingers that exhibit no hyperphalangy (compare "From Legs to Swimming Paddles," p. 39).

Most pachypleurosaurs—for instance, *Keichousaurus*—exhibit pachyosteosclerotic ribs (see "The Secrets of Bone," p. 129). We imagine that their ballasted skeleton allowed them, like the placodonts, to linger near the seabed for relatively long stretches without needing to spend much energy. Pachypleurosaurs were therefore small reptiles that lived in shallow waters and that probably moved fairly slowly.

Keichousaurus (fig. 2.26) is probably the most famous pachypleurosaur. Numerous adults and juveniles of this species, 5–25 centimeters long, were discovered in China starting in the 1950s. The specimens are generally complete and allow for detailed studies of anatomy, most notably variations within a single species. This is how paleontologists were able to observe that in some specimens, the humerus (upper front limb bone) and femur (upper hind limb bone) were the same size, while in others the humerus was both more massive and longer than the femur. It was hypothesized that this was a case of sexual dimorphism … but which specimens were the males and which were the females? The answer came in 2004, when a Chinese team published an essay accompanied by photographs of fossils of adult *Keichousaurus* containing embryos. And these pregnant *Keichousaurus* had a humerus and a femur that were the same size. For a long time, it had been supposed that sauropterygians, which were probably completely independent of the terrestrial environment, gave birth to live young, but never had a pregnant sauropterygian been found, so proof of viviparity had been lacking. Importantly, each gravid female discovered by the Chinese team contained between four and six embryos at

Simosaurus

Simosaurus ("lizard with a blunt snout") was a Middle Triassic nothosaur 3 to 4 meters long, found mostly in Europe. Its large and relatively flat skull lacked the long muzzle of *Nothosaurus*, and its blunt teeth support the notion that it subsisted on a diet of tough foods. The genus *Simosaurus* comprises a single species, *S. gaillardoti*, first described by German paleontologist Herbert von Meyer in 1842.

► Fig. 2.27. *Simosaurus*, a nothosaur from the Middle Triassic in Europe.

the level of the rib cage, just ahead of the pelvic girdle. *Keichousaurus* must have therefore given birth, in the water, to young that were already formed and capable of swimming. This adaptation shows that sauropterygians became independent of a terrestrial environment very early in their evolutionary history.

Coastal Fishers: The Nothosaurs

The nothosaurs inhabited the Tethysian and Pacific seas of the Triassic. They weren't very diverse and are represented by only four genera. Their skull was longer and slenderer than pachypleurosaurs', and their temporal fossae (see p. 25) were larger than their eye sockets. Overall, nothosaurs were larger than pachypleurosaurs as well, even though one species (*Nothosaurus winkelhorsti*) had a skull only 5 centimeters long.

Nothosaurs were probably piscivorous but could also feed on soft-shelled invertebrates. Their slender jaws, with thin, pointed teeth, like those of *Lariosaurus* (fig. 2.28), probably did not allow them to latch on to tougher prey. There are nevertheless always exceptions: *Simosaurus* (fig. 2.27), with its shorter rostrum (another word for snout or muzzle) and more robust teeth, could certainly feed on invertebrates with harder shells.

▲ Fig. 2.28. *Lariosaurus*, a nothosaur from the Middle Triassic in the eastern Pyrenees (France), paleontology collections of the Sorbonne University (Paris, France). This skull, as fine as lace, is only 6 centimeters long.

Because, like pachypleurosaurs, nothosaurs had long bodies and limbs resembling those of terrestrial animals, they seem unlikely to have lived in the open ocean. In addition, in an open environment, where food resources might be spread out across long distances, good acceleration and maneuverability are indispensable. The high bone mass that is characteristic of some nothosaurs would have hampered them in these regards. It is therefore probable that most of these species were not very active swimmers and lived near the coast in shallow marine environments.

A Collection of Stars: The Pistosaurs

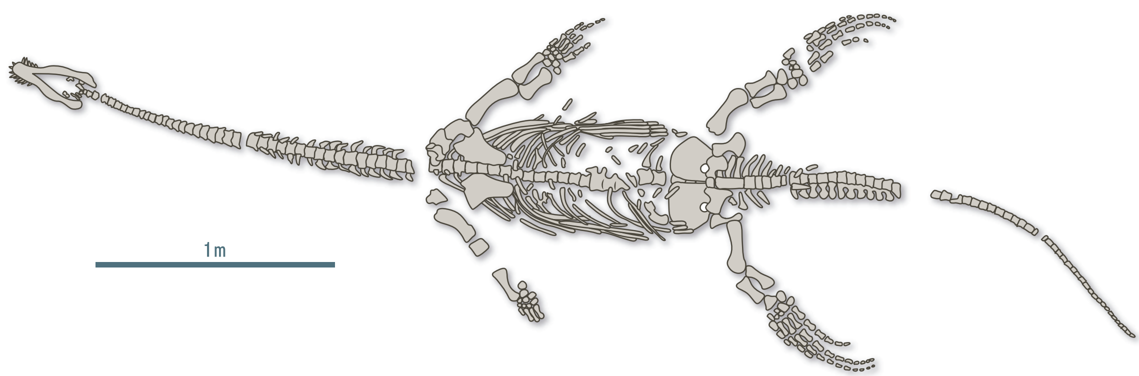
The pistosaurs, just like the nothosaurs, lived in the Tethysian and Pacific seas of the Triassic. Considered the closest relatives of the plesiosaurs and pliosaurs, they are known for six genera, among them *Yunguisaurus* (fig. 2.29) and *Bobosaurus*. The latter has, however, been recently placed among the plesiosaurs; its kinship relations are still debated.

The first pistosaurs do not seem to have varied much, in comparison with the plesiosaurs. They have, however, been found widely—principally in Europe, but also in China and the United States. They are known from the Lower Triassic to the Upper Triassic and were of respectable proportions, with *Bobosaurus* reaching about 3 meters in length.

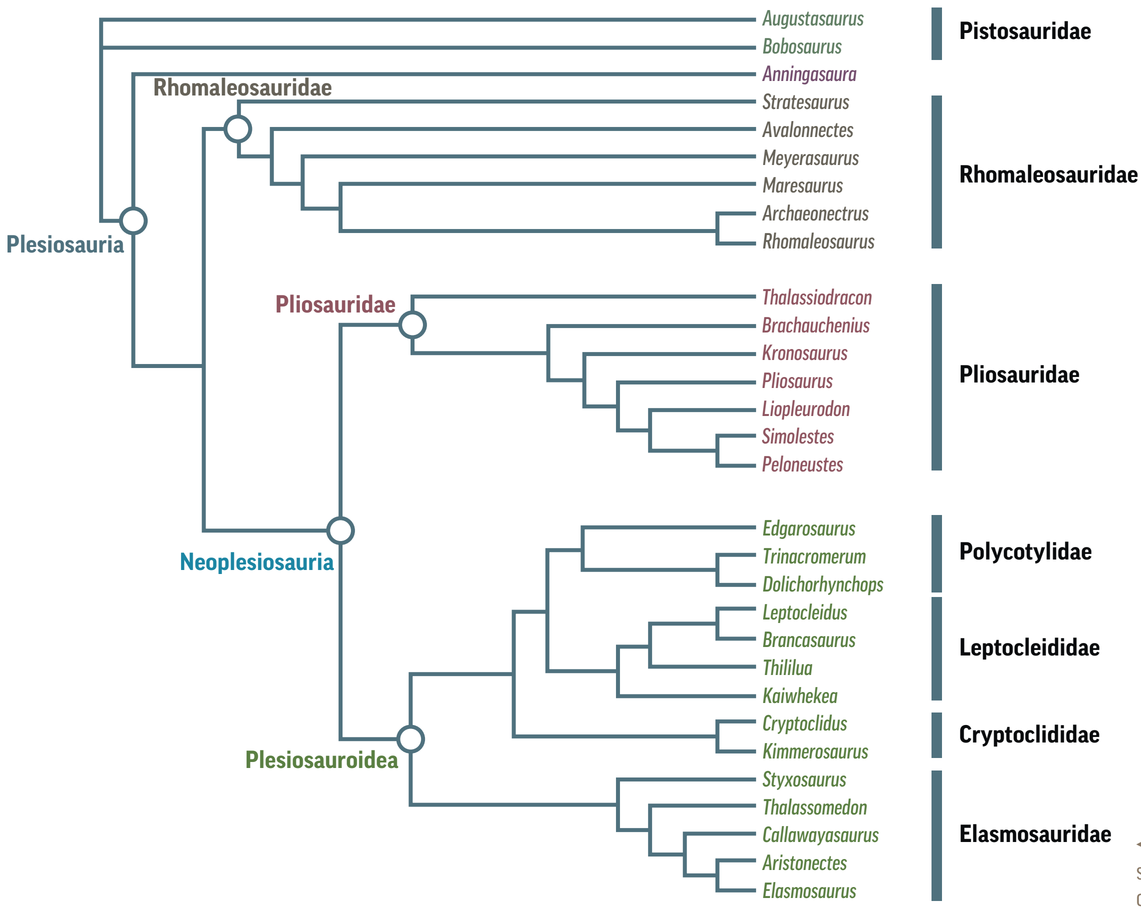
From "Sea Giraffes," the Plesiosaurs, to the "Teeth of the Sea," the Pliosaurs

Phylogenetically, the plesiosaurs are part of the large clade of the pistosaurs (fig. 2.30). But unlike the Triassic pistosaurs, the plesiosaurs (from the Greek *plesios*, "close to," and *sauros*, "lizard") thrived for most of the Mesozoic. They are distinguishable from Triassic pistosaurs by several characteristics of their skeletons—for example, hyperphalangy and the shape of the radius and the ulna (the two bones in the lower part of each forelimb).

