Taxonomy, phylogeny and palaeoecology of the plesiosauroids (Sauropterygia, Reptilia) from the Posidonia shale (Toarcian, Lower Jurassic) of Holzmaden, south west Germany

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Contents

Die Plesiosauroiden aus dem Posidonienschiefer (Toarcium, Unterer Jura) von Holzmaden (Baden-Württemberg) wurden detailliert studiert, ihre taxionomische und phylogenetische Position analysiert und revidiert, und ihre Palökologie untersucht.

Dafür wurden 10 vollständige Skelette detailliert aufgenommen, vier beschriebene und sechs unbeschriebene. Unter den Stücken befinden sich die Holotypen der drei Arten *Plesiosaurus guilelmiimperatoris* Dames, 1895, *Plesiosaurus brachypterygiu*s v. Huene, 1923 und *Plesiopterys wildii* O'Keefe 2004, sowie ein weiteres beschriebenes Stück der Art *P. guilelmiimperatoris* (Fraas 1910). Anhand von morphologischen Merkmalen und einer statistischen Analyse wurden die unbeschriebenen Stücke, sofern möglich, vorhandenen Arten zugeordnet.

P. brachypterygius und *P. guilelmiimperatoris* unterscheiden sich deutlich von der Typus Art der Gattung *Plesiosaurus*, *P. dolichodeirus,* und auch untereinander, und beide Arten wurden eigenen Gattungen zugeordnet. Für *P. guilelmiimperatoris* wurde die Gattung *Seeleyosaurus* White, 1940 wieder belebt, während für *P. brachypterygius* die neue Gattung *Hydrorion* aufgestellt wurde. *Plesiopterys wildii* stellt ein jüngeres taxionomisches Synonym von *P. guilelmiimperatoris* dar.

Eine phylogenetische Analyse zeigte, daß beide deutschen Gattungen zu der Familie der Elasmosauriden gehören. *Seeleyosaurus guilelmiimperatoris* ähnelt stark der englischen Gattung *Muraenosaurus*, während *Hydrorion brachypterygius* mit den Gattungen *Microcleidus* und *Occitanosaurus* eine monophyletische Gruppe bildet, welche die Schwestergruppe der kretazischen Elasmosaurier ist.

Die Schädelmuskulatur beider Gattungen wurde rekonstruiert und analysiert. Dabei stellte sich heraus, daß *Hydrorion* höhere Beißkräfte ausüben konnte als *Seeleyosaurus*, letzterer konnte dagegen sein Maul schneller schließen. Der Vergleich der Flossen zeigte, daß *Hydrorion* ein sehr wendiger Schwimmer war, während *Seeleyosaurus* eher für ausdauerndes und schnelles Schwimmen angepaßt war. Diese Eigenschaften der beiden Gattungen wurden mit dem möglichen Beutespektrum aus dem Posidonienschiefer verglichen. Vermutlich spezialisierte sich *Hydrorion* auf den Schwarmfisch *Leptolepis*, während *Seeleyosaurus* eher Tintenfische jagte.

Der Vergleich von Plesiosauriern aus dem Lias von Europa zeigte, daß eine deutliche paläobiogeographische Zonierung auf Art- und Gattungsniveau bestand.

Abstract

The plesiosauroids from the Posidonia shale (Toarcian, Lower Jurassic) of Holzmaden (south west Germany) were examined in detail, their taxonomic and phylogenetic position was analysed and revised and their palaeoecology studied.

Ten complete specimens were studied, including the type specimens of *Plesiosaurus guilelmiimperatoris* Dames, 1895, *Plesiosaurus brachypterygius* v. Huene, 1923 and *Plesiopterys wildii* O'Keefe, 2004, as well as a described specimen of *P. guilelmiimperatoris* (Fraas 1910). Where possible, the six undescribed specimens were assigned to one of the existing species, on the basis of morphological characters and a statistical analysis.

P. brachypterygius and *P. guilelmiimperatoris* differ sufficiently from the type species of the genus *Plesiosaurus*, *Plesiosaurus dolichodeirus,* and from each other to be assigned to separate genera. The genus *Seeleyosaurus* White, 1940 was re-established for *P. guilelmiimperatoris*, and the new genus *Hydrorion* was introduced for *P. brachypterygius*. *Plesiopterys wildii* turned out to be a junior synonym of *P. guilelmiimperatoris*.

A phylogenetic analysis placed both German genera within the family Elasmosauridae. *Seeleyosaurus guilelmiimperatoris* resembles strongly the English genus *Muraenosaurus*. *Hydrorion brachypterygius* forms a monophyletic group with *Microcleidus* and *Occitanosaurus*, which is the sister taxon to the cretaceous elasmosaurs.

The cranial musculature of both German taxa was reconstructed and analysed. It could be shown that *Hydrorion* was able to exert higher biting forces than *Seeleyosaurus*, whereas the latter could close his jaws faster. A comparison of the flipper morphology indicated that *Hydrorion* was a highly manoeuvrable swimmer. In contrast to this, *Seeleyosaurus* was better adapted for stamina and speed. These qualities were compared to the possible prey from the Posidonia shale. *Hydrorion* probably specialised on the swarm-fish *Leptolepis*, whereas *Seeleyosaurus* is more likely to have caught coleoids (squid and cuttlefish).

The comparison of Liassic plesiosaurs from Europe showed that palaeobiogeographic zonation was present at species and genus level.

INTRODUCTION

Despite having been studied for 185 years, plesiosaurs remain an enigmatic group. With their four flipper-like limbs and their elongated neck, they have no modern analogue that would contribute to the understanding of their locomotion, diet and ecological preferences.

Plesiosaurs belong to the Sauropterygia, an extinct group of marine reptiles that lived from the Triassic until the end of the Cretaceous. The plesiosaurs, which appear in the uppermost Triassic (TAYLOR & CRUICKSHANK 1993a, STORRS 1994a, STORRS & TAYLOR 1996), are the most derived members of this group (Fig. 1.1), and show a high degree of adaptation to the marine environment. Their four limbs have the form of hydrofoil-shaped flippers, and are used for locomotion. The trunk and tail are relatively short and the neck is elongated. The plesiosaurs are divided into two groups: (1) the pliosauroids, with relatively short necks and large skulls (Fig. 1.2), and (2) the plesiosauroids, with small skulls and elongated necks (Fig. 1.3). In some Cretaceous members of the family Elasmosauridae the neck can be twice as long as the trunk.

