

Mesozoic marine reptiles: an overview

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Abstract

During the Mesozoic era, the evolution of numerous reptilian groups resulted in secondary adaptation to life in water. As a consequence, most clades were involved to various extents in the exploitation of marine resources. A description of the major taxa of Mesozoic aquatic reptiles is conducted below, with an account of the present state of knowledge on their biology and ecology.

Introduction: brief definition of a broad concept

In extant faunas, marine tetrapods are mainly represented by birds and mammals. Reptiles are rare and sparse in the oceans, although the marine iguana (*Amblyrhynchus cristatus*) some turtles (Dermochelyidae, Cheloniidae), snakes (Acrochordidae, Elapidae hydrophiinae), and the estuarine crocodile, *Crocodylus porosus* (a species that can be encountered at sea several hundreds kilometres from the shore; cf. BUSTARD and CHOUDHURY, 1980) regularly exploit marine resources. The present situation is far from reflecting the amazing diversity of marine reptiles during Mesozoic times. However, it is noteworthy that, in fresh water environments, these animals (including turtles, lizards, snakes, crocodylians) are more numerous and diverse today.

The expression “Mesozoic marine reptiles” has no definite systematic meaning; it rather refers, like the term “marine mammals”, to a complex assemblage of various zoological groups sharing the same habitat. Hence, Mesozoic marine reptiles by no means constitute a taxon, but rather a collection of taxa that can be phylogenetically quite different in spite of obvious morphological or ecological convergent adaptations. The aim of this article is not to conduct a detailed, comprehensive description of all these groups (a task that would itself involve a big volume), but to give a synthetic account of its spectacular (but often ignored) biodiversity.

Several groups of Mesozoic marine reptiles, with variable degrees of independence from the terrestrial environment, are commonly acknowledged: the Placodonts (littoral forms from the Triassic, sometimes armoured, and characterised by crushing teeth); the Pachypleurosaurs (small lizard-like reptiles from Triassic littoral environments, often displaying pachyostotic bones); the Nothosaurs (lizard-like medium to large-sized reptiles from the Triassic, phylogenetically close to the plesiosaurs and pliosaurs); the Plesiosaurs (large marine forms with a characteristic neck lengthening); the Pliosaurs (large super-predators closely related to the previous ones); the Ichthyosaurs (fish-like reptiles highly adapted to an aquatic life); the Mosasaurs (varanoid lizards lately adapted to the marine environment during the Cretaceous); the Thalattosuchian Crocodiles (“true” marine crocodiles, mainly diversified during the Jurassic); and the turtles, which invaded the seas during the Upper Jurassic. Other forms, such as the Thalattosaurs and several littoral diapsid reptiles, could be added to this list. However, they were relatively sparse in time and space and, as amphibious

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organisms, they largely remained dependent on the terrestrial environment.

Though some early attempts by reptiles to adapt to marine conditions are revealed by the fossil record, most of this radiation occurred during Mesozoic times. Nearly all Mesozoic reptilian groups were involved with variable success (Fig. 1), except the Dinosaurs, although some of them are supposed to have been related to fresh-water habitats.

More than 400 marine reptile species, representing about 225 genera and some 50 families, are acknowledged for the Mesozoic. The course of their evolution clearly shows that their richest diversification, as also the highest frequency of attempts to re-adapt to marine conditions, occurred during the Triassic, an epoch when marine reptiles were still basically dependent on littoral environments (placodonts, pachypleurosaurs, nothosaurs, early ichthyosaurs, thalattosaurs, etc.). New forms, further freed from terrestrial and littoral environments, such as the plesiosaurs, the pliosaurs, the “classical” ichthyosaurs and, later on, the mosasaurs, appeared by the end of the Triassic, and, for most of them, during the Jurassic and the Cretaceous.

The degrees of marine adaptation of the tetrapod are unevenly perceptible in the fossils. This adaptation is quite evident and unquestionable when very specialised forms, like the ichthyosaurs, are considered. However, accurate assessments can be much more delicate for littoral, Triassic forms such as the placodonts or certain nothosaurs. Marine reptiles generally display a number of unambiguous adaptive characteristics, that are also shared by all aquatic amniots. These can be grouped into three categories, very unevenly revealed by the fossils: a) Morphological specialisations bearing on the organs involved in propulsion, trim control and buoyancy regulation, but also on skull structure (especially the position of air ducts), or teeth morphology and arrangement. In some exceptional occasions, soft parts may also be preserved. b) Clues to physiological characteristics, e.g. reproductive adaptations, bone histology, bio-geochemistry, etc. c) Clues to eco-ethological characteristics: taphonomic indications of environment, fossilised faeces or stomach contents, etc.