The earliest plesiosaur fossils date from the Upper Triassic. They were found in the United Kingdom and in Russia, in sediments roughly 225 to 215 million years old. However, it is believed these creatures differentiated themselves about 10 to 20 million years earlier, in the geologic age known as the Carnian, around 235 million years ago. After enduring for more than 150 million years, the plesiosaurs disappeared (as did the non-avian dinosaurs) during the famous Cretaceous/Paleogene crisis.



► Fig. 2.29. *Yunguisaurus*, a pistosaur from the Middle Triassic in China. Its anatomy indicates that it had evolved past needing to undulate its body in order to swim; it did, however, still have a long tail, like anguilliform swimmers.



◄ Fig. 2.30. A simplified phylogeny of Plesiosauria.

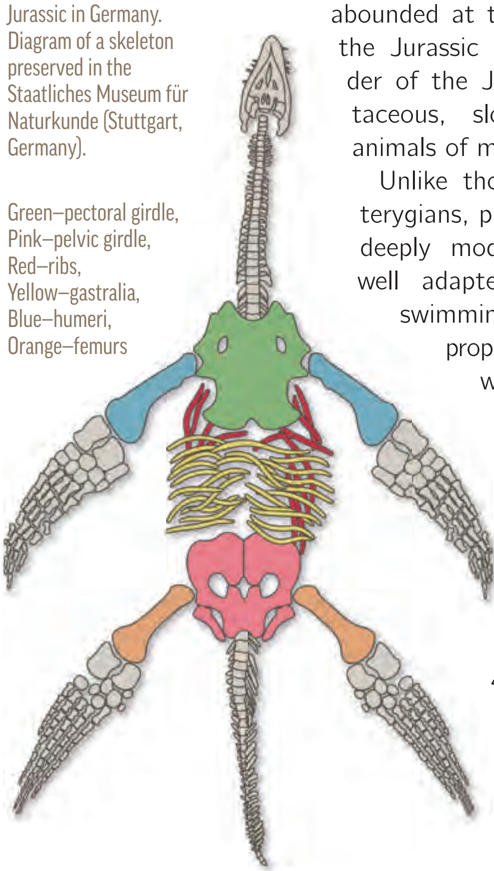
The plesiosaurs (suborder Plesiosauria) (fig. 2.30) are traditionally, according to their physical features, divided into two groups: plesiosaurs and pliosaurs. Plesiosaurs thus in the narrowest sense of the term correspond to forms with a small head and a long neck; pliosaurs are those with a massive skull and a short neck. (But we shall see that looks can be deceiving.)

Plesiosauria was one of the most diverse groups of aquatic vertebrates. About one hundred species are known. Having spread worldwide starting in the Early Jurassic, members of Plesiosauria have been found fossilized on all continents and at all latitudes, from the Antarctic to the Artic. This suggests that they were active swimmers, capable of migrating over long distances. Their fossilized remains are abundant in marine deposits; in addition, fossils in England, Canada, and even Australia have been found in sediments of continental origin. These deposits correspond to ancient lagoons, rivers, or deltas; because the remains are mostly those of juveniles, some researchers have ventured that these shallow environments functioned as plesiosaur nurseries.

These highly successful marine reptiles were characterized by a massive body, four swimming paddles, and a long neck, although neck length was somewhat variable. In terms of overall length, they ranged from less than 2 meters for *Thalassiodracon* to 10 meters or more for the largest pliosaurs, such as *Kronosaurus* and *Liopleurodon* (roughly 10 meters), *Thalassomedon* (12 meters), and *Pliosaurus* (15 meters!). The smallest among them, such as *Thalassiodracon* and *Avalonnectes*,

▲▼ Fig. 2.31. **Above**, *Rhomaleosaurus*, from the Lower Jurassic in England. This gigantic rhomaleosaurid was more than 7 meters long. **Below**, *Meyerosaurus*, a rhomaleosaurid from the Lower Jurassic in Germany. Diagram of a skeleton preserved in the Staatliches Museum für Naturkunde (Stuttgart, Germany).

Green–pectoral girdle,
Pink–pelvic girdle,
Red–ribs,
Yellow–gastralia,
Blue–humeri,
Orange–femurs



abounded at the very beginning of the Jurassic but, for the remainder of the Jurassic and the Cretaceous, slowly gave way to animals of much larger size.

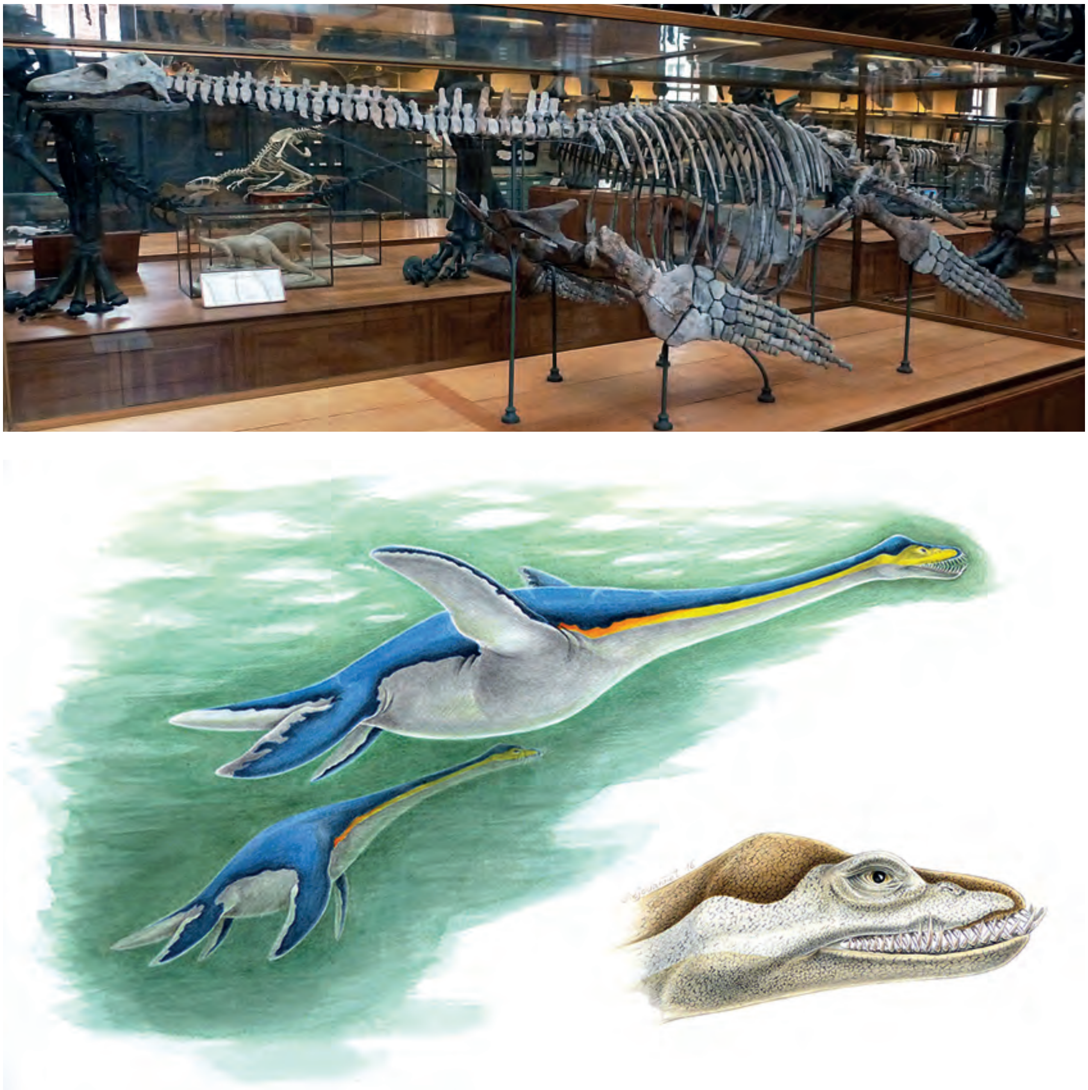
Unlike those of other sauropterygians, plesiosaurs' limbs were deeply modified and extremely well adapted to the work of swimming. These creatures propelled themselves not with spine or tail movements but by using their swimming paddles in underwater flight (see "Locomotion in Ichthyosaurs and Sauropterygians," pp. 148–49). The front and rear swimming paddles were fairly similar, although plesiosaurs in the narrow sense of the term generally had longer front swimming paddles, whereas pliosaurs generally had longer rear ones, which is a good way to distinguish between them. The upper bones of the limbs (the humerus and femur, respectively) were the longest bones, while zeugopod (radius and ulna; tibia and fibula) length was reduced; these disc-shaped elements were not elongated as in the Triassic sauropterygians. There were five fingers to a swimming paddle, and different species had different degrees of hyperphalangy. Unlike in ichthyosaurs, among plesiosaurs there was no hyperdactyly (see "From Legs to Swimming Paddles," p. 39). The surface area of the swimming paddles, which were not very flexible, increased considerably thanks to the increase in the number of phalanges, and the paddles' efficacy for locomotion was assured by strong muscles connecting the front paddles to the large pectoral girdle and connecting the rear ones to the pelvic girdle (fig. 2.31, bottom). As in ichthyosaurs, the

underside of the rib cage was reinforced by gastralia. Last, their tails were shorter in comparison with Triassic sauropterygians.