All plesiosaurs were predators, feeding mainly on fish and cephalopods. Due to their small head, the prey of plesiosauroids was restricted to small forms. In contrast to this, pliosauroids also attacked

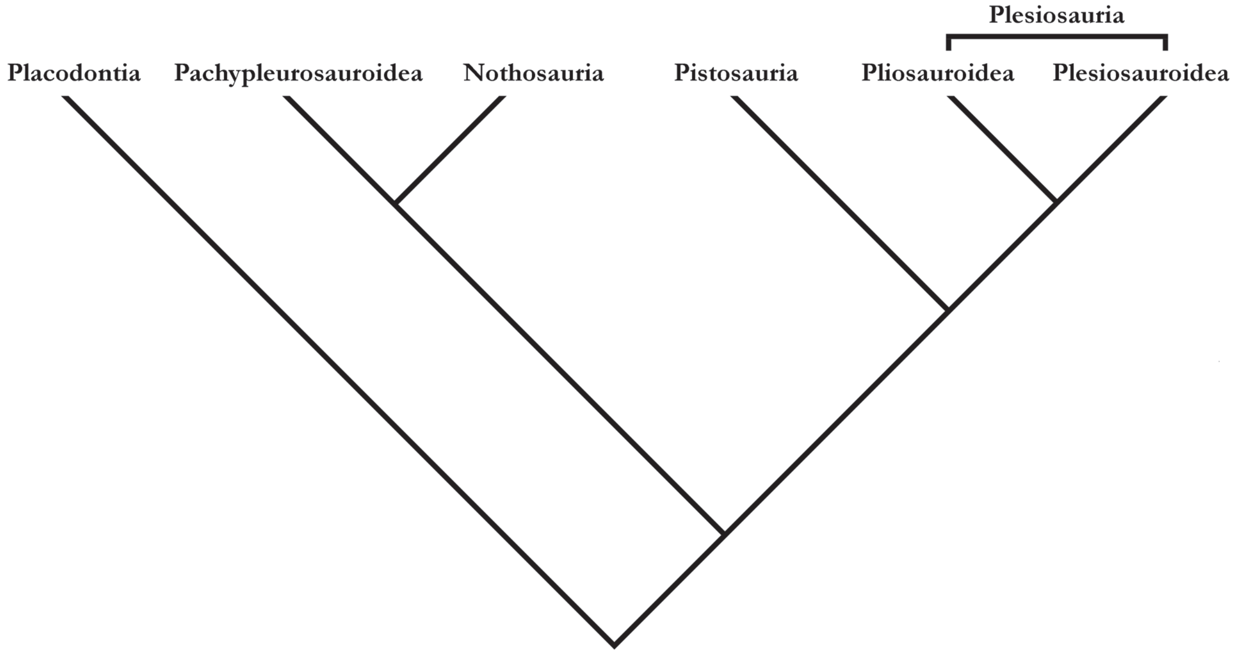


Fig. 1.1: Phylogeny of the Sauropterygia (modified after RIEPPEL 1999).

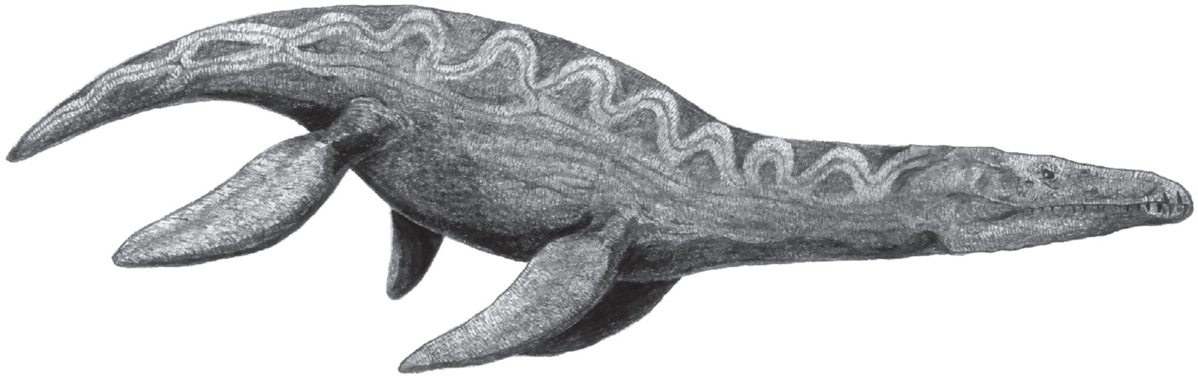


Fig. 1.2: *Liopleurodon ferox*, a typical pliosauroid from the Callovian (Lower Jurassic) of England. (Artwork courtesy of A. S. Smith.)

prey larger than themselves, including other marine reptiles. With their strong jaws and sharp teeth they were able to dismember their prey after the kill.

The four limbs were used for under-water flight, a method of locomotion used by turtles, penguins and otariids. The limbs have a cross-section similar to that of a bird wing or an aeroplane wing, and like these they work by creating lift by inducing differential velocities of the surrounding medium above and below the wing (Fig. 1.4). Tilting the wing produces a forward drag.

History of plesiosaur research

Plesiosaurs were amongst the first vertebrate fossils studied at the beginning of palaeontology. de la Beche & Conybeare (1821) described some vertebrae, naming them "*Plesiosaurus*". Descriptions of other, more complete specimens followed soon (Conybeare 1822 & 1824, Hawkins 1834 & 1840, Owen 1838), and plesiosaurs were also discovered in America (Harlan 1824 & 1825), Germany (v. Meyer 1841) and New Zealand (Hutton 1844). These early descriptions are still remarkable for their quality, both in the detailed descriptions and in the beautiful and highly accurate illustrations. Although much work has been done since then, concerning the taxonomy (for example: Welles 1952, Tarlo 1960, Brown, D. S. 1981 & 1983, Carpenter 1996 & 1999, Storrs 1997, O'Keefe 2001a, Kear 2003), phylogeny (for example: Bardet *et al.* 1999, O'Keefe 2001a & 2004, Gasparini *et al.* 2002), diet (for example: Massare 1987, Clarke & Etches 1991, Martill 1992, Taylor *et al.* 1993, Thulborn & Turner 1993, Geister 1998, Kanie 1998, Cicimurri & Everhart 2001, McHenry *et al.* 2005) and locomotion (for example: Robinson 1975 & 1977, Frey & Riess 1982, Tarsitano & Riess 1982, Godfrey 1984, Massare 1988 & 1994, Halstead 1989, Riess & Frey 1991, Lingham-Soliar