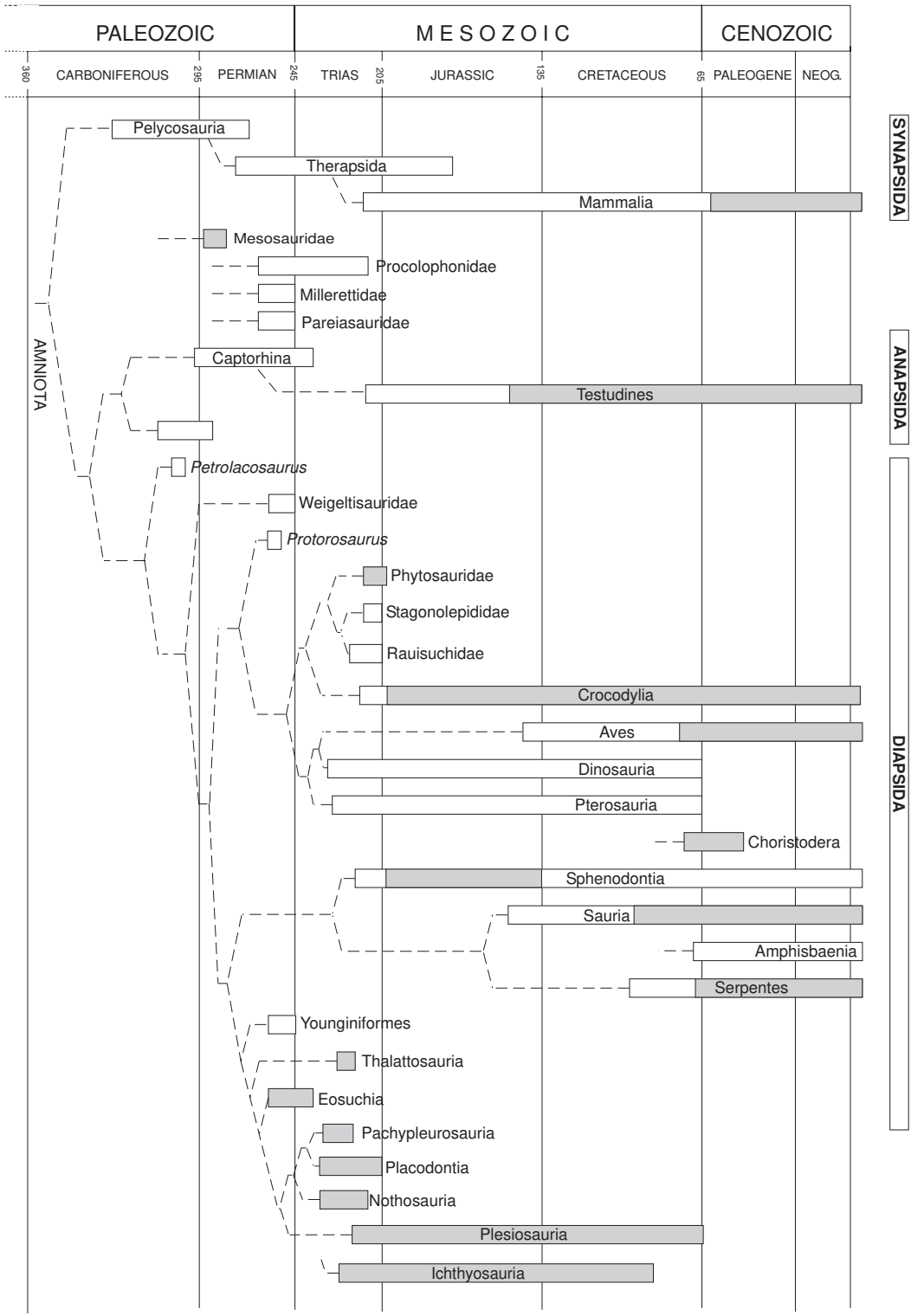
Key to abbreviations used in figures

a:	angular	l:	lachrymal	Rad:	radius
astr:	astragalus	mx:	maxilla	rad:	radial
calc:	calcaneum	n:	nasal	sa:	surangular
d:	dentary	p:	parietal	sp:	splenial
f:	frontal	pmx:	premaxilla	sq:	squamosal
Fem:	femur	po:	postorbital	st:	supratemporal
Fib:	fibula	prf:	prefrontal	Tib:	tibia
Hum:	humerus	ptf:	postfrontal	Uln:	ulna
int:	intermedial	q:	quadrate	uln:	ulnare
j:	jugal	qj:	quadratojugal		

