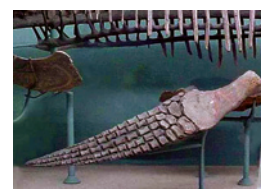


Fossils explained 54



Plesiosaurs

Plesiosaurs are an unusual and intriguing group of extinct aquatic reptiles (Fig. 1). They are sauropterygians, a group known from an array of semi-aquatic forms during the Triassic period: placodonts, pachypleurosaurs and nothosaurs. The first plesiosaurs are known from the very latest Triassic, but by the Early Jurassic plesiosaurs were cosmopolitan in distribution and lasted successfully to the latest Cretaceous, when they became victims of the K-T extinction event. Plesiosaurs were predominantly marine organisms, although their fossils are not uncommon in brackish or even fresh water deposits. We know that all plesiosaurs were carnivorous; many of them were top predators in their respective ecosystems. But with no living descendants (or analogues) plesiosaurs are mysterious fossil organisms—as we will see, many questions regarding their biology remain unanswered or contentious. However, plesiosaurs are currently undergoing renewed scientific attention.

Plesiosaur classification

The closest known relatives of plesiosaurs are the pistosaurids, a group of Middle Triassic (Anisian and Carnian) sauropterygians known from a number of genera around the world: *Pistosaurus* from Germany, *Augustasaurus* from the USA, *Bobosaurus* from Italy, and *Yunguisaurus* from China. The pistosaurids are plesiosaur-like in many aspects (and some classifications have considered them plesiosaurs), but they lack some of the adaptations seen in true plesiosaurs.

A clarification of plesiosaur terminology is given in Table 1. Strictly speaking the term 'plesiosaur' is reserved for the order Plesiosauria, but it is also popularly applied to the Plesiosauroidea, one of the two superfamilies recognized within Plesiosauria (One should be cautious not to confuse these names with the family Plesiosauridae or the genus *Plesiosaurus*).

Recent studies recognize four plesiosauroid families: Plesiosauridae (Fig. 2A), Cryptoclididae (Fig. 2B), Elasmosauridae (Fig. 3), and Polycotylidae (Fig. 4). The second major plesiosaur superfamily is the Pliosauroidae, often termed 'pliosaurs', of which three families are recognized, Rhomaleosauridae (Fig. 1), Pliosauridae (Fig. 2C) and Brachauchenidae (Fig. 5).

Morphotypes

Plesiosaurs may be divided into two general morphotypes, based on body shape. 'Pliosauromorphs' have a large head and a short neck—traditionally thought to be pliosaurs, while 'plesiosauromorphs' have a small head and long neck, and have been seen as plesiosauroids. This is in fact an oversimplification, and today, detailed analysis and investigations of plesiosaur anatomy suggest that these morphotypes actually evolved independently many times—such that there are short-necked plesiosauroids and long-necked pliosaurs. This confusing state of affairs is illustrated by the convergence of morphologies seen in the short-necked Family Polycotylidae. Historically, this group was classified as pliosaurs, yet recent analyses indicate that it may be an offshoot of the Plesiosauroidea, with their short necks acquired independently.

Despite this variation in the head and neck of plesiosaurs, the gross morphology of the rest of the body is widely considered to have been conservative throughout the evolution of the group, with all plesiosaurs having four flippers, a short body, and a short tail (Fig. 1). Plesiosaurs vary in size from 1.5 m (e.g., *Thalassiodracon* from the Lower Jurassic) to 15 m long giants (e.g., *Pliosaurus* from the Middle Jurassic). Iso-