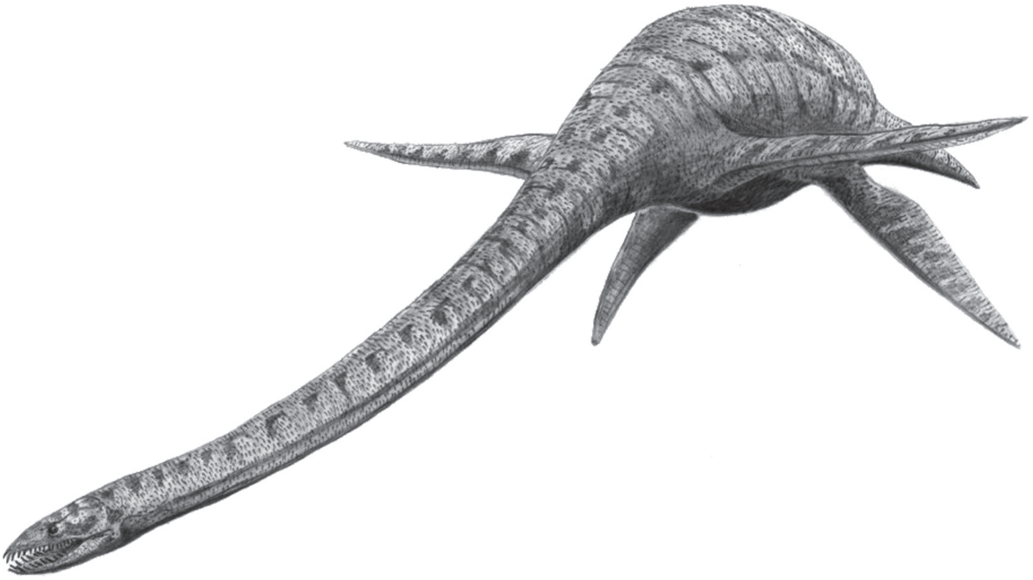


Fig. 2.3: Reconstruction of *Elasmosaurus platyurus* from the Campanian (Upper Cretaceous) of Kansas, USA. It is a member of the plesiosauroid family Elasmosauridae, whose members have very elongated necks. (Artwork courtesy of A. S. Smith.)

2000, Taylor 2000, Massare & Sperber 2001, O'Keefe 2001b, Motani 2002) of plesiosaurs, many questions remain unanswered.

The Posidonia shale

The Posidonia shale is known worldwide for its exceptionally well-preserved fossils. It represents the deposits of a shallow epicontinental sea, which covered most of Europe in the Lower Jurassic. Today its main outcrops in Germany are along the northern margin of the Swabian and Franconian Alb (Fig. 1.5), but it can also be found in the area around Braunschweig, northeast Lower Saxony. Posidonia shale or equivalent black shale sediments are also present in Luxembourg, Belgium, the Paris basin, and Yorkshire, England.

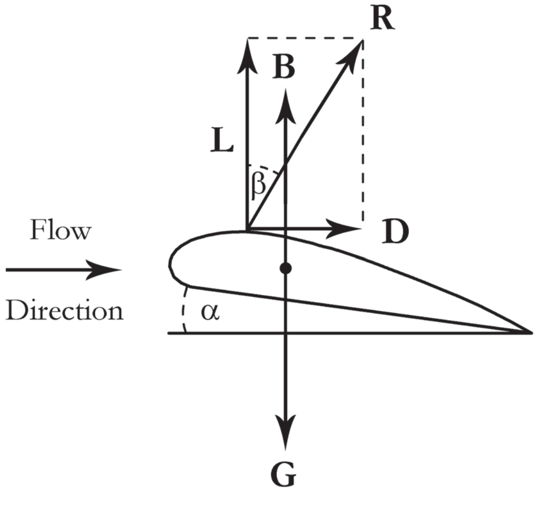


Fig. 1.4: Schematic illustration of the forces of drag, lift, buoyancy and gravity on a theoretical, neutrally buoyant hydrofoil for horizontal progression. Centres of buoyancy and gravity (indicated by dot) are equivalent in this example, but need not be in reality. B = buoyancy, D = drag, G = gravity, L = lift, R = resultant force, a = angle of attack, b = angle from vertical of resultant force vector (determined by lift/drag ratio) (after Storrs 1993).

In Germany, the foreland of the Swabian Alb and especially the area around Holzmaden, Bad Boll and Ohmden yield the largest number

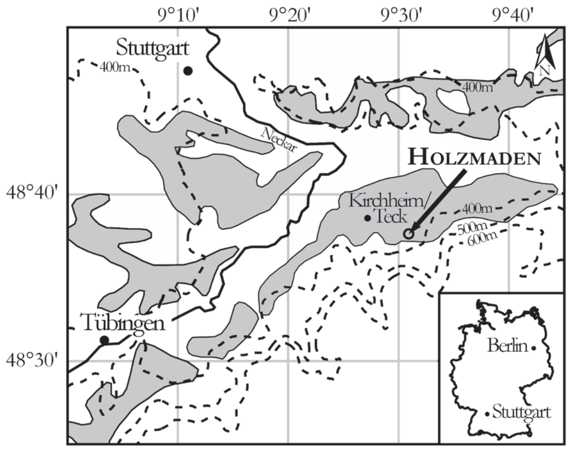


Fig. 1.5: Location map of Holzmaden and the outcrop of the Posidonia shale, indicated by the shaded areas. The 500 and 600 m contours mark the northern boundary of the Swabian Alb.

of the best-preserved fossils. The first fossils were found in the 16th century during the study of a thermal spring in Bad Boll. Early discoveries from the 18th century were often misinterpreted, especially extinct marine reptiles like ichthyosaurs. This changed with the beginning of modern palaeontology, and the exceptionally good preservation of the Posidonia shale fossils, including soft-part preservation and pregnant female ichthyosaurs, was recognised.

The systematic preparation of fossils from the Posidonia shale started around 1890. B. Hauff senior, son of an owner of several quarries in Holzmaden, was the first to prepare the preserved skin impressions around a complete ichthyosaur. His detailed study of the distribution of fossils in different layers (Hauff 1921) led the way to modern studies of the Posidonia shale.