Early re-adaptations to an aquatic habitat in reptiles

The earliest reptilian attempt to return to an aquatic life occurred in the family Mesosauridae. These small to medium-sized reptiles (0.3 to 1 m in length) were relatively common during the Early Permian (around –280 Ma) in the southern parts of Africa and America. They displayed a series of common, original specialisations (Fig. 2). Their body was slender, with a very long, laterally compressed tail. Their pentadactyl limbs were characterised by finger lengthening; pelvic limbs being larger than thoracic ones. Their neck and skull were stretched antero-posteriorly, and there was only one pair of temporal openings occupying a lower position. The slender jaws of these reptiles bore numerous thin teeth. In some taxa, like *Mesosaurus*, teeth were needle-like and interlocked at occlusion, thus forming an efficient tool for catching small preys. These various morphological features strongly suggest that the mesosaurs were indeed aquatic reptiles, retaining the ability to

Fig. 1. General phylogeny of the Amniota showing, in grey, the clades which have had aquatic adaptation stages in their history. ▸



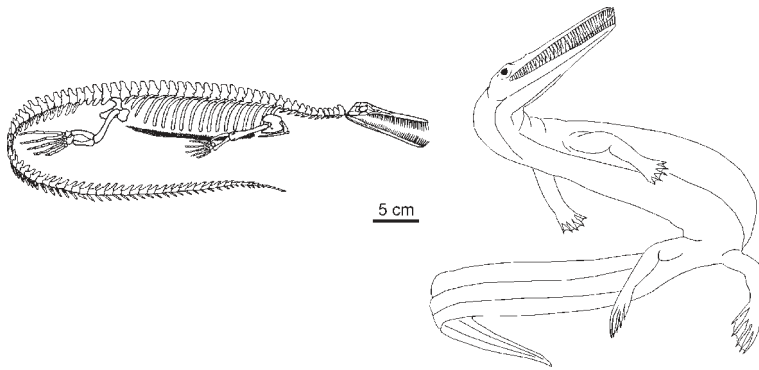


Fig. 2. *Mesosaurus*, Early Permian of South Africa (skeleton after CARROLL, 1987).

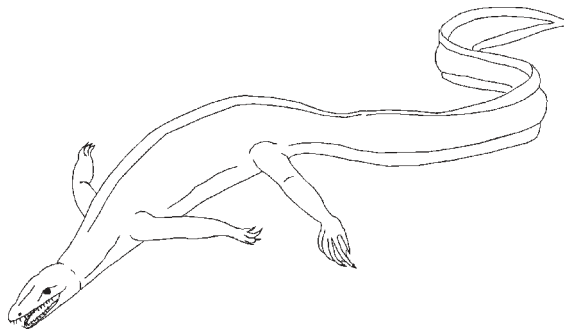


Fig. 3. *Hovasaurus* life restoration.

move on land, and feeding on small elusive swimming preys.

The affinities of the Mesosauria remain poorly understood. Available phylogenetic analyses (Fig. 1) indicate that they were primitive amniots totally unrelated to the other clades of Mesozoic marine reptiles.

A second wave of reptilian attempts to re-adapt to an aquatic life occurred by the end of the Permian up to the very Early Triassic (–250 to –235 Ma), with small diapsid eosuchians that were probably related to some of the major Mesozoic groups such as the Euryapsida. Indeed, several genera from the Permo-Triassic of Madagascar, e.g. *Claudiosaurus* and *Hovasaurus* (Fig. 3), seem to have acquired a good ability for aquatic locomotion (CARROLL, 1981). These were small reptiles some tens centimetres long, with a slender body and a very long, laterally compressed tail. Their limbs were moderately specialised, but the pelvic ones were longer than the thoracic and had very developed autopodial bones. These features, as also the presence of pachyostosis in some skeletal parts (BUFFRÉNIL and MAZIN, 1989) and the littoral or marine nature of the geologic layers where these genera are found, altogether suggest that they were coastal forms with an efficient adaptation to swimming.