Some species possessed a long and slender snout, while others had a short rostrum and still others a large and robust skull. Most had long, conical and pointed teeth, with fine grooves running from the base of the crown all the way to the point. These teeth could be small and delicate (as generally in "true" plesiosaurs) or large and robust (as in pliosaurs), according to whether they ate mollusks, fish, or other marine vertebrates. Although it is likely most species were active predators, some may have been scavengers. Dentition might seem to have been fairly uniform among this group, but there are nevertheless exceptions, because some forms (e.g., *Kaiwhekea*) had very small teeth crowded closely together and others (e.g., *Pliosaurus*) had large teeth that were triangular in cross section.

Animals resembling the pliosaurs—for example, rhomaleosaurids such as *Rhomaleosaurus* (7 meters)—are known beginning from the Lower Jurassic (fig. 2.31, top). The pliosaurids (plesiosaurs of the group Pliosauroidea) swam the seas mostly from the Middle Jurassic to the Late Cretaceous. The pliosaurids of the Early Jurassic were usually of modest dimensions, but starting in the Middle Jurassic they grew tremendously, giving us some of the most terrifying mega-predators: *Liopleurodon* (fig. 5.20, pp. 158–59),

▲ Fig. 2.32. *Occitanosaurus*, an elasmosaurid plesiosaur from the Lower Jurassic in the Aveyron (France).



► Fig. 2.33. *Cryptoclidus*, a cryptoclidid plesiosaur from the Middle Jurassic in Europe, and its skeleton preserved at the Muséum national d'Histoire naturelle (Paris, France).

Pliosaurus, and *Kronosaurus* (fig. 6.3, pp. 165–66). The largest specimen of *Liopleurodon*, from the Middle Jurassic in Great Britain, exhibits a skull 1.5 meters long. The pliosaurids of the Late Jurassic and the Cretaceous grew even larger, and some, such as *Kronosaurus* and *Pliosaurus*, had a skull more than 2 meters long. A pliosaurid mandible found in England actually reached the 3-meter mark! These leviathans all had a powerful, long triangular muzzle, equipped with conical, sharp, and slightly curved teeth. They must have fed on fish of all sizes, as well as on other marine reptiles. In their short neck they had at most about twenty vertebrae; *Kronosaurus*, for instance, only had twelve.

The plesiosaurs proper (or "true" plesiosaurs) belong to Plesiosauroidea, which divides into lineages with very different characteristics: the plesiosaurids, the cryptoclidids, and the elasmosaurids (fig. 2.30). The plesiosaurids were creatures of relatively modest dimensions, known mostly from the Lower Jurassic in Europe. Their neck was long in proportion to their body and contained more than thirty vertebrae. It is within this group that we find *Plesiosaurus*, the very first genus of Plesiosauria to have been discovered and described (see

Plesiosaurus

Plesiosaurus was the first plesiosaur to be discovered, and by no less than noted paleontologist Mary Anning (see pp. 40–41). It was also the very first plesiosaur to be scientifically studied, described, and named. *Plesiosaurus* was an animal of modest size (3 to 4 meters in length) that lived around 190 million years ago, during the Early Jurassic.

Several relatively complete specimens found on the southern coast of England, at Lyme Regis, in Dorset (fig. 2.18), helped paleontologists gain more knowledge about *Plesiosaurus*'s anatomy. Its long neck contained about forty cervical vertebrae. Its tail was short, and its swimming paddles well developed, which indicates that it moved not by undulating its body but by use of its paddles. Its small skull, as well as the fifty delicate, sharp conical teeth that lined its jaws, probably did not allow it to hunt large prey. It must have subsisted on fish and invertebrates.

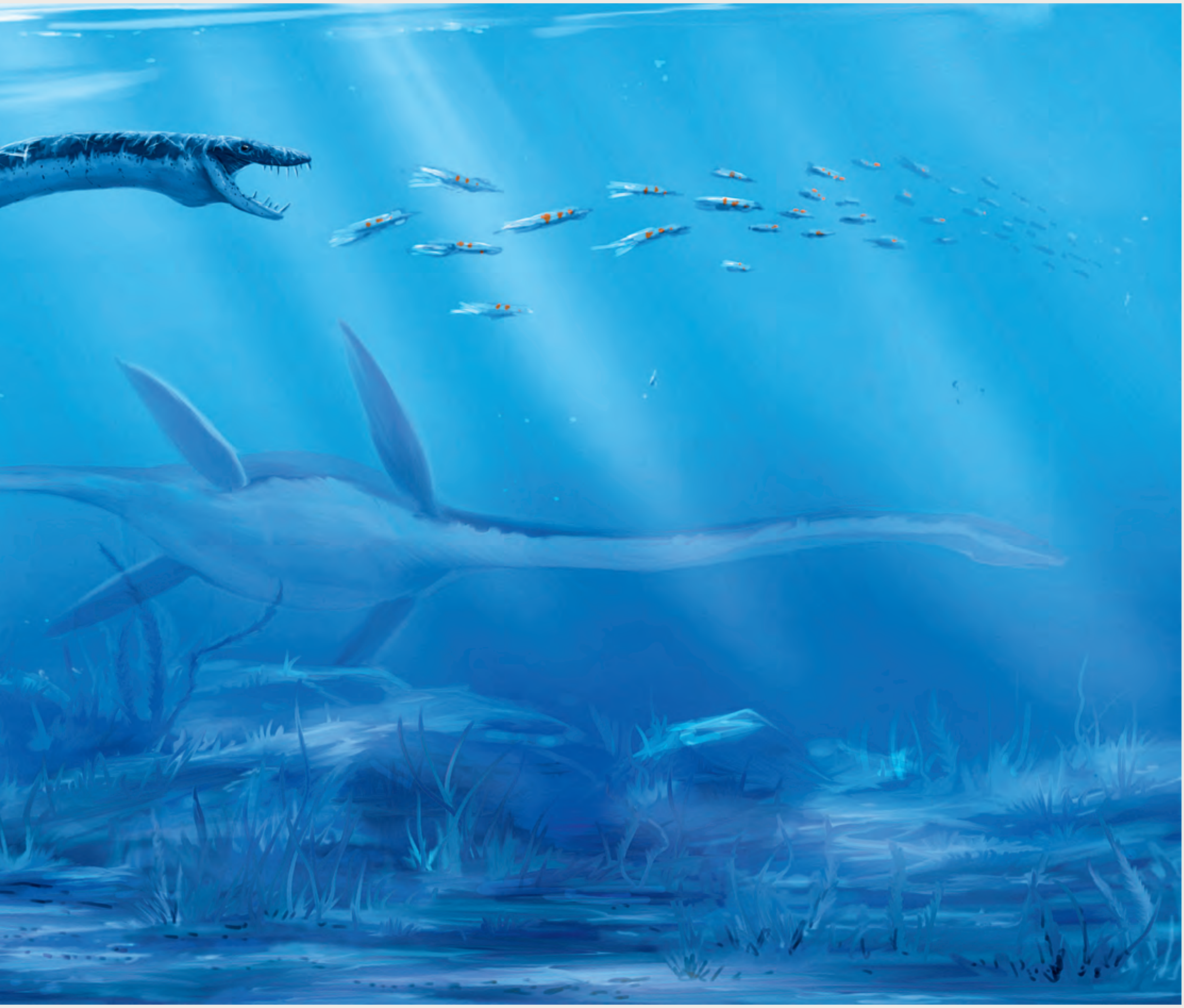
▲ Fig. 2.34. *Plesiosaurus*, a plesiosaurid plesiosaur from the Lower Jurassic in England.