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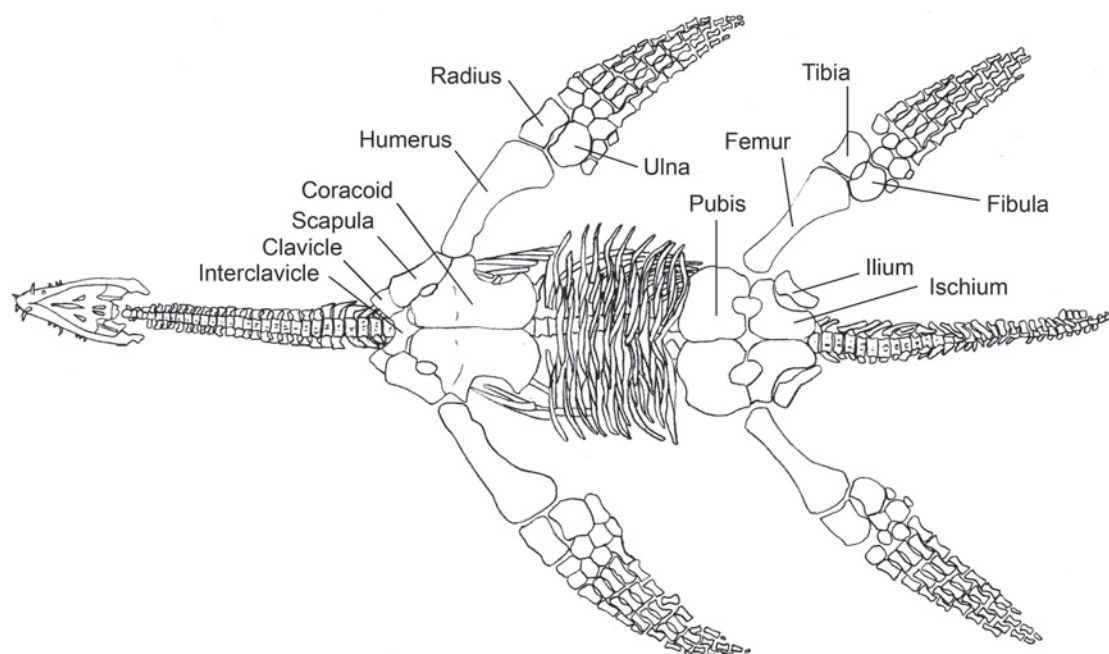


Fig. 1. The beautifully preserved skeleton of the plesiosaur *Rhomaleosaurus victor* seen in ventral view, from the Lower Jurassic (Toarcian) of Holzmaden, Germany (total length 3.44 m). Redrawn from Fraas (1910).

lated remains, including a 3-m long mandible indicate that these animals perhaps exceeded 17 m in length.

Skull

There is huge variation in the size and shape of plesiosaur skulls, but the general structure remains consistent (Fig. 2). They possess a single pair of large upper temporal fenestrae or openings at the rear of the skull, a condition known as euryapsid. A pineal foramen is situated between the temporal fenestrae: in life this would have contained a light-sensitive pineal organ. The external nostrils are small and positioned close to the large upward-facing orbits. The internal nostrils of the palate are situated near the front of the skull, and there is always a pair of openings at the rear of the palate, exposing the braincase. Additional openings on the palate may or may not be present. All plesiosaurs possessed pointed teeth, set in individual sockets; in life these were constantly replaced. However, there is plenty of variation in plesiosaur dentition. Whilst many species possess a uniform dentition of long and conical teeth with fine ridges running along the length of each tooth (Fig. 2A), there are also plesiosaurs with hundreds of tiny smooth pin-like teeth (Fig. 2B); and at the other extreme there are plesiosaurs with large robust coarsely ridged teeth (Fig. 2C).

Vertebral column

A pair of nutritive foramina (a pair of small holes) are

situated on the ventral surface of each vertebral centrum. This conspicuous character is one of the easiest to help identify isolated fossil plesiosaur vertebrae. In the cervical (neck) vertebrae the articulating surfaces range from slightly concave to flat. The main body (centrum) of each neck vertebra has facets for the cervical ribs, which are double faceted in early plesiosaurs, but reduced to a single rib facet in later forms.