The Euryapsida

General taxonomy

The phylogenetic analysis of the various groups of Mesozoic marine reptiles has been deeply changed during the last decades. A classical interpretation settled the existence of a sub-class Euryapsida composed of the Ichthyosauria, Sauropterygia (nothosaurs, plesiosaurs and pliosaurs), and Placodontia. The diagnostic feature of this taxon referred to a peculiar temporal architecture, with just one

pair of temporal openings in an upper position (see e.g. ROMER, 1966). The demonstration that this temporal fenestration was independently derived from a diapsid pattern in the Sauropterygia (KUHN-SCHNYDER, 1961, 1962, 1967; RIEPPEL and GRONOWSKI, 1981) and in the Ichthyopterygia (MAZIN, 1982; TARSITANO, 1982, 1983), even though the latter conclusion can be discussed (MAISCH, 1997), led to consider these two groups as highly derived diapsid reptiles (STORRS, 1991; RIEPPEL, 1993). Among the subclass Diapsida, they are included in the infraclass Lepidosauromorpha and, according to recent phylogenetic studies (BENTON, 1985; STORRS, 1991; RIEPPEL, 1993, 1998), their actual systematic position would be the following:

Infraclass Lepidosauromorpha
 Division Euryapsida
 Superorder Sauropterygia
 Order Placodontia
 Order Pachypleurosauria
 Order Nothosauria
 Order Plesiosauria
 Division Ichthyopterygia

This systematic hierarchy is adopted in the present article. It actually bears three main taxonomic consequences:

1. The Sauropterygia now include the placodonts, once considered as an independent clade.
2. The pachypleurosaurs, once considered as Nothosauria are now excluded from this group and represent the sister-group of the Nothosauria.
3. The ichthyosaurs are now excluded from the Euryapsida and form a distinct division, the affinities of which among the Lepidosauromorpha remain obscure.

Placodontia

The history of the Placodonts was brief and marked by a number of original adaptations to life in water. This order includes four families (Placodontidae, Cyamodontidae, Placochelyidae, and Henodontidae) and 20 species forming a dozen genera, distributed in time from the top of the Early Triassic to the end of the Late Triassic (–240 to –205 Ma). Placodont fossils are found in the Germanic and west Tethyan realms of western and central Europe, the Middle East, and northern Africa, exclusively. Two very distinct morphological patterns are described among them: a placodontoid type, with the so-called “non armoured” placodonts, was characterised by a moderate development of osteoderm shields; conversely, the cyamodontoid type (armoured, or turtle-like placodonts) displayed numerous osteoderms forming a carapace (Fig. 4). The gastralia constituted a robust ventral shield. Placodont teeth were set in shallow sockets (the thecodont condition), and their peculiarities are typical of the order (Fig. 4C,E). Maxillary and palatine teeth, together with their mandibular antagonists, had very low crowns, a crushing morphology, and rounded or flat occlusal surfaces covered by a thick layer of enamel. Front teeth (on the premaxillae and the mandible), when present, could be “incisor-like” and organised as a rake (in e.g. *Placodus*), or very reduced. Placodont skull was extremely bulky, and had a single pair of temporal openings in upper position, that have been secondarily closed in some taxa (e.g. *Henodus*). The vertebrae were amphicoelous, with a narrow, but high, neural canal, and very large transverse apophyses. Neural spines were either long and robust (placodontoids) or, conversely, low or even absent. The latter feature is typical of the cyamodontoids, the spine of which was ankylosed on a large part of its length. Placodonts had rather unspecialised limbs, and these could be very weak in shielded forms (Fig. 4A,B,D). The tail was long, robust, slightly compressed in the placodontoids, but whip-like in shielded forms.

The presence of a massive skull, associated with crushing teeth, are indicative of a durophagous diet. This diet probably relied on molluscs and crustaceans living in shallow coastal waters (MAZIN and PINNA, 1993). Moreover, the weakness of the limbs, the absence of specialised propelling organs, the development of a heavy dermal shield in the cyamodontoids, and the local increase in skeletal