Stratigraphically the Posidonia shale is placed into the Lower Toarcian (185 Ma) or Lias ε. Based on the lithological division of the sediment used by the quarry workers, Hauff (1921) erected a stratigraphy that is still in use today (Fig. 1.6).

Palaeoenvironmental models. Several models have been proposed to explain the exeptional preservation of fossils in the Posidonia shale. It is generally agreed that it results from anoxic conditions, but the cause for these conditions is still debated. The first model to be proposed was the "stagnant basin model", which favours long-term stagnant conditions due to restricted water circulation (Pompeckj 1901, Brockham 1944, Hallam & Bradshaw 1979, Seilacher 1980 & 1982, Küspert 1982 & 1983). Oxygen was absent in deeper waters, and therefore little or no benthos could exist. Life was restricted to nektonic, epibiontic, or pseudoplanktonic organisms. According to the model, no currents existed at the bottom. Only very rare occurrences, such as major storm events, were able to mix the water masses and allow for short periods with benthic life, causing bioturbation of the sediment. The contrasting "benthic island model" of Kauffmann (1978 & 1981) assumes a generally oxic condition of the water column with a redox boundary that fluctuated between a position a few centimetres below the sediment surface and a point slightly above it. Benthic life could exist during most of the time by using slightly elevated secondary substrates, like large ammonite shells, to evade the anoxic conditions in the sediment. The bivalve, crinoid and even arthropod taxa to which Seilacher (1980 & 1982) assigned an epibiontic or pseudoplanctonic lifestyle due to the hostile anoxic condition at the bottom have a normal benthic way of life in this model. Nearly constant bottom currents explain the aligning of dead shells and vertebrate skeletons.

The latest studies (Schmid-Röhl *et al.* 1997, Röhl *et al.* 2001, Schmid-Röhl *et al.* 2002) suggest that anoxic conditions prevailed during most of the deposition of the Posidonia shale. They were

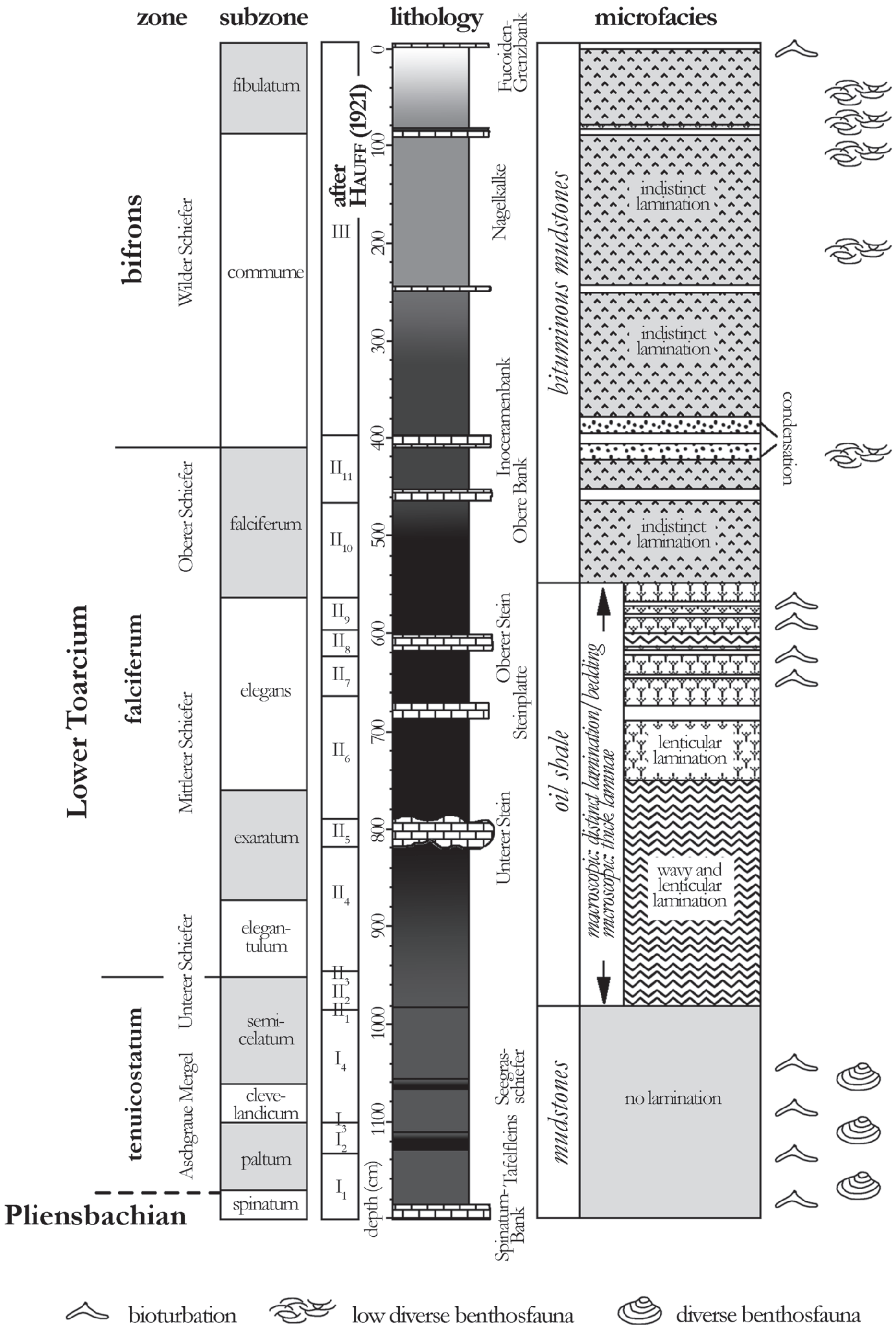


Fig. 1.6: Stratigraphy, lithology and microfacies of a Posidonia shale section from Dotternhausen (modified after Röhl *et al.* 2001). Darker shading in the lithology indicates higher amounts of total organic carbon.