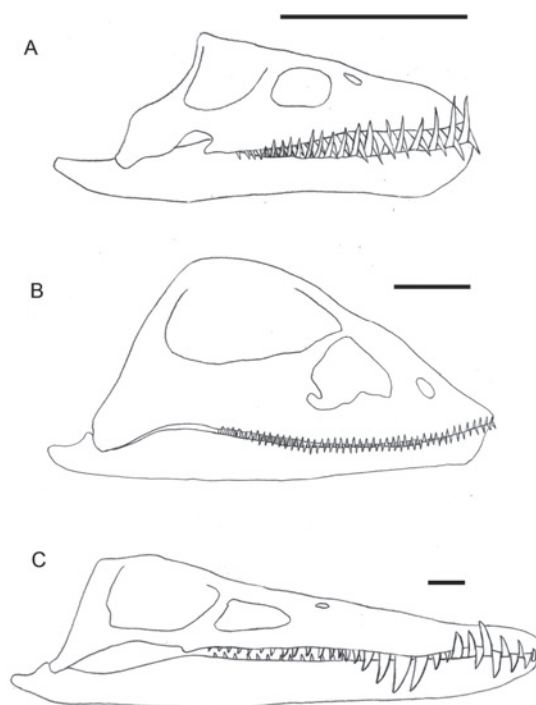


Fig. 2. Variation in plesiosaur skulls and dentitions. **A.** *Hydrorion brachypterygius*, a plesiosaurid from the Toarcian of Germany (Based on Brown, 1993). **B.** *Kaiiweheka katiki*, a cryptoclidid from the Maastrichtian of New Zealand (Redrawn from Cruickshank and Fordyce, 2002). **C.** *Liopleurodon ferox*, a plesiosaurid from the Callovian of Europe. Redrawn from Noë *et al.* (2003). Scale bar = 10 cm.

The cervical series merges into the dorsal (back) series through a transitional series of 'pectoral' vertebrae. During this transition the rib facets migrate from the centrum onto the neural arch above, where they become long processes in the dorsal vertebrae to support long ribs. From the dorsal series we pass through the sacral (pelvic) and caudal (tail) vertebrae, where the rib facets return to the centrum. The caudal vertebrae also bear facets for additional bones, chevrons, on their lower surfaces.

Girdles and gastralia

The pectoral and pelvic girdles of plesiosaurs are expanded ventrally into plates. The main elements in the pectoral (shoulder) girdle are the plate-like coracoids and scapulae—these form a facet to accommodate the forelimb. In the pelvic girdle the facet for the hindlimb is formed by the plate-like pubis and ischium bones, and a small rod-like ilium bone that attaches the pelvic girdle to the vertebral column. Bridging the wide gap between the pectoral and pelvic girdles is a mesh of gastralia (also called the 'ventral ribs', 'gastral basket' or 'plastron'). This structure consists of a central row of more-or-less symmetrical median ribs and a number of overlapping lateral ribs.

Limbs

Both the fore and hind limbs are developed into wing-like flippers, which closely resemble each other. The largest bones in the limbs are the humerus and femur, whereas most of the other limb bones are shortened, and the phalanges (finger bones) are elongate. An increase in the number of finger bones, known as hyperphalangy, occurred during the evolution of plesiosaurs, plus there are often additional bones in the limbs. All four limbs curve backwards slightly and taper to a sharp tip.

The mystery of the long neck

The long neck is an iconic feature of many plesiosaurs (Fig. 3). The cervical region attained great length in these forms via at least two evolutionary mechanisms. First, there is an increase in the number of vertebrae—the neck of *Elasmosaurus* from the Upper Cretaceous of the USA, for example, contains 72 cervical vertebrae, the largest number documented in any plesiosaur. Second, there is an increase in the length of individual vertebrae. The function of the long neck remains unresolved; that it was a successful adaptation is demonstrated by its duration throughout the long evolutionary history of the group. Contrary to suggestions by early workers who thought the long neck was flexible and acted like a 'harpoon', the flexibility