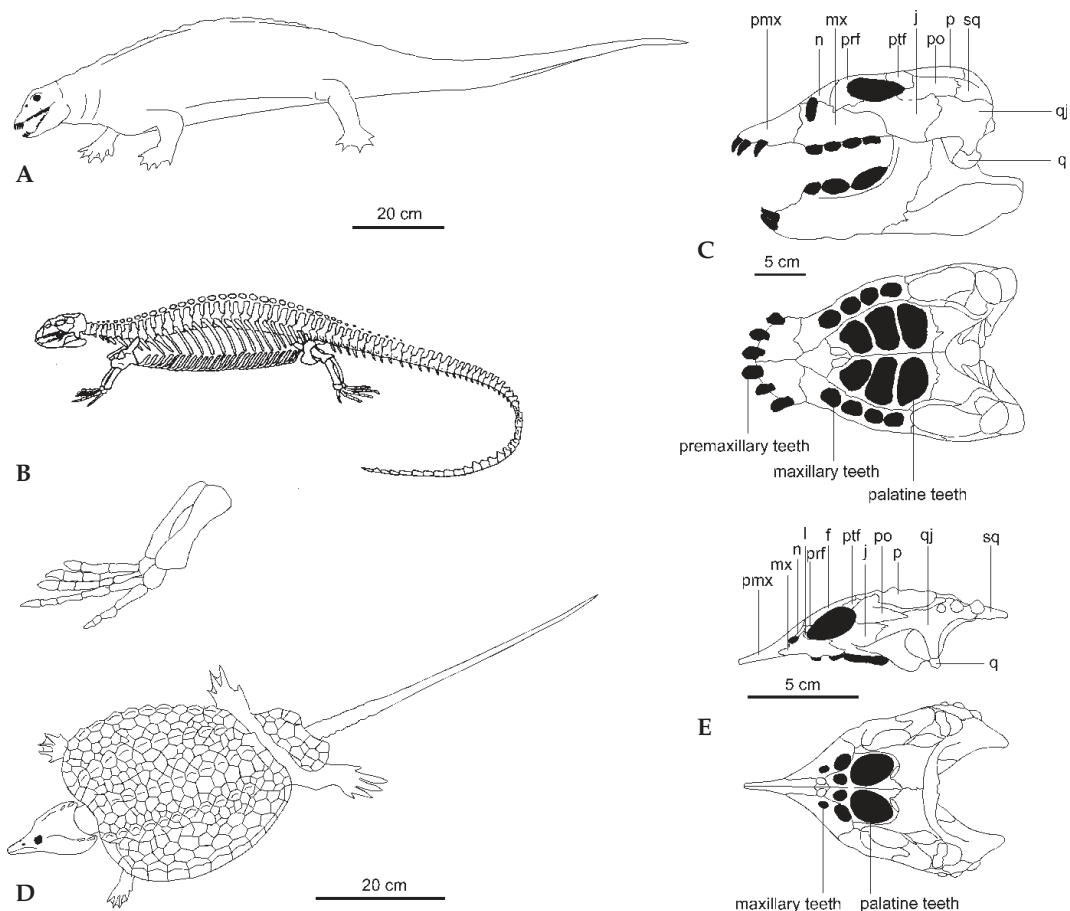


Fig. 4. Placodontia. **A**, *Placodus gigas* AGASSIZ 1833, Placodontoidea, Placodontidae, Early and Middle Triassic of Europe, life restoration. **B**, *Placodus gigas*, skeleton and left fore limb. **C**, *Placodus gigas*, skull in lateral and ventral views. **D**, *Psephoderma alpinum* MEYER 1858, Cyamodontoidea, Placochelyiidae, Late Triassic of western Europe, life restoration. **E**, *Psephoderma alpinum*, skull in lateral and ventral views. (B, after PEYER, 1950; C, after PEYER and KUHN-SCHNYDER, 1955; D, E, after PINNA and NOSOTTI, 1989).

mass by pachyostosis (BUFFRÉNIL and MAZIN, 1992), altogether suggest that these animals had poor locomotion capabilities in both water and land (MAZIN and PINNA, 1993).

It is noteworthy that a strange form, *Helveticosaurus*, from the Middle Triassic of Switzerland, has long been interpreted as a primitive, atypic placodont (PEYER and KUHN-SCHNYDER, 1955), and the absence of crushing teeth and dermal ossifications led to consider it as an *incertae sedis* among the placodonts (MAZIN and PINNA, 1993). For the present *Helveticosaurus* is regarded as an aquatic diapsid form, supposedly close to the placodonts, but with poorly understood phylogenetic relationships (RIEPEL, 1989a).

Pachypleurosauria

The pachypleurosaur (Fig. 5) were small (total body length: 0.2 to 1 m), slender reptiles with a lizard-like design. Their morphology was characterised by a small head, a relatively long neck, flipper-like limbs, a long tail, a loose attachment of the pectoral and pelvic girdles to the spine, and a certain