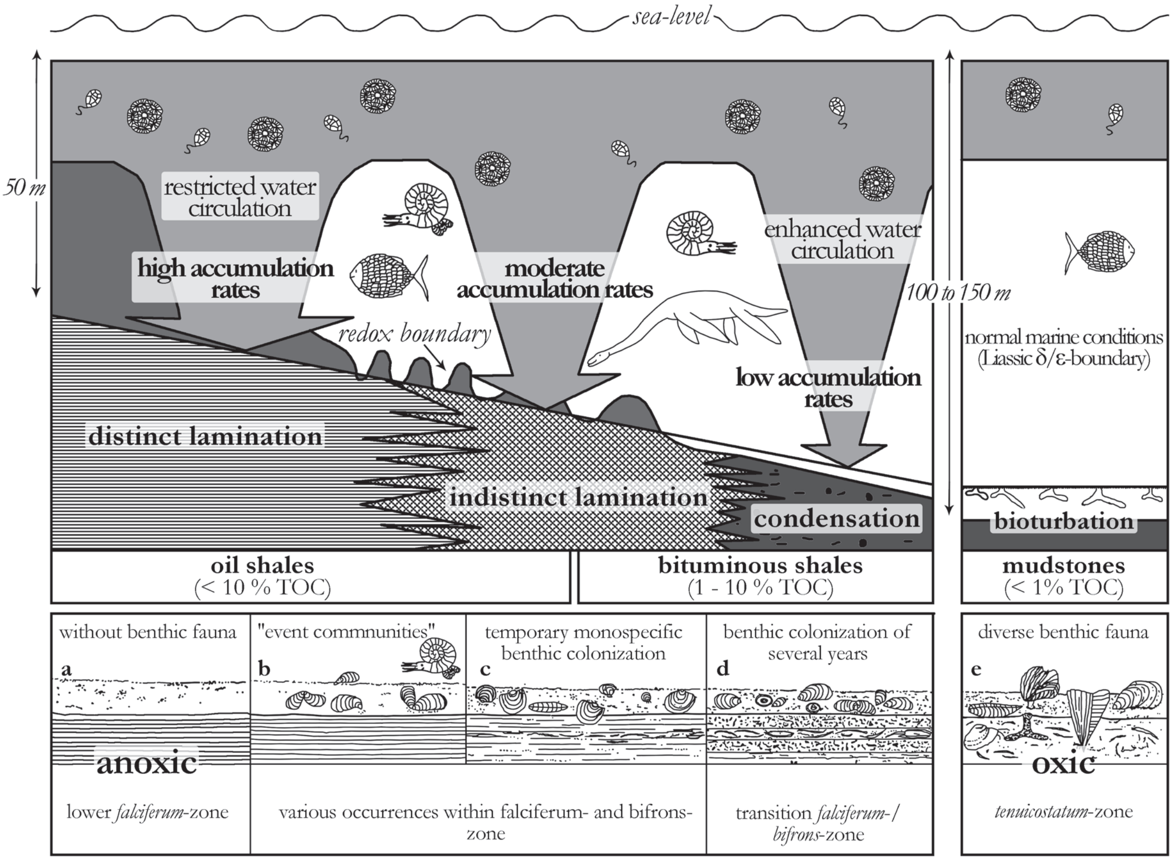


Fig. 1.7: Temporary sequence of facies zones during the Lower Toarcian related to water depth and redox conditions. Restricted water circulation during sea level low stand led to long-term anoxic conditions excluding benthic fauna. Distinctly laminated sediments with high organic carbon content were deposited (a). Anoxia was only interrupted by very short oxygenated periods indicated by event communities (b). Benthic colonisation of several years occured during high sea level with enhanced water circulation. Sediments are characterised by condensation and reduced total organic carbon (TOC) values (d). An intermediate position of sea level allowed temporary benthic colonisation and indistinc laminated sediments were deposited (c). Bioturbated mudstones with low organic carbon content and a diverse benthic fauna point to normal marine conditions during the *tenuicostatum*-zone (e). (After Röhl *et al.* 2001.)

caused by stratification of the water column, which in turn was controlled by sea-level changes and the climate. At times of relative low sea level stand, the stratification reached its maximum, and no benthic life existed. During intermediate sea level positions a seasonal reversal of a trade- and monsoon-wind circulation pattern caused seasonal fluctuations in surface water salinity, which enabled temporal colonisation of the bottom of the sea. Longer oxygenated periods during high sea level stand, which probably lasted several years to decades, even allowed a moderately diverse colonisation and bioturbation of the sediment. According to the amount of available oxygen, Röhl *et al.* (2001) distinguished several oxygen levels, ranging from "long-term anoxic" to "long-term oxic" (Fig. 1.7).

Hauff (1921) suggested a very fast covering of the fossils in addition to the anoxic conditions to enable the excellent preservation. Martill (1993) studied the taphonomy of ichthyosaurs from the Posidonia shale, and concluded that their preservation is mainly a factor of the consistency of the sediment. The softer the sediment, the faster and deeper a carcass can sink into it, and the better the preservation. According to Martill (1993), the best preserved, articulated fossils from the Posidonia shale were embedded in a soupy substrate, where the entire body could sink into the sediment. Harder substrates allowed only for a partial sinking of the carcasses, and any parts outside of the sediment were prone to decay. Additionally he claimed that such soupy substrates would act as a concentrating mechanism for articulated fossils. During times of low sedimentation, several carcasses can intrude into the sediment. The depth at which these bodies finally lie is correlated to their density and not to the time of arrival, and therefore later arrivals can sink to greater depths than early ones. During diagenesis the sediment is substantially compacted, and the carcasses are concentrated.

The high compaction of the soft sediment during diagenesis caused severe flattening of the majority of fossils. This makes study of specimens more difficult, as details are often lost, the form of the bones is altered, and overlying bones obscure those underneath. Some fossils are preserved in calcareous concretions, which protected them from compaction, and are preserved three-dimensionally. Preparation of fossils is normally undertaken from the lower side, since this is usually better preserved (Martill 1993). As most specimens remain partly in the original sediment, usually only one side of the specimen is available for study.

Palaeoecosystem. The fossil content of the Posidonia shale probably covers most of the former ecosystem. Wood and other terrestrial plants are often converted by the high diagnetic pressures into lignite, which obscures details and makes most specimens unidentifiable. Large logs, occasionally greater than 10 metres in length have been found, often associated with crinoids and bivalves, and are interpreted as driftwood.

Among invertebrates, ammonites are the most abundant forms, occurring throughout the Posidonia shale. The ammonites are usually flattened because their aragonitic shell was dissolved during diagenesis, and only the outer membrane, the periostracum, is preserved. Other cephalopods include belemnites, phragmotheutids and decapodiforms (squid and cuttlefish). Some species of bivalves like *Bositra buchi* and *Steinmannia bronni* (both formerly placed into the genus *Posidonia*) and *Pseudomytoloides* can be very common in certain layers. Gastropods and brachiopods are rare, as are crustaceans. Among echinoderms, crinoids are the most beautiful fossils from the Posidonia shale. Their colonies, sometimes attached to large driftwood, can be very large; the largest covers an area of 108 m^2. Apart from the crinoids, small echinoderms are known to occur in three layers. Only in the oldest layer they are preserved complete; in the other two only isolated spikes are found.