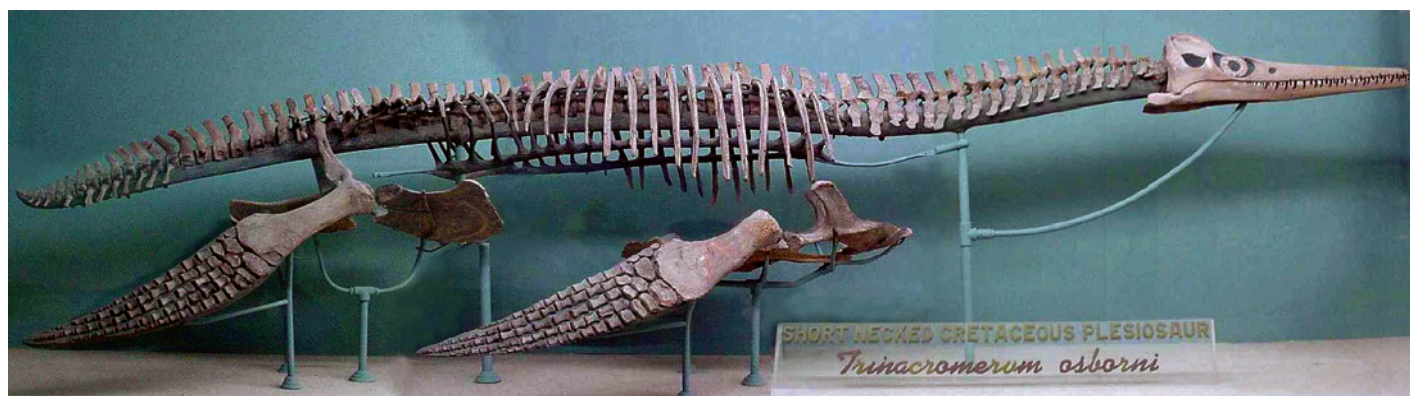


Fig. 3. Mounted skeleton of *Thalassomedon*, an elasmosaurid from the Cenomanian of the USA. (Photograph used with the kind courtesy of Mike Everhart)

of the plesiosaur neck was quite limited due to the close and rigid articulation between successive cervical vertebrae. Therefore the neck could not coil up or adopt a swan-like posture; instead, it possibly served as a mechanism for approaching prey—say a school of fish—without the large body of the plesiosaur being detected. It has also recently been suggested that the long neck may have been an adaptation for feeding on the sea bottom. In contrast to the long-necked forms, the vertebrae of short-necked taxa (pliosaurids, polycotylids) are short and their number decreased; the shortest neck belongs to *Brachauchenius* from the Upper Cretaceous of the USA, a pliosaur with only 13 cervical vertebrae.

Underwater olfaction

A specialized underwater olfactory system has been suggested as a common adaptation in the Plesiosauria. The internal nostrils—or choanae—are situated anteriorly on the palate and are sometimes associated with palatal grooves, which have been interpreted as adaptations to channel water into the internal nares. The flow of water through the nasal passage may have been maintained by hydrodynamic pressure over the retracted external nostrils during locomotion, and during its passage through the nasal ducts,



water would have been ‘tasted’ by olfactory epithelia. Under this scenario, the nostrils had no role in air intake; inhalation would have been accomplished via the mouth only. However, this long-standing model was recently challenged and an alternative interpretation of the palate was proposed, in which the openings at the rear of the palate are regarded as the internal nostrils. In this model, the openings traditionally regarded as choanae in plesiosaurs are re-identified as vacuities associated with salt excreting glands.

Gastroliths

Plesiosaurs are known to have intentionally swallowed stones—gastroliths are commonly preserved in the abdominal region. When present, these gastroliths are usually found in quite small numbers (sometimes just one or two) although concentrations of more than 600 are known for some elasmosaurid specimens. These stones may have been used for grinding food in the stomach or may have had a role in buoyancy control, offering a less physiologically expensive way of attaining negative buoyancy than pachyostosis (the production of thickened or dense bone). Although pachyostosis is rare amongst plesiosaurs, it is present in the ribs of the genus *Pachycostasaurus* from the Middle Jurassic of England, and in the ribs of *Kronosaurus boyacensis* from the Lower Cretaceous of Colombia. More recently a computational study of the effects of gastroliths in plesiosaurs showed that rather than influencing buoyancy, the presence of these stones would have increased stability and equilibrium of the body in water. Gastroliths may, of course, have had a dual or even multi-purpose in these animals.