Elasmosaurus

Elasmosaurus was discovered in sedimentary layers dating to about 80 million years ago in Kansas (in the central United States) and was described by American paleontologist Edward Drinker Cope (1840–1897) in 1868. This animal's anatomy—and notably its exceptionally long neck—were so troubling that young Cope made a monumental error when describing it: he placed its neck where the tail should have been, thinking that, like some dinosaurs, this animal had a long tail and a short neck. This error was the basis of a memorable quarrel with another American paleontologist, Othniel Charles Marsh (1831–1899), who publicly humiliated Cope by placing the neck where it belonged. The mutual hatred that animated these two men for the rest of their lives as a result of this quarrel gave rise to an extraordinary scientific competition between them (later called "The Bone Wars"), in which each raced to find more fossils than the other. Thanks to the Bone Wars, dozens of species were discovered, and hundreds of specimens of both dinosaurs and marine reptiles found, in just a couple of decades. This earned both Cope and Marsh enduring fame.

Because of this history, and because of *Elasmosaurus*'s immeasurably long neck, with more than seventy cervical vertebrae, it is the most famous genus of plesiosaur today. Its celebrity notwithstanding, the anatomy of *Elasmosaurus* is not well known, because remains of its limbs and part of its skull have never been found. Fortunately, the discovery of closely related plesiosaurs has allowed us to fill in some of those gaps. *Elasmosaurus* must have had a slender triangular skull equipped with needlelike teeth that decreased in size toward the back of the jaw. The upper and lower rows of teeth must have meshed perfectly once the animal closed its mouth. Its front limbs must have been longer than its rear limbs, and its tail must have been relatively short. It was a gigantic animal, just under 10 meters long.

▼ Fig. 2.35. *Elasmosaurus*, an elasmosaurid plesiosaur from the Upper Cretaceous in North America.



"*Plesiosaurus*," p. 55). Certain plesiosaurids exhibit a remarkable elongation of the neck; some, like *Occitanosaurus* (fig. 2.32), had a neck twice the length of their trunk.

Cryptoclidids were of modest dimensions too. *Cryptoclidus* (fig. 2.33) could reach up to 3 meters in length, with a long neck composed of thirty to forty vertebrae. These plesiosauroids are known mainly from fossils dating from the Middle Jurassic in England.

The elasmosaurids, known only from the Cretaceous, with their extremely long neck, were of a much more impressive size. The greatest numbers of cervical (neck) vertebrae belong to *Elasmosaurus* (which had seventy-two) (fig. 2.35) and *Albertonectes* (seventy-six). The latter sported a neck that was roughly 7 meters long! *Mauisaurus* had sixty-eight cervical vertebrae, *Hydralmosaurus* sixty-three, and *Styxosaurus* (which had a neck almost three times the length of its trunk) sixty-two. Despite the unknown ecological function of such an extreme elongation, elasmosaurids came in a wide variety, and they have been found at all latitudes, in sediments dating right up to the very end of the Cretaceous. The greatest number of specimens have been found in the United States.

The leptocleidids and the polycotylids are two other groups within Plesiosauria, but their precise fit is the subject of controversy. Some paleontologists classify them within Pliosauroidea; others, within Plesiosauroidea. They do exhibit a confusing mix of features—their skull was long, like pliosaurids', but slender, like plesiosaurids'. The polycotylids, such as *Dolichorhynchops and Thililua*, had a very long rostrum, and their neck, although relatively short, contained up to thirty vertebrae. These animals could reach considerable dimensions—*Pahasapasaurus* (fig. 2.36), for instance, was almost 6 meters long. A polycotylid fossil about 80 million years old, found in the United States, has provided proof of their viviparous nature, in the form of a juvenile preserved within the abdomen of an adult. The bones of the juvenile seem not to have been subjected to any degradation due to predation, so they

must be those of an embryo. It is likely that all species in Plesiosauria gave birth to live young, especially because a viviparous nature was already present in their close relatives, the pachypleurosaurs, back in the Triassic (see p. 48).

▲ Fig. 2.36. *Pahasapasaurus*, a polycotylid plesiosaur from the Upper Cretaceous in South Dakota (United States), shown giving birth. Its name comes from a Sioux (Lakota dialect) word meaning "black hills," referring to the name of the mountain chain where the fossil was found (the Black Hills).

The Fall of the Sauropterygians

Sauropterygians experienced an evolutionary success without equal among marine reptiles, but most went extinct before the end of the Mesozoic. Even though many hypotheses have been advanced, the causes of sauropterygians' slow disappearance are not completely clear. The only group that endured until the very end of the Cretaceous was the plesiosaurs proper, represented by the elasmosaurids.

At the beginning of the Cretaceous, plesiosaurs in the wide sense were still extremely diverse, with four large groups: the elasmosaurids, the polycotylids, the leptocleidids, and the pliosaurids. During the Late Cretaceous, the leptocleidids and the pliosaurids disappeared, and the polycotylids followed them. Did the plesiosaurs become extinct gradually? It is possible that the mosasaur boom (see p. 90) during the Late Cretaceous entailed sharp competition and a battle for survival that plesiosaurs lost over time. But during the Maastrichtian (the last age of the Cretaceous, 70–66 Ma), elasmosaurids still existed worldwide, in a wide variety of species—this apparent continued success does not fit such a pattern. Perhaps, of all the plesiosaurs, elasmosaurids' peculiar characteristics allowed them to avoid direct competition with the mosasaurs. We do not know. What we do know is that the consequences of the environmental upheavals that occurred at the very end of the Cretaceous were fatal to them.

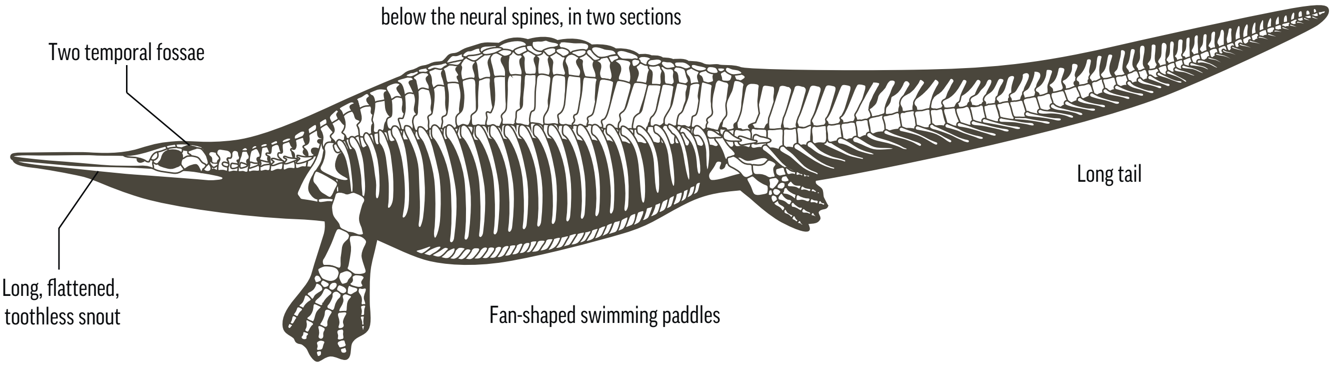
VII
The Hupehsuchians: An Exclusive Group

The hupehsuchians were both a short-lived and a geographically very limited group: they are known exclusively from around 248 million years ago, in the Lower Triassic (the Spathian stage), and from two very close counties in Hubei province—from which their name derives—in eastern central China (see fig. 4.8, p. 122).

Although we have known about hupehsuchians since the 1950s, only very recently, thanks to the unearthing of new fossils, has a clear picture of their phylogenetic relationships been established. They were actually first considered sauropterygians, then "**thecodonts**" within the archosaur group, and then a separate order of marine reptiles, closer to the ichthyosaurs. The new fossils have allowed researchers to identify hupehsuchians as diapsids closely related to the ichthyosaurs, with whom they form the clade Ichthyosauromorpha.

The hupehsuchians comprise five genera, all of them monospecific (one species only) and often based on very few specimens—sometimes only one. The diversity of this isolated group, all the specimens of which have come from the same deposit (or from deposits in very close proximity) and the same stratigraphic level, may be overestimated, even though the differences among specimens justify assigning them different genera.