The vertebrates are mostly comprised of fish and marine reptiles. The fish – Chondrichthyes, Actinopterygia and Sarcopterygia – are diverse and, in some layers, common. About 90 per cent of them are ganoid fish (Jäger 1985), which are covered with a carapace of hard ganoid scales. Among the marine reptiles, the ichthyosaurs are best known. Due to the exceptional preservational qualities of the Posidonia shale, soft parts and body outlines were preserved, allowing accurate reconstructions. Since many ichthyosaurs were found with embryos in the body, a viviparous reproduction system is known definitively for this group. Several taxa of crocodiles that are well adapted for a marine life are also known from the Posidonia shale. Terrestrial reptiles are rare, but several pterosaurs are known, as well as one sphenodontid and the dinosaur *Ohmdenosaurus*.

The plesiosaurs from the Posidonia shale

Compared to the abundance of other marine vertebrates, few plesiosaurs have been found in the Posidonia shale. 12 complete specimens are known, five of which are on display and two more in the collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS), two in the galleries of the Naturkundemuseum Berlin (MB), two in the small Urweltmuseum Hauff (MH) in Holzmaden and one in the museum of the Institut für Geowissenschaften of the University of Tübingen (GPIT). In addition there are approximately 10 incomplete plesiosaur remains in the collection of the SMNS.

Quenstedt was the first to describe plesiosaur remains from the Posidonia shale, an articulated

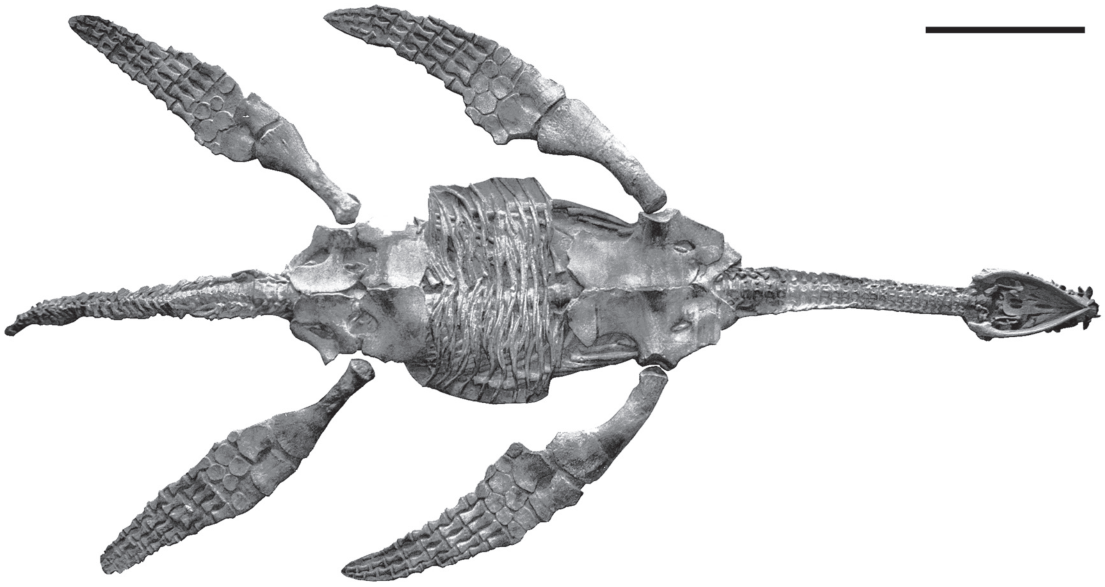


Fig. 1.8: Photograph of SMNS 12478, the type specimen of *Rhomaleosaurus* (*Thaumatosaurus*) *victor* (Fraas, 1910), as mounted in the SMNS (scale bar represents 500 mm).

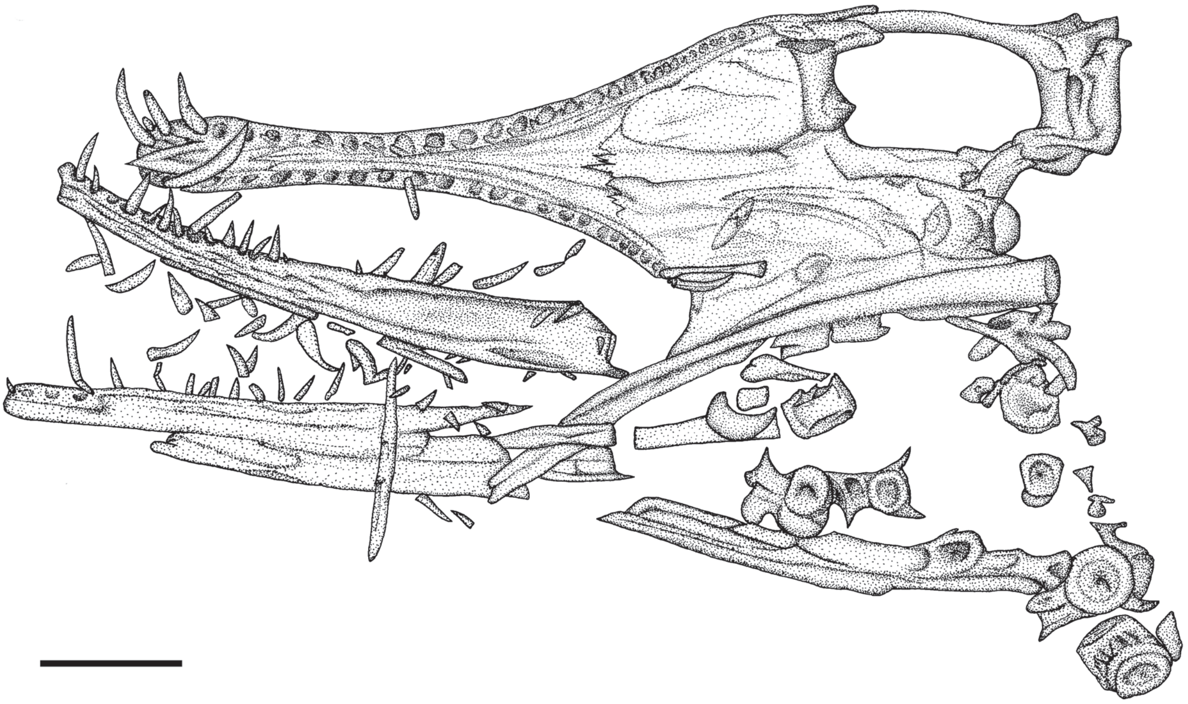


Fig. 1.9: Drawing of the skull of the type specimen of *Hauffiosaurus zanoni* O'Keefe, 2001 (MH Nr.9); scale bar represents 50 mm.