Locomotion

The ventrally expanded plate-like pectoral and pelvic girdles, together with the closely packed and well-formed ‘gastral basket’ and tightly articulated spine provided a sturdy base for movement of the four hydrofoil-shaped flippers; these adaptations reflect a shift

from an axial to a paraxial lift-based locomotory repertoire. There was only one mobile joint in the plesiosaur limb (i.e. the glenoid/acetabulum) and the fifth digit is shifted proximally relative to the other digits, serving to reduce flexibility and maintain a stiff limb or ‘wingfin’. The precise function of these wingfins is uncertain; because plesiosaurs are extinct they cannot be subject to experimental hydrodynamic study. Plesiosaurs were once interpreted as rowers with their limbs functioning as oars, providing a strong backstroke coupled with a feathered recovery stroke. However, this model was subsequently discounted using a number of clear lines of evidence—particularly the construction of the glenoid and the acetabulum (the only moveable limb joints in plesiosaurs), and the ‘wing-like’, rather than ‘oar-like’, shape of the limbs.

Plesiosaur limbs are certainly efficient for flying, with tapered tips for reducing drag, the rowing model was therefore replaced with an ‘underwater flying’ scenario. An updated repertoire was later introduced, now known as ‘rowing flight’. In this model, plesiosaurs employed a modified form of flying combining principles of both rowing and flying, in which the downstroke provides both thrust and lift, and the feathered recovery stroke is more-or-less passive. Locomotion is still a poorly understood and actively researched area of plesiosaur palaeobiology.

Plesiosaurs are the only known vertebrate organisms possessing two pairs of fins with a function in propulsion—this raises the question of how these

Fig. 4. Mounted skeleton of *Dolichorhynchops osborni* (labeled as *Trinacromerum*), a polycotyloid from the Cenomanian of the USA (Photograph used with the kind courtesy of Mike Everhart).

Table 1. The taxonomy of the Plesiosauria, with colloquial terminology given in brackets

Plesiosauria [= plesiosaur]
Plesiosauroidea [= plesiosauroid]
Plesiosauridae [= plesiosaurid]
Cryptoclididae [= cryptoclidid]
Elasmosauridae [= elasmosaurid = ‘elasmosaur’]
Polycotyliidae [= polycotyloid]
Pliosauroida [= pliosauroid = ‘pliosaur’]
Rhomaesauridae [= rhomaesaurid = ‘rhomaesaur’]
Leptocleididae [= leptocleidid]
Pliosauridae [= pliosaurid]
Brachauchenidae [= brachaucheniid]

Fig. 5. Mounted skeleton of *Kronosaurus queenslandicus*, a brachaucheniid from the Albian of Australia. (Photograph used with the kind courtesy of Hector Rivera).



limbs moved relative to each other: the so-called 'four wing problem'. The pectoral and pelvic girdles of plesiosaurs are predominantly reinforced ventrally for muscle attachment to enable a very powerful downstroke but only a weak upstroke. It has been proposed that the fore and hind limbs alternated to compensate for the lack of thrust during the weak upstroke of one pair of limbs (i.e. the other pair would provide the thrust), hypothetically, this could provide efficient and constant forward motion. Some researchers regard the rear limbs as being of little or no use in a flying propulsive locomotion, instead being used only for steering and stability while others endorse a repertoire in which all four flippers move in synchrony. Recent research into the efficiency of these different models using robots, suggests that these repertoires may have been interchangeable and depended on the specific speed and manoeuvrability desired by the animal. Short bursts of speed would have been possible by combining the down stroke of both pairs of limbs simultaneously. Gait may have varied between taxa too, for example, pliosauromorph plesiosaurs have been interpreted as more rapid and manoeuvrable swimmers than other plesiosaurs.

The ability of plesiosaurs to move on land is another point of contention. The mechanics of their skeletons imply a completely aquatic existence: the limb girdles are only weakly connected to the axial skeleton and this would inhibit the transfer of force from limbstrokes into movement on land. However, small plesiosaurs may have been relatively unaffected by these constraints and might have used their pow-

erful limb downstrokes to propel themselves forward in short 'hops'.

Reproduction

A fully aquatic existence presents problems for egg-laying reptiles because they must make nests on land. Plesiosaurs, however, almost certainly overcame this problem by evolving viviparity, the ability to give live birth. Pregnant mothers and isolated embryos are known as fossils amongst basal sauropterygians (not-hosaurs and pachypleurosaurs) indicating viviparity in these taxa, so their close relatives, the plesiosaurs, were probably also viviparous. No fossil plesiosaur embryos have been described to empirically verify this behaviour, however, some undescribed plesiosaur material represents the first solid evidence for this conjecture.

Suggestions for further reading

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