Hupehsuchians' anatomy (fig. 2.37) is surprising. They had a massive body; a long muzzle; a long tail; and, generally, large, fan-shaped swimming paddles. They can be divided into three size categories: *Nanchangosaurus* and *Eohupehsuchus* were the smallest (roughly 40 centimeters long), *Hupehsuchus* and *Eretmorhipis* were roughly 1 meter long, and *Parahupehsuchus* could attain a length of almost 2 meters. Their skull exhibits two temporal fossae, indicating



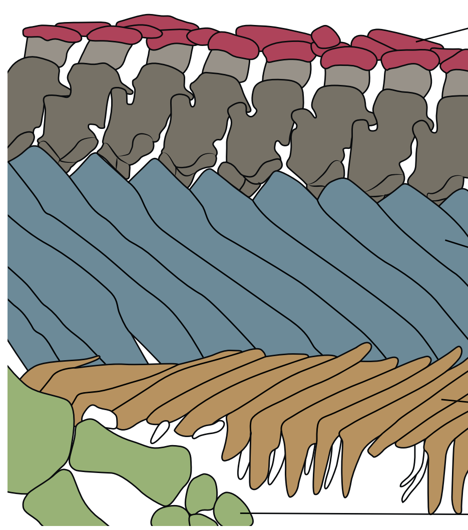
▲ Fig. 2.37. The very peculiar features of hupehsuchians, shown in *Hupehsuchus*, from the Lower Triassic in China.

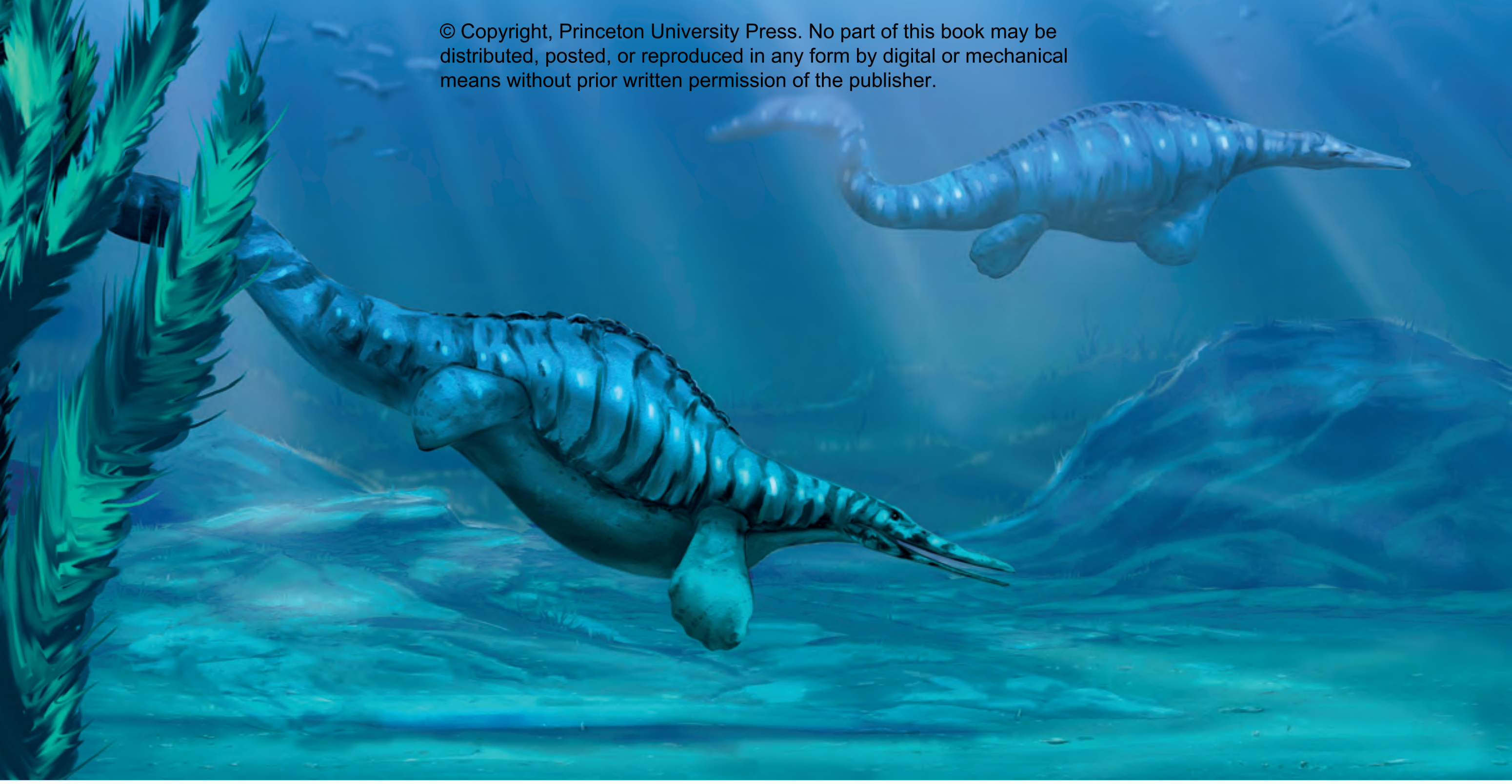
that they belong to the diapsids, and a very long, slim muzzle, formed almost exclusively by the premaxillary bone. Their muzzle was laterally compressed, somewhat like the beak of a wading bird, and completely toothless. Their neck was generally longer than that of other vertebrates, containing nine or ten cervical vertebrae, with the exception of *Eohupehsuchus*'s six.

The hupehsuchians' body formed a unique "bony tube" (fig. 2.38) that was more pronounced in some genera and that extended from the pectoral girdle to the pelvic girdle. It was formed by the overlap of the ribs and the gastralia, both components being pachyostotic—similar to a turtle's shell (see p. 76), except that the girdles remained on the outside. This means that the ribs and gastralia coming together to form a protective shell, either externally (in turtles) or internally (in hupehsuchians), has happened at least twice in the history of the vertebrates. The bony tube extended along the entirety of the body in *Parahupehsuchus* but was limited to the pectoral region in the case of *Eretmorhipis*. In the case of *Hupehsuchus*, a faint space still existed between the ribs. This tube must have made each hupehsuchian's body considerably rigid, meaning that in order to swim it must have depended on the undulation of its powerful tail, like a crocodile.

Hupehsuchians' neural spines were all very short and, uniquely, composed of two separate parts. These spines were also sculpted toward the tip, which allows the possibility that they protruded from the skin. Another remarkable characteristic of the hupehsuchians was the presence of three layers of dermal plates (except in the case of *Nanchangosaurus*, which had only one layer) above the neural spines of the trunk and the base of the tail. These osteoderms were stacked in an alternating arrangement, like tiles, to leave no chinks in the animal's armor. In *Eohupehsuchus* the plates in all three rows were very small, whereas in the case of *Eretmorhipis*, *Hupehsuchus*, and *Parahupehsuchus* the ones in the third row were large, each covering several vertebrae—up to four in the case of *Eretmorhipis*!

▼ Fig. 2.38. A diagram showing the "bony tube," formed by the conjoined and overlapping ribs and gastralia; the neural spines in two parts (two shades of gray); and the three rows of osteoderms in the hupehsuchian *Parahupehsuchus*. All this, which formed a robust bony armor, must have provided the animal with good protection from predators.





▲ Fig. 2.39. *Hupehsuchus*, a hupehsuchian from the Lower Triassic in China.

With the exception of *Nanchangosaurus*, the hupehsuchians' swimming paddles were well developed. In *Parahupehsuchus* they were slender; in *Hupehsuchus* (fig. 2.39) and *Eretmorhipis* they were fan-shaped. Hupehsuchians with wide and short paddles also exhibit hyperdactyly. This hyperdactyly is different from that found in ichthyosaurs but reminiscent of the first tetrapods of the Devonian, such as *Ichthyostega* and *Acanthostega*: another example of convergence (see "Convergence," pp. 198–99).

Although the deposits in which hupehsuchians have been found are otherwise rich in fossils, they are characterized by both a surprising absence of fish and a plethora of small marine reptiles about 20 centimeters to 1 meter long (comprising the ichthyosaur *Chaohusaurus* and the sauropterygians *Hanosaurus* and *Keichousaurus* in addition to five types of hupehsuchians). These creatures must all have been potential prey of the ecosystem's assumed mega-predator, an undiscovered sauropterygian 3–4 meters long. All of this shows that the trophic networks were fairly well established about 4 million years after the catastrophic Permian/Triassic crisis. The joint presence in hupehsuchians of a "bony tube" and of neural spines covered by up to three rows of osteoderms represents a unique and sophisticated mode of protection against predators. These defensive features must have made hupehsuchians heavy and somewhat inflexible. Considering their long free tail and powerful swimming paddles as well, this suggests that the area they lived in was a shallow sea, in which they typically kept to the bottom. Their slender, flat, and toothless muzzle seems to point to their being **filter feeders**, somewhat in the manner of modern beaked whales. The differences between these animals in terms of size, the length of the "bony tube," dermal armor, and paddle shape probably reflect a partitioning of the ecological niches among them so as to best exploit the food resources of the region they shared.