series of six vertebrae, which he named *Plesiosaurus suevicus* (Quenstedt 1858), and an incomplete hindlimb named *Plesiosaurus posidonia* (Quenstedt 1885). In his treatise on the plesiosaurs from the Liassic of south Germany, Dames (1895) described the first complete plesiosaur from the Posidonia shale. He named the new species *Plesiosaurus guilelmi imperatoris*, in honour of Kaiser Wilhelm II, German emperor of that time. Fraas (1910) presented another two complete specimens, of which he referred one to *P. guilelmi imperatoris*, and described the other as the new pliosauroid taxon *Thaumatosaurus victor* (Fig. 1.8). V. Huene (1923) described another complete specimen and named it *Plesiosaurus brachypterygius*. Despite new findings, little work had been carried out on the plesiosaurs from the Posidonia shale until 2000, when Maisch & Rücklin (2000) published a modern description of the skull of *P. brachypterygiu*s. Recently, two new taxa have been described: *Hauffiosaurus zanoni* (O'Keefe 2001a) (Fig. 1.9) and *Plesiopterys wildii* (O'Keefe 2004).

Storrs (1997) clarified the genus *Plesiosaurus*, and excluded nearly all species previously referred to this taxon. He suggested that the two German species *P. brachypterygius* and *P. guilelmiimperatoris* might belong to a single taxon, but he decided to postpone a definitive taxonomic decision until personal observation of the specimens could be made. However, despite these suggestions, no further work has been carried out.

A number of recent phylogenetic analyses (Bardet *et al.* 1999, O'Keefe 2001a & 2004) have included the German plesiosaurs, but in the case of *P. guilelmiimperatoris* and *P. brachypterygius* (Bardet *et al.* 1999, O'Keefe 2001a), character coding was based only on the original (Dames 1895, Fraas 1910, v. Huene 1923) descriptions.

Aims of the thesis

Since few modern works exist about the plesiosauroids of the Posidonia shale, one of the aims of this thesis is to close this research gap. This work is restricted to the plesiosauroids because a greater amount of material is available for study than for pliosauroids, of which only two are known. A larger sample size allows a better definition of the morphology of a species as it can give greater insight into intraspecific and ontogentic variation. It is acknowledged, however, that the pliosauroids from the Posidonia shale are as much in need of a taxonomic and phylogenetic revision as the plesiosauroids; the descriptions of both taxa, *Rhomaleosaurus victor* (Fraas, 1910) (Fig. 1.8) and *Hauffiosaurus zanoni* O'Keefe, 2001 (Fig. 1.9) suffer from being either quite old (Fraas 1910), or very short (O'Keefe 2001a). A detailed study of both species, clarifying their morphology and comparing them to English material, is desirable.

The principal aim of this work is to get a better understanding of the lifestyle of the plesiosauroids from the Posidonia shale, including differences between the coexistent taxa. For this, four successive steps were undertaken.

1) A revision of the taxonomy. All available plesiosauroid specimens are studied. Morphological differences of the cranium and postcranium are gathered, to determine species-specific characters (Chapter 2). A comparison of the material with other Liassic plesiosauroids helps to clarify existing taxa, find new ones if present and synonymise species if necessary (Chapter 3).
2) "The clarification of phylogeny is a necessary precursor to any understanding of functional evolution." (Storrs 1993, p. 65)

   The newly found morphological characters as well as previously published ones (Bardet *et al.* 1999, O'Keefe 2001a, Gasparini *et al.* 2002) are included in a phylogenetic analysis with all major Liassic taxa and representatives of the plesiosauroid families Plesiosauridae, Cryptoclididae and Elasmosauridae. This allows the referral of the German taxa to one of these families and clarification of their phylogenetic position, as well a better understanding of the early evolution and radiation of the plesiosauroids in general. (Chapter 4)

3) The functional analysis of the skull includes reconstructions of the cranial musculature of all determined species. The skull in reptiles serves mainly as a food-gathering organ, and is therefore well suited to deduce adaptations for diet and feeding from both cranial morphology and musculature.

   Since plesiosaurs use their four hydrofoil-shaped limbs for propulsion, a functional analysis of these highlights differences in the swimming style of the taxa from the Posidonia shale. The differences in feeding and swimming allow the assignation of a mode of predation to each taxon studied. (Chapter 5)

4) These different feeding strategies are then compared to the known fauna of the Posidonia shale to deduce possible prey. Further palaeoecological studies include the habitat and the distribution of the plesiosauroids within the Posidonia shale as well as a palaeobiogeographic analysis of all Lower Jurassic plesiosauroids. (Chapter 6)

Chapter 2

MATERIAL AND CLASSIFICATION

Introduction

As a first approach to the available material, all 10 plesiosauroid specimens from the Posidonia shale were studied in detail. Measurement of the total body length, length of skull, neck, trunk and tail, length and width of fore- and hind limbs, length of pro- and metapodials were taken (see appendix B) Every measurement was taken three times and the arithmetic average was calculated to enhance accuracy. Each specimen was photographed and a separate photograph of the skull and additional detailed pictures of the limbs or other body-parts if necessary were taken. Detailed drawings of each skull were made. Each specimen was described in detail from the specimens themselves, and distinguishing features (for example number of cervical, dorsal and sacral vertebrae, number of phalanges in fore- and hind limb, number and ornamentation of teeth, form of pectoral and pelvic girdles, form and ornamentation of the snout, ornamentation of teeth, etc.) listed.