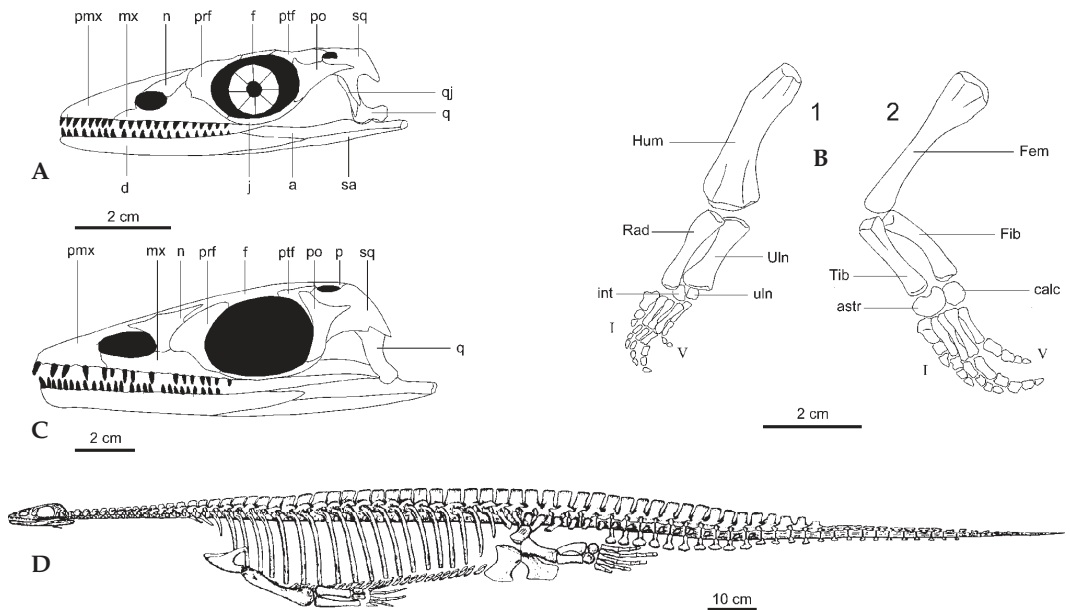


Fig. 5. Pachypleurosauria. A, *Serpianosaurus mirigiolensis* RIEPPEL 1989, Middle Triassic, Alpine Europe, skull. B, *Serpianosaurus mirigiolensis* RIEPPEL 1989, fore and hind limbs. C, *Neusticosaurus edwardsii* (Cornalia 1854), Middle Triassic, western Europe, skull. D, *Neusticosaurus edwardsii* (CORNALIA 1854), skeletal restoration. (A and B, after RIEPPEL, 1989b. C and D, after SANDER, 1989).

tendency to develop pachyostosis, at least in axial and appendicular regions (ZANGERL, 1935). All these features agree with an aquatic habitat. The skull of the pachypleurosaur was robust, though rather short, with small temporal openings and sharp, widely spaced teeth that were often procumbent at the front of the jaws (Fig. 5A,C). The pachypleurosaur is known by 13 species distributed in eight genera. They are commonly found in Middle Triassic layers from Europe and China (CARROLL and GASKIN, 1985; SANDER, 1989; RIEPPEL, 1989b).

In addition to the morphological characteristics quoted above, the fossils of these reptiles originate from marine deposits, a double series of evidence that lets no doubt on their effective adaptation to life in water. Moreover, the weakness of their skeletal girdles suggests that their ability to move on land was poor.

Nothosauria

The Triassic order Nothosauria, with some 32 species representing 17 genera unevenly adapted to marine conditions (Fig. 6), was particularly rich and diversified. Nothosaurian fossils are found from the end of the Early Triassic to the Late Triassic (–240 to –215 Ma) of central and western Europe, Asia, northern Africa, Middle East and North America. Specific sizes (snout-to-tail length) ranged from some tens centimetres to several metres. Nothosaurs classification has been deeply revised during last years, and this group should no longer be regarded as a monophyletic unit, but rather as an assemblage of several distinct clades within the superorder Sauropterygia.

The general body design of the nothosaurs was that of amphibious forms, adapted to swimming and foraging in water, but nevertheless still able to move on land for most of them. Their skull was generally long and widely fenestrated, and their neck, body and tail were stretched. However, the limbs, though ended by broad autopodials, were not transformed into true flippers. The jaws of the nothosaurs bore numerous thecodont teeth that were most often long and sharp.

The general morphology of the various nothosaurians, as also their supposed degree of aquatic