VIII

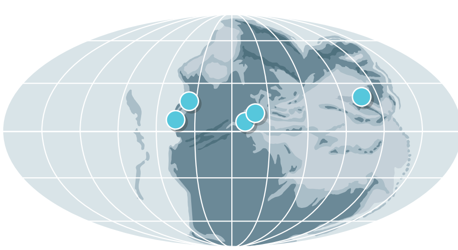
The Thalattosaurs: Enigmatic Reptiles

The name "thalattosaur" comes from the Greek *thálassa*, "sea," and *sauros*, "lizard," and therefore means "sea lizard." It refers to a group of Triassic marine reptiles that were widely distributed in the northern hemisphere, from Alaska to China, by way of Canada and Europe. Although this group's representatives were well distributed geographically (fig. 2.40), as well as relatively diverse, their fossils are fairly rare. Thalattosaurs roughly resembled lizards and were between 1 and 4 meters in length.

The oldest known thalattosaurs are from the Lower Triassic in North America. The great marine transgression of the Middle Triassic would facilitate their diversification and dispersal throughout the Tethys and the eastern portion of Panthalassa. Their transoceanic distribution is all the more remarkable since these animals were of only medium size and were not completely adapted to a pelagic way of life (in the open sea). Their disappearance at the end of the Triassic is unexplained. Did competition with the ichthyosaurs (see p. 30), which were constantly growing in number and above all were increasingly specialized, help vanquish the thalattosaurs, animals of a rather generalist nature? Because they are so rare in the fossil record to begin with, we have little to go on.

Thalattosaurs' anatomy indicates that, although they were adapted to an aquatic way of life, they were probably amphibious and therefore capable of returning to land for both warmth and purposes of reproduction. Their limbs were short and probably ended in flippers, but they retained some impressive front claws, which must have allowed these animals to move about on the shore, as well as to resist swells while they rested on the rocks, like today's marine iguanas. In illustrations, their tail is often represented as raised (in other words, stretched dorso-ventrally), like salamanders' and newts', but there is no reason to believe that it wasn't slender and whip-shaped like that of iguanas (see fig. 1.2, p. 9). Their tail was exceptionally long, even for a reptile—up to twice the length of their trunk! Coupled with the undulation of the entire body, that tail probably ensured efficient propulsion in water. Their snout was generally long and slender. Their nostrils, like those of many animals that have returned to a marine way of life, were situated behind the snout, near the eyes. Also, like those of many aquatic animals (but not exclusive to them), their eyes were protected by sclerotic rings (see "Diving and Underwater Vision," p. 150–51).

Thalattosaurs' exact position within the class Reptilia remains extremely fluid and

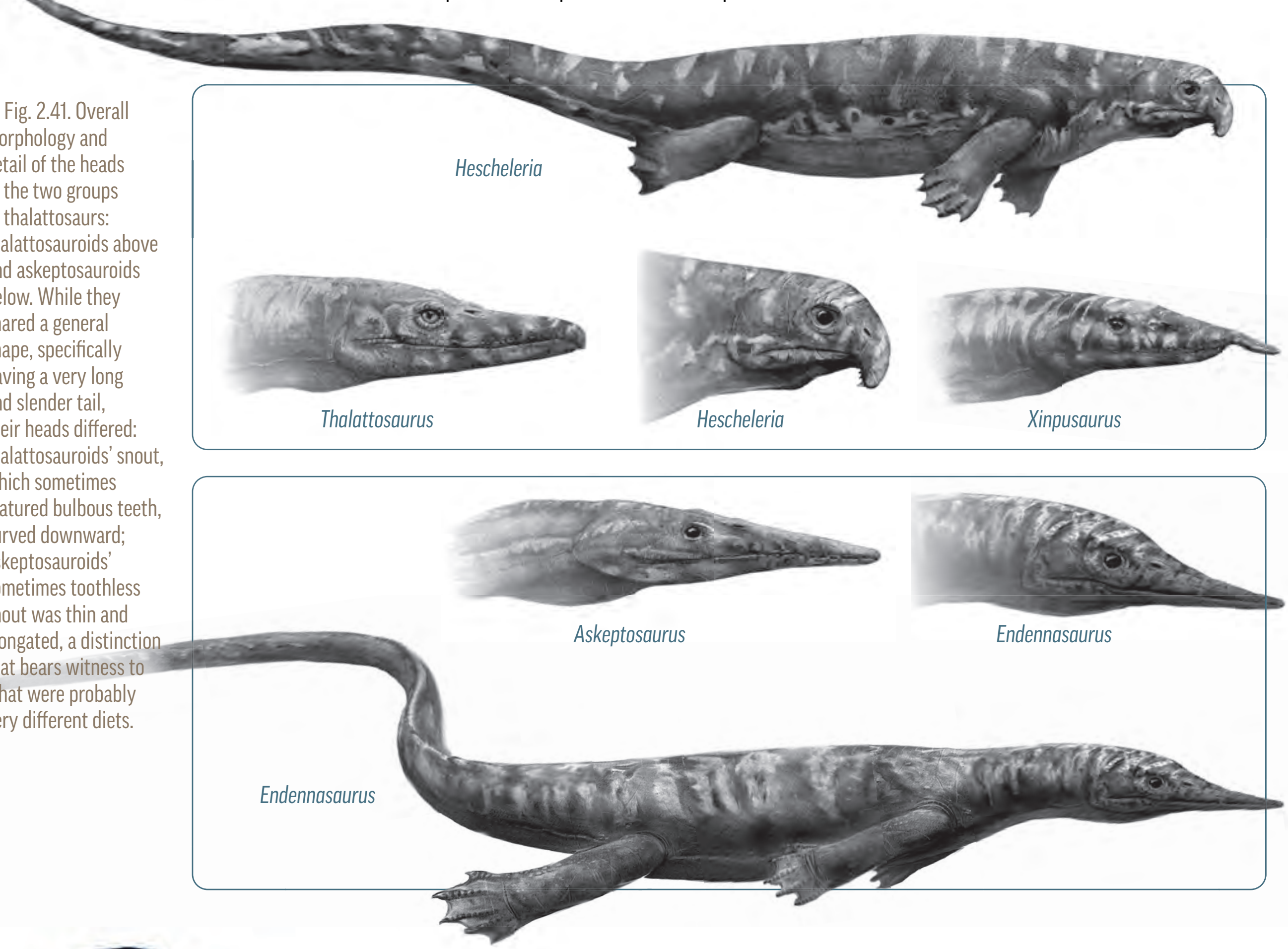


Early and Middle Triassic

Late Triassic

◄ Fig. 2.40. The distribution of the thalattosaurs over the course of the Triassic.

► Fig. 2.41. Overall morphology and detail of the heads of the two groups of thalattosaurs: thalattosauroids above and askeptosauroids below. While they shared a general shape, specifically having a very long and slender tail, their heads differed: thalattosauroids' snout, which sometimes featured bulbous teeth, curved downward; askeptosauroids' sometimes toothless snout was thin and elongated, a distinction that bears witness to what were probably very different diets.



► Fig. 2.42. Skeleton of *Askeptosaurus* (roughly 2 meters long), a thalattosaur from the Middle Triassic in Switzerland and Italy. Muséum national d'Histoire naturelle (Paris, France).

controversial. While they are most often considered diapsids (see p. 25), they have at different times been regarded as close to the sauropterygians, the lepidosauromorphs, and the archosauromorphs. Whatever the case might be, the thalattosaurs themselves can be clearly divided into two groups: the thalattosauroids and the askeptosauroids (fig. 2.41).

In most thalattosauroids, the end of the snout curved downward, and the short, massive round teeth of some species seem to indicate a diet of tough prey. Their curved snout might have helped them manipulate shelled creatures and other mollusks or aided their foraging on the seafloor. Thalattosauroids occupied numerous ecological niches and were perfectly adapted to life in shallow coastal waters and reef systems.

Askeptosauroids, such as *Askeptosaurus* (figs. 2.42 and 2.44), with their short pointy teeth, were probably opportunistic surface predators that ate fish and any prey within their reach. Some, like *Endennasaurus* (fig. 2.41), were practically toothless.

Hescheleria

Hescheleria was a small, very particular thalattosauroid discovered in the 1930s in Middle Triassic deposits (from 247 to 235 Ma) at Monte San Giorgio, on the border between Switzerland and Italy (see chapter 4, p. 113). Although its overall appearance, like that of other thalattosaurs, was that of a lizard, with a very long tail and short limbs, its snout was strange. Its lower jaw was short, and the end of its upper jaw was turned downward, almost vertically, covering the front part of the mandible when the creature's mouth was closed.

At the time of its original description in 1936, *Hescheleria* was thought to most likely have fed on mollusks, the curved part of the skull helping hold the shells while the lower teeth crushed them. Yet some experts expressed doubts, since some of the teeth in the mandible closed upon a diastema (a section devoid of any teeth) in the upper jaw, which obviously would have made crushing difficult. Therefore the function of this snout remains somewhat a mystery.

▲ Fig. 2.43. *Hescheleria* (roughly 1 meter long), a thalattosaur from the Middle Triassic in Switzerland.

Askeptosaurus

Askeptosaurus was an askeptosauroid about 2.5 meters long, found in both Italy and Switzerland. Its tail accounted for about half of the animal's entire length and must have allowed it to swim using undulation. Its limbs, short and relatively weak, probably allowed it to move about on land for only short distances, for purposes such as laying eggs.

Askeptosaurus means "unsuspected lizard," and its discovery in 1925 was indeed fortuitous. Hungarian paleontologist Franz Nopcsa von Felső-Szilvás was at the time studying the remains of a small ichthyosaur, *Mixosaurus*, which had been provided by the Natural History Museum in Milan, when he noticed some bones that did not belong to the ichthyosaur's skeleton. The baron proceeded to describe this new species, and several more specimens were found thereafter.

▲ Fig. 2.44. *Askeptosaurus*, a thalattosaur from the Middle Triassic in Switzerland and Italy.

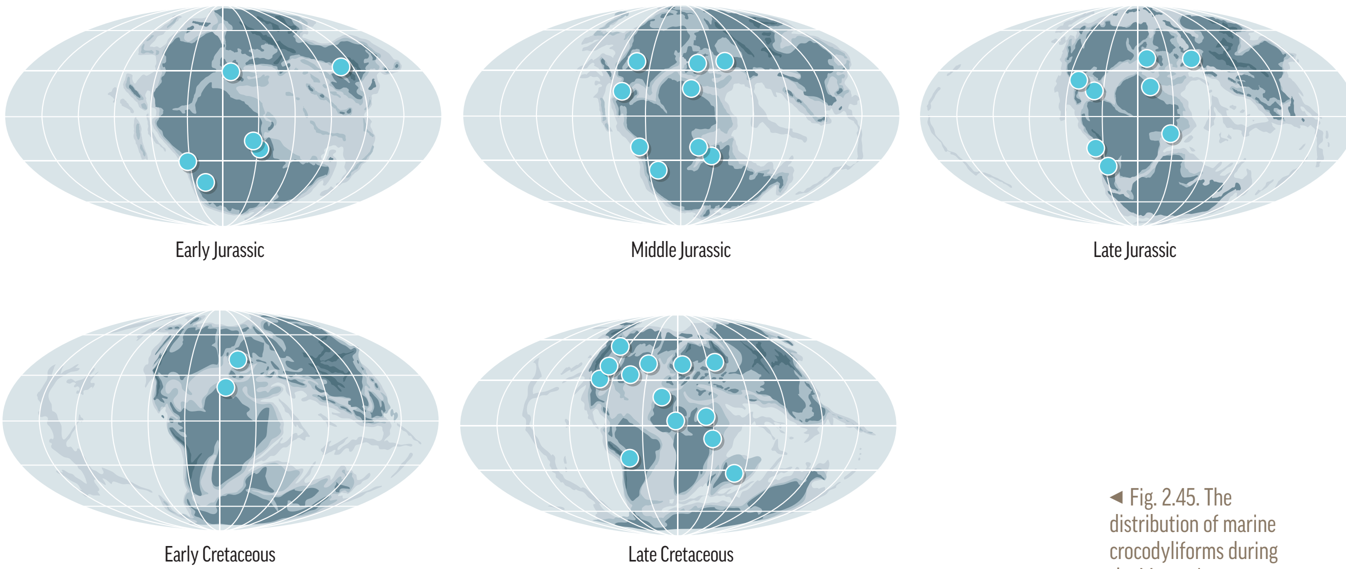
IX

The Crocodylomorphs: Variations on a Crocodile

Like dinosaurs and pterosaurs, crocodylomorphs are archosaurs (figs. 2.3 and 2.4). In today's natural world they are represented only by the crocodiles (or crocodilians). But that was not always the case. During the Mesozoic, crocodylomorphs came in an impressive variety: they occupied many ecological niches, and their physical attributes differed much more substantially than they do today.

Amphibious Crocodiles? Not Necessarily

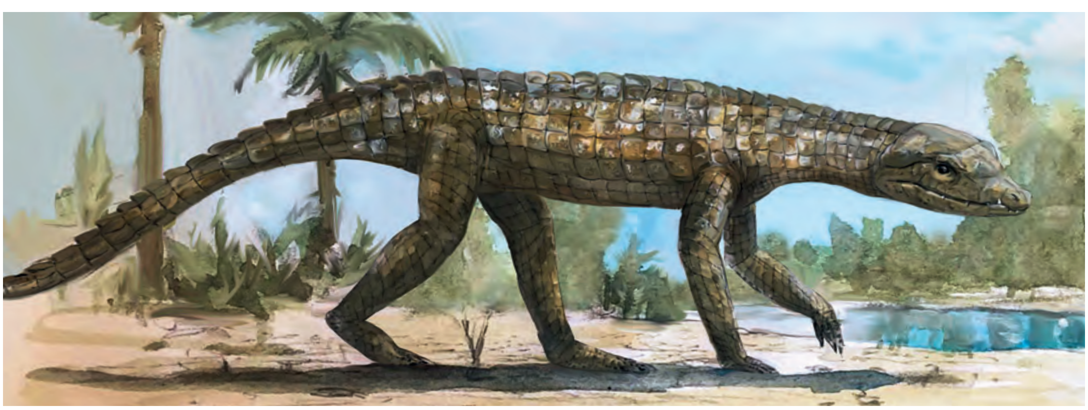
All of today's crocodylomorphs, whether we are talking about crocodiles, caimans, alligators, or gavials, are amphibious, and only *Crocodylus porosus* (see chapter 1, p. 10), the saltwater crocodile, occupies the marine environment in a recurring fashion. Their Mesozoic cousins were a much more mixed



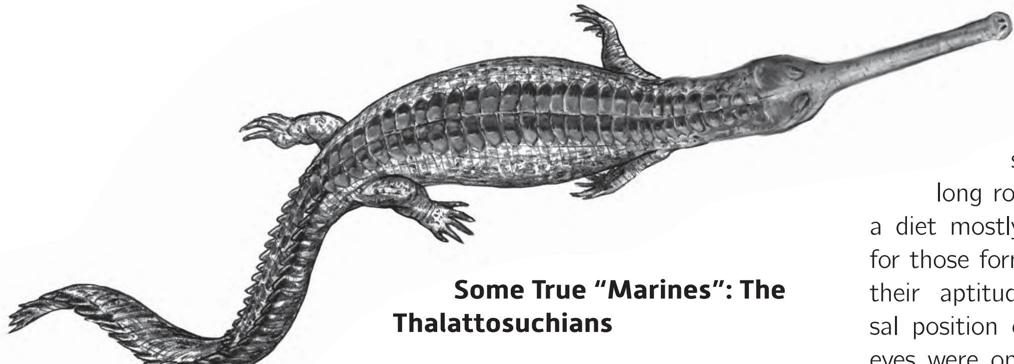
◄ Fig. 2.45. The distribution of marine crocodyliforms during the Mesozoic.

group. Numerous forms were completely terrestrial, such as *Bretesuchus* and *Sebecus*, the skull of which more closely resembles that of a tyrannosaur than that of other crocodilians. Some notosuchians, such as *Simosuchus*, were even herbivorous. The most basal (least evolved) crocodylomorphs, such as the protosuchians (fig. 2.46), were terrestrial, and it therefore seems that creatures in this group only subsequently began to adapt to aquatic environments.

Aquatic forms are numerous among the fossil crocodylomorphs, and it is sometimes difficult to distinguish the forms that were completely marine from those that only occasionally visited the ocean or only frequented brackish estuaries or mangrove swamps. Bear in mind that, like today's saltwater crocodile, some fossil species must have spent the first years of their lives in fresh water. We know this because the largest specimens of those species are found in areas that correspond to the sea and smaller ones are found in areas corresponding to rivers. In addition, river currents sometimes transport the corpses of non-marine aquatic animals to the sea, where they can become fossilized in marine sediments. Rather than discuss these groups with an uncertain lifestyle, we will consider only the groups that can frequently be found in marine sediments.



◄ Fig. 2.46. *Gobiosuchus*, a terrestrial protosuchian from the Upper Cretaceous in the Gobi Desert, Mongolia.



▲ Fig. 2.47. *Teleosaurus*, a thalattosuchian from the Middle Jurassic in Normandy (France), showing the rows of osteoderms.

Some True "Marines": The Thalattosuchians

As their name reveals, the thalattosuchians (from the Greek *thálassa*, "sea," and *suchos*, "crocodile") were, with few exceptions, exclusively marine crocodylomorphs. The oldest traces of representatives of this group go back to the Sinemurian stage (Lower Jurassic sediments roughly 195 million years old). Thalattosuchians' geographic origin is not clear, since the most ancient of their fossils come from very distant locations: South America, India, and France (fig. 2.45). Thalattosuchians from the end of the Early Jurassic and later are known mostly from Europe and the Neuquén Basin in Argentina.