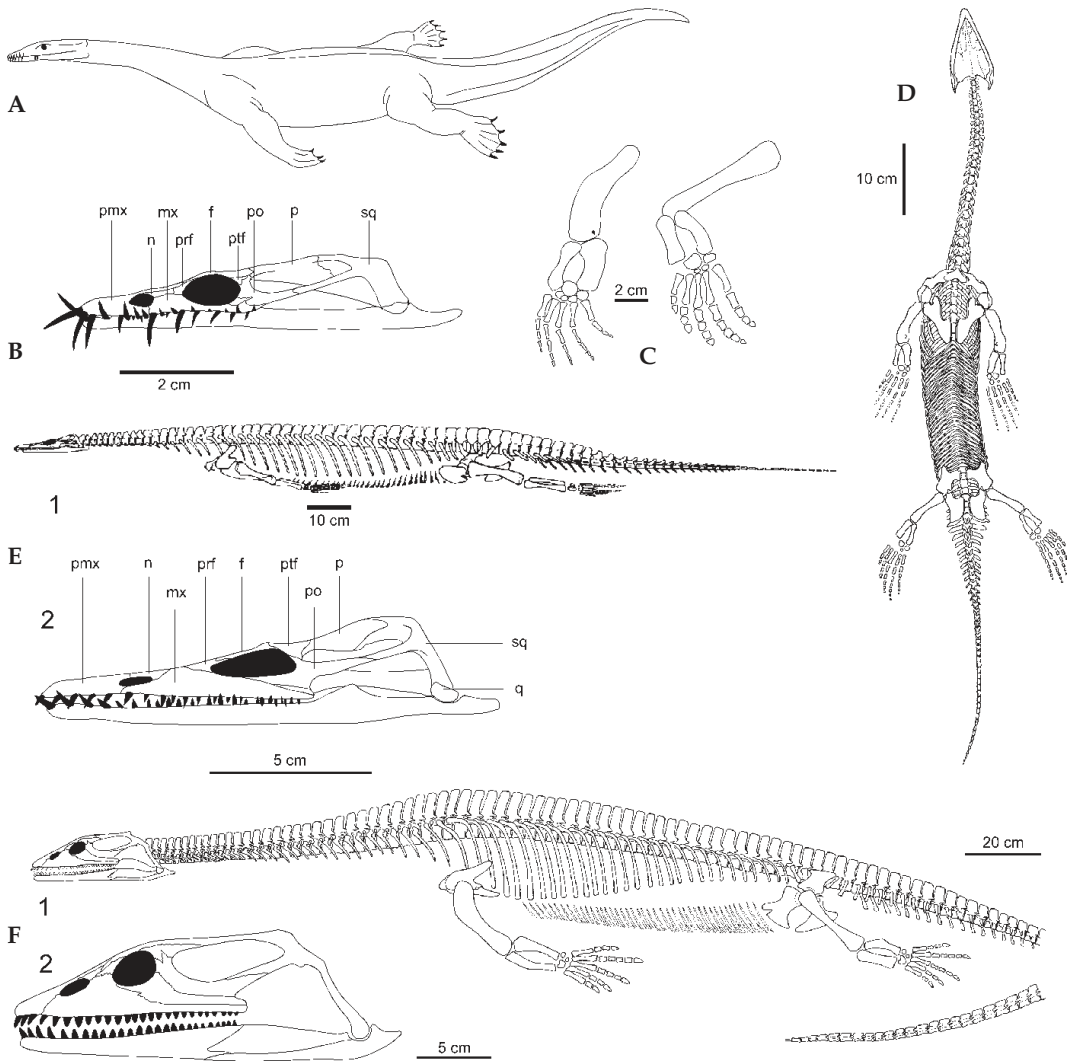


Fig. 6. Nothosauria. **A**, *Nothosaurus* MÜNSTER 1934, Early to Late Triassic of Europe, North Africa and Middle East, life restoration. **B**, *Lariosaurus balsami* CURIONI 1847, Middle Triassic of western Europe, skull. **C**, *Lariosaurus balsami* CURIONI 1847, left fore and hind limbs. **D**, *Ceresiosaurus calcagnii* PEYER 1931, Middle Triassic of western Europe, skeleton in ventral view. **E**, *Corosaurus alcovensis* CASE 1936, Middle Triassic of North America, 1, skeleton in lateral view, 2, skull. **F**, *Simosaurus gaillardoti* MEYER 1842, Middle Triassic of western Europe, 1, skeleton, 2, skull. (B, after MAZIN, 1985; D, after PEYER, 1931; E, after STORRS, 1991; F, after RIEPPEL, 1994).

adaptation, clearly differed among taxa (SCHMIDT, 1985). The family Nothosauridae is by far the most frequent in the fossil record, and was apparently the outstanding nothosaurian taxon during the Middle Triassic in Europe, northern Africa, Middle East and China. Some species of the genus *Nothosaurus* could be more than two metres long. The marine sediments in which they are found, together with their general morphology (long, laterally compressed tail, very mobile head, stretched jaws with sharp teeth and two pairs of lateral fangs), suggest that they were predators feeding in shallow, coastal waters. Other genera, such as *Lariosaurus*, a small nothosaurid from the Triassic of Europe (Fig. 6B,C), or *Ceresiosaurus* a form from the Middle Triassic of Europe with a long neck and