The thalattosuchians are traditionally divided into two large groups: the teleosauroids and the metriorhynchoids. The teleosauroids, the more ancient of the two, exhibit much less pronounced adaptations to the aquatic environment, with an overall anatomy not much different from that of other amphibious crocodylomorphs (fig. 2.47). They were equipped with dorsal and ventral shields, made of bony plates formed in the skin (osteoderms). Propulsion was supplied by a long, supple, muscular tail. The forelimbs were certainly a little small, but they still allowed for movement on land both to lay eggs and to warm up in the sun. All teleosauroids were equipped with a long rostrum (fig. 2.49), which suggests a diet mostly of fish, or sometimes tortoises for those forms with more robust teeth. Given their aptitude for swimming and the dorsal position of their orbits in the skull (their eyes were on top of their heads), most likely these animals evolved in coastal environments, avoiding the open ocean and preferring to hunt by ambush from below.

The origin of teleosauroids, and therefore of thalattosuchians, is still much debated (fig. 2.50). For a long time, paleontologists were guided by the fact that thalattosuchians' skull, especially the palate and the bones around the ear, was very primitive for crocodylomorphs. However, most recent phylogenetic research places them closer to other, more evolved, long-snouted saltwater crocodylomorphs: the pholidosaurids and the dyrosaurids. It is possible that this grouping is actually an artifact: these groups' similarly long muzzles might simply be a result of shared ways of life and shared dietary regimens, rather than a result of close evolutionary kinship (i.e., an example of convergence; see "Convergence," p. 198–99). Only the discovery of really ancient fossils resembling the first thalattosuchians but still retaining some ancestral characteristics would allow experts to decide. Unfortunately, the oldest known significant thalattosuchian forerunner, *Peipehsuchus*, from about 180 million years ago (the Toarcian) in China, was already a very long-snouted form exhibiting all the

► Fig. 2.48. *Pelagosaurus*, a thalattosuchian from the Lower Jurassic in Calvados (France), Muséum national d'Histoire naturelle (Paris).

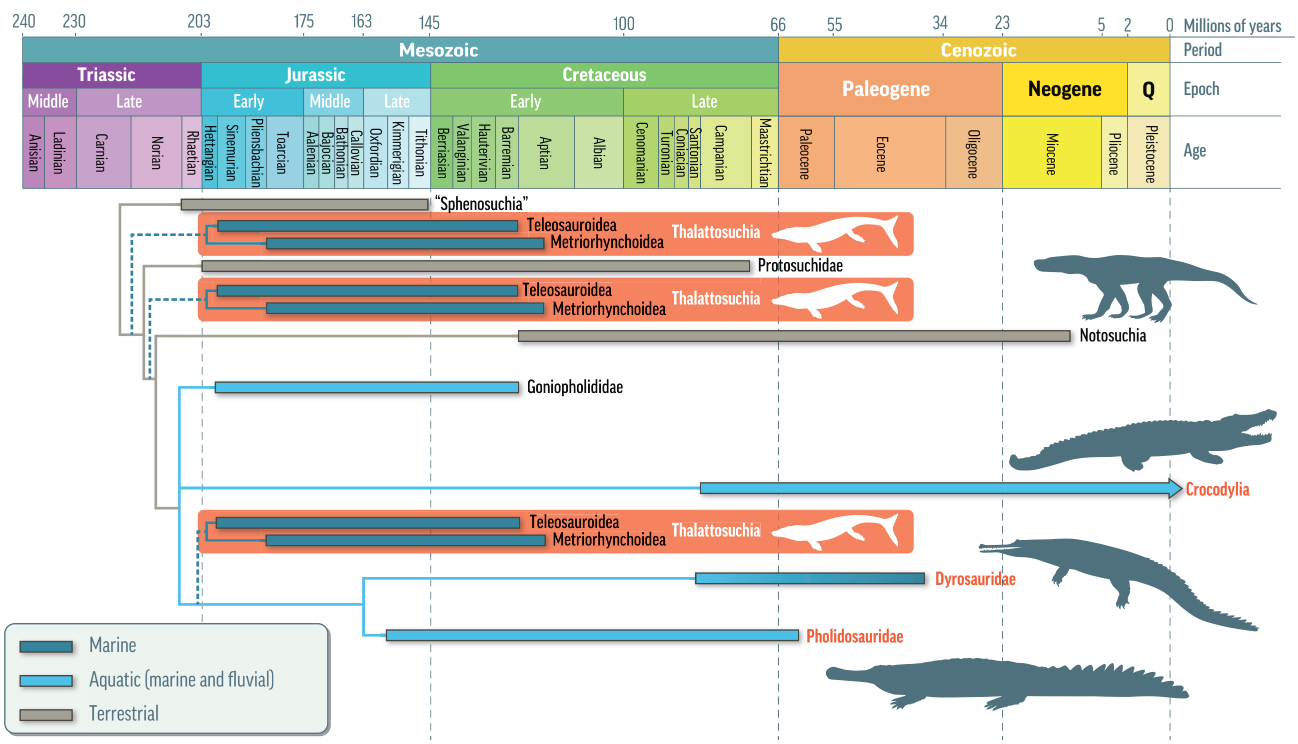
characteristics of the thalattosuchians and of the teleosauroids specifically.

The oldest fossil metriorhynchoids all come from the Toarcian, as *Peipehsuchus* does, and have been found in Europe. They exhibit increasingly marked skeletal modifications that point to a much more exclusive aquatic life: the forelimbs are short, and the fingers of both hands and feet are flat but show no hyperphalangy or hyperdactyly (compare "From Legs to Swimming Paddles," p. 39); in addition, their skeleton was light, composed of spongy and not very compact bones, and they lacked a protective shield, either dorsal or ventral. They were equipped with a hypocercal tail—one with a smaller upper lobe than in ichthyosaurs, the presence of which nonetheless demonstrates a high degree of adaptation to the aquatic environment and to rapid swimming. As in the case of the ichthyosaurs, the caudal vertebrae supported the lower lobe (fig. 2.51).

Curiously, while the metriorhynchoids' forelimbs had shrunk, their hind limbs remained very long, comparable to the hind limbs of today's crocodilians. But the muscle insertion areas on the bones are not very marked, revealing a certain muscular weakness that would have limited the involvement of the hind limbs in locomotion. It must have been difficult, if not impossible, for metriorhynchoids to move about on land as modern crocodiles do. Perhaps these hind limbs served only directional or stabilizing purposes, like **hydrofoils** on ships and submarines.

Metriorhynchoids' skull presents numerous innovations that testify to a lifestyle that was more marine than that of the teleosauroids. First, certain fossils show evidence of an enlarged salt gland, which would have helped these creatures eliminate any excesses of salt

▲ Fig. 2.49. Skull of *Proexochokefalos*, a thalattosuchian from the Middle Jurassic in Calvados (France), Muséum national d'Histoire naturelle (Paris).



▼ Fig. 2.50. A simplified phylogeny of the crocodylomorphs, showing the groups mentioned in the text and the different possible positions for the thalattosuchians.

in the body that had not been excreted by the kidneys. Situated in a sort of bony visor in front of and below the eye sockets, this gland most likely was present in all metriorhynchoids. Moreover, the eyes were oriented no longer upward but laterally, which attests to a modification in predation behavior. The metriorhynchoids were therefore probably open-ocean hunters, capable of actively pursuing their prey (fig. 2.52).

No fossilized metriorhynchoid embryos have been found, but given these animals' great degree of adaptation to the aquatic environment, it should not be ruled out that they gave birth to live young. Nevertheless, metriorhynchoids may have used their hind limbs to move about on land to lay eggs. If so, given their feeble musculature, it must have presented a real challenge!

The metriorhynchoids seem to have favored different prey than the teleosauroids did. Metriorhynchoids had a significantly shorter muzzle and, overall, their teeth were more robust, which seems to reveal a more varied and opportunistic diet. *Dakosaurus* (see fig. 5.21, p. 161) pushed these characteristics to the extreme, with a very high, short, and squat skull containing teeth that were far apart but were massive and **ziphodont** (serrated). This morphology, a classic one in predatory dinosaurs, as well as in terrestrial crocodylomorphs, is rare among marine crocodylomorphs. Imagine the head of a *Tyrannosaurus* placed on a body capable of swimming extremely efficiently!

Thalattosuchians began to decline at the end of the Jurassic. For a long time, researchers supposed they became extinct shortly thereafter, at the beginning of the Early Cretaceous; however, recent reinterpretation of some fragmentary fossilized remains suggests that they died out about 20 million years later, at the end of the Early Cretaceous. What doomed them? For the time being, there seem

▼ Fig. 2.51. Skeleton of *Cricosaurus*, a thalattosuchian from the Upper Jurassic in Germany.

At almost 7 meters in length, *Plesiosuchus manselii* is the largest known metriorhynchoid. Discovered in Kimmeridgian–Tithonian sediments (from 155 to 150 Ma) in England, its short muzzle and serrated teeth made it a redoubtable predator, at the top of the food chain. It lived next to another mega-predator, *Dakosaurus maximus* (fig. 5.21, p. 161), a close cousin that was just as formidable; this

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