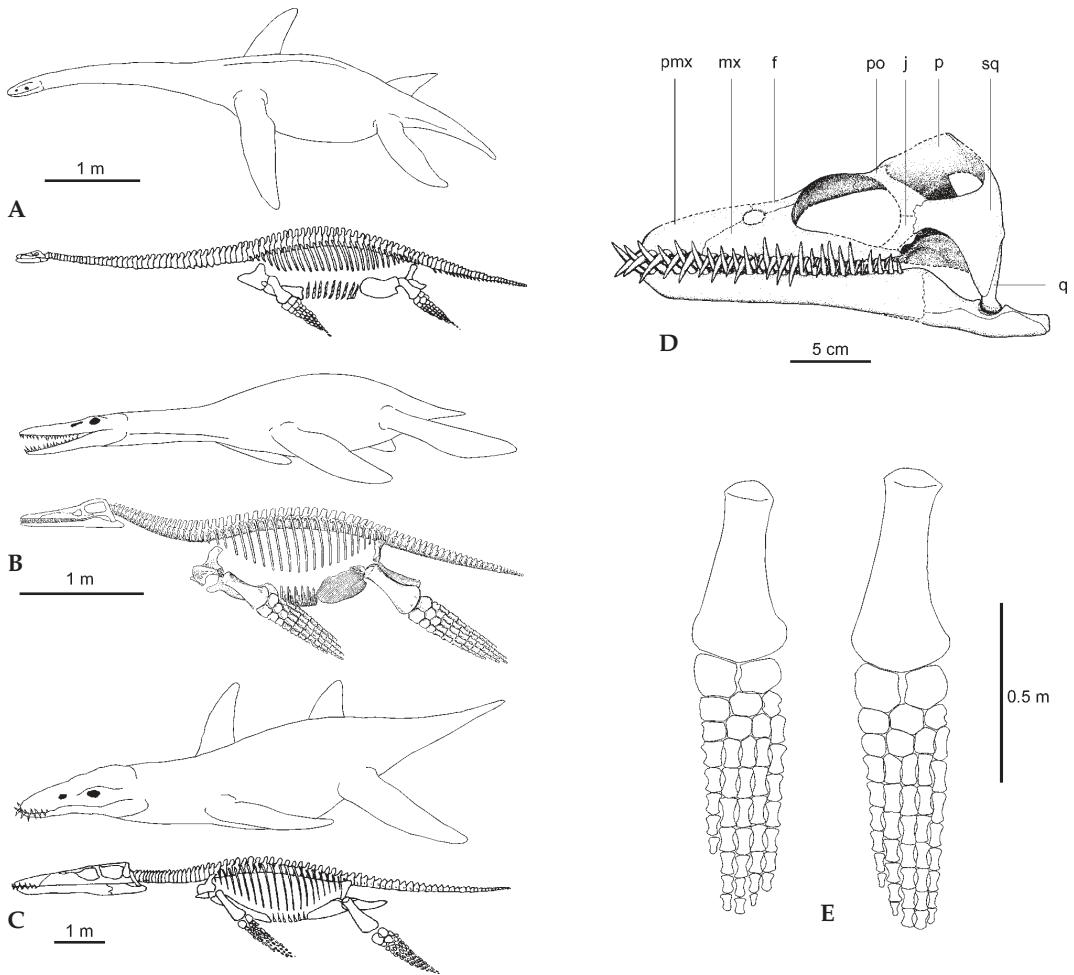


Fig. 7. Plesiosauria. **A**, *Muraenosaurus* SEELEY 1874, Elasmosauridae, Middle Jurassic of western Europe, life restoration and skeleton. **B**, *Peloneustes* LYDEKKER 1889, Pliosauridae, Middle Jurassic of western Europe, life restoration and skeleton. **C**, *Liopleurodon* SAUVAGE 1873, Middle-Late Jurassic of Europe and South America, life restoration and skeleton. **D**, *Cryptoclidus eurymerus* (PHILLIPS, 1871), Cryptoclididae, Middle Jurassic of western Europe, skull. **E**, *Peloneustes*, fore and hind limbs. (skeletons A and C, after ROBINSON, 1975; skeleton B and E, after ANDREWS 1913; D, after BROWN, 1981).

large autopodials (Fig. 6D), are supposed to have been much more aquatic than *Nothosaurus*. Other nothosaurian families are known, such as, for example, the Simosauridae (Middle and Late Triassic of Europe, northern Africa, Middle East and Asia), that were rather large animals with a long neck and low-crowned teeth (Fig. 6F); or the Corosauridae (Middle Triassic of North America) that displayed a long neck and a proportionately small head (Fig. 6E).

Plesiosauria

The plesiosaurs appeared during the Late Triassic, and are supposed to have been closely related to the Nothosauria. About 43 genera and 65 species are presently acknowledged. Plesiosaurs were medium to large-sized (up to 15 m) reptiles, characterised by a bulky body, a short tail, and paddle-