Institutional abbreviations. BMNH (for specimen numbers) or NHM (for the institution), Natural History Museum, London, UK; GPIT, Institut für Geowissenschaften der Universität Tübingen, Tübingen, Germany; MB, Naturkundemuseum Berlin, Berlin, Germany; MH, Urweltmuseum Hauff, Holzmaden, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Description of specimens

SMNS 12039 (Lias εII4, Holzmaden). (Fig. 2.1)

Originally described as *Plesiosaurus guilelmi imperatoris* (Fraas 1910). White (1940) regarded it as belonging to the new genus and species *Seeleyosaurus holzmadensis*. Most of the specimen was destroyed during World War II, and only the skull and several fragments of the ribcage, the vertebral column and the limbs could be found in the ruins of the old museum. Nevertheless a cast of the complete specimen exists in the collections of the SMNS. Figured in Jäger (1985, fig. 17) as *Plesiosaurus guilelmi imperatoris*. Due to poor illumination and the quality of the cast, no photographs were taken. As the original postcranial is lost, only a brief description of it is given here. For more detailed information

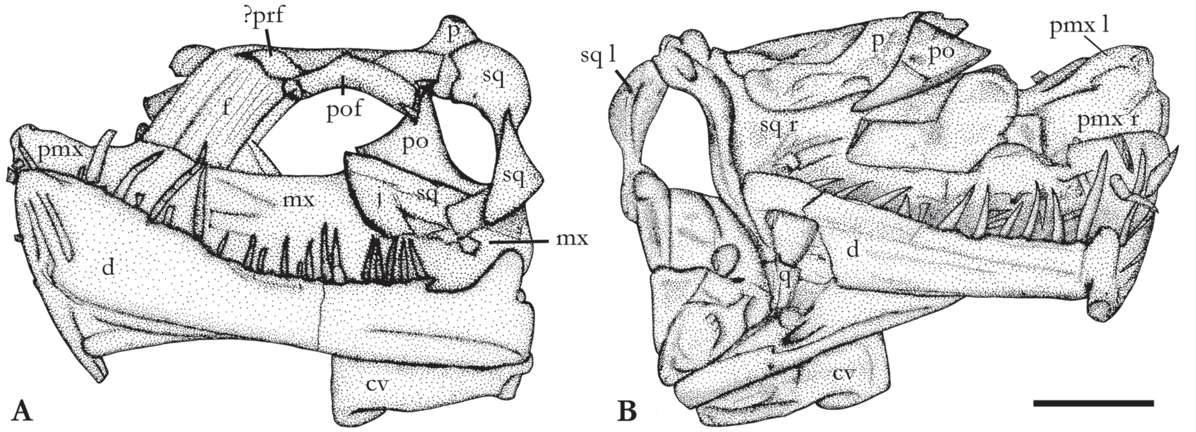


Fig. 2.1: SMNS 12039, the specimen of *Plesiosaurus guilelmiimperatoris* described by Fraas (1910). Drawing of the skull in (A) left lateral and (B) right lateral view (scale bar represents 50 mm); for abbreviations, see appendix A.

see Fraas (1910).

The specimen is complete, in right lateral view. During preparation the disarticulated left hind-limb, which originally lay under the anterior caudal vertebrae and facing the opposite direction to the right hind limb, had to be prepared completely, as the surrounding sediment was brittle. The bones were rearranged based on the bones of the right extremity, and the reconstructed limb was inserted into the sediment in its present position (Fraas 1910).

The three dimensionally prepared skull is nearly complete and articulated, but was severely compressed laterally and distorted during fossilisation. Both frontals are now lying on the left side of the skull (Fig. 2.1 A), whereas both premaxillae are on the right side (Fig. 2.1 B). The maxillae still show some small pits in its anterior portion. The position of the external nares cannot be determined. The nearly complete occiput is on the right side and between the posterior rami of the squamosals lie the exoccipital-opisthotic and the supraoccipitals, but the basioccipital is missing. The symphysis of the lower jaw is situated completely on the left side of the skull. The dentary is also covered with small pits, which are difficult to see due to the preservation of the bone. The posterior part of the lower jaw is only preserved on the right side, separated from the dentary. The jaw articulation is well visible, and the right quadrate is lying next to it.

The exact number of teeth cannot be given; 14 remain in the dentary on the left side, 15 on the right. The ventral margin of the premaxilla and maxilla is covered by the dentary on both sides. The teeth are slender, recurved and have fine striation only on the lingual side of the tooth crown. In the anterior part of the snout the teeth are distinctly larger.

The cervical vertebrae are slightly elongated and all vertebrae are amphicoelous. There are 35 cervical, four pectoral, 16 dorsal, two sacral and 43 caudal vertebrae preserved. Both pectoral and pelvic girdle are well exposed and complete from the right side, whereas the left side is partly hidden. In the pelvic girdle, the pubis and ischium meet along the midline, forming a pelvic bar. The forelimbs are incompletely preserved, with several phalanges missing. The slightly posteriorly curved humerus is laterally expanded at its posterior distal ending. A distinct foramen can be observed between the radius and ulna. There are four proximal and three distal carpals preserved.

The left hind limb is well and completely preserved, the right one was repositioned as noted above. The tibia and fibula are comparable in form to the radius and ulna, but slightly smaller. Four proximal and three distal tarsals exist. The maximum number of phalanges in the complete hind limb is 14 for the third digit.

SMNS 16812 (Lias εII4, Holzmaden). (Figs 2.2 – 2.4)

Described as *Plesiopterys wildii* by O'Keefe (2004). Figured in Urlichs *et al.* (1994, fig. 105) as ?*Microcleidus*.

This is a complete juvenile specimen, of which the body has been three dimensionally prepared and mounted for display (Fig. 2.2 A). The skull on display is a reconstruction, as the original is not completely three dimensionally prepared and stored in the collection.

The skull is complete but disarticulated and significantly dorsoventrally compressed. Most of the skull is embedded in a piece of sediment but visible from both sides. (Remark: The side of the slab exhibiting the dorsal side of the snout (Fig. 2.2 B, C) is here called the upper side, and the one displaying the palate (Fig. 2.2 D, E) the lower side. The original location of the skull in the sediment is unknown.) Several bones of the occiput and the posterior parts of the lower jaw are prepared three dimensionally (Fig. 2.3). The skull roof is separated from the ventral side of the skull and has been rotated by approximately 90° and is turned over, now displaying the ventral side of the braincase. This condition is indicated by the form of the suspensoria, which are concave on the upper side of the slab and slightly convex on the lower, as well as by the sutures of the parietal and squamosal. On the upper side the parietals continue until the posterior end of the skull, whereas on the lower side of the slab the squamosals form the posterior end of the skull, meeting in a median suture. This is usually seen on the dorsal side of the skull in plesiosaurs (Andrews 1910 & 1913, Storrs 1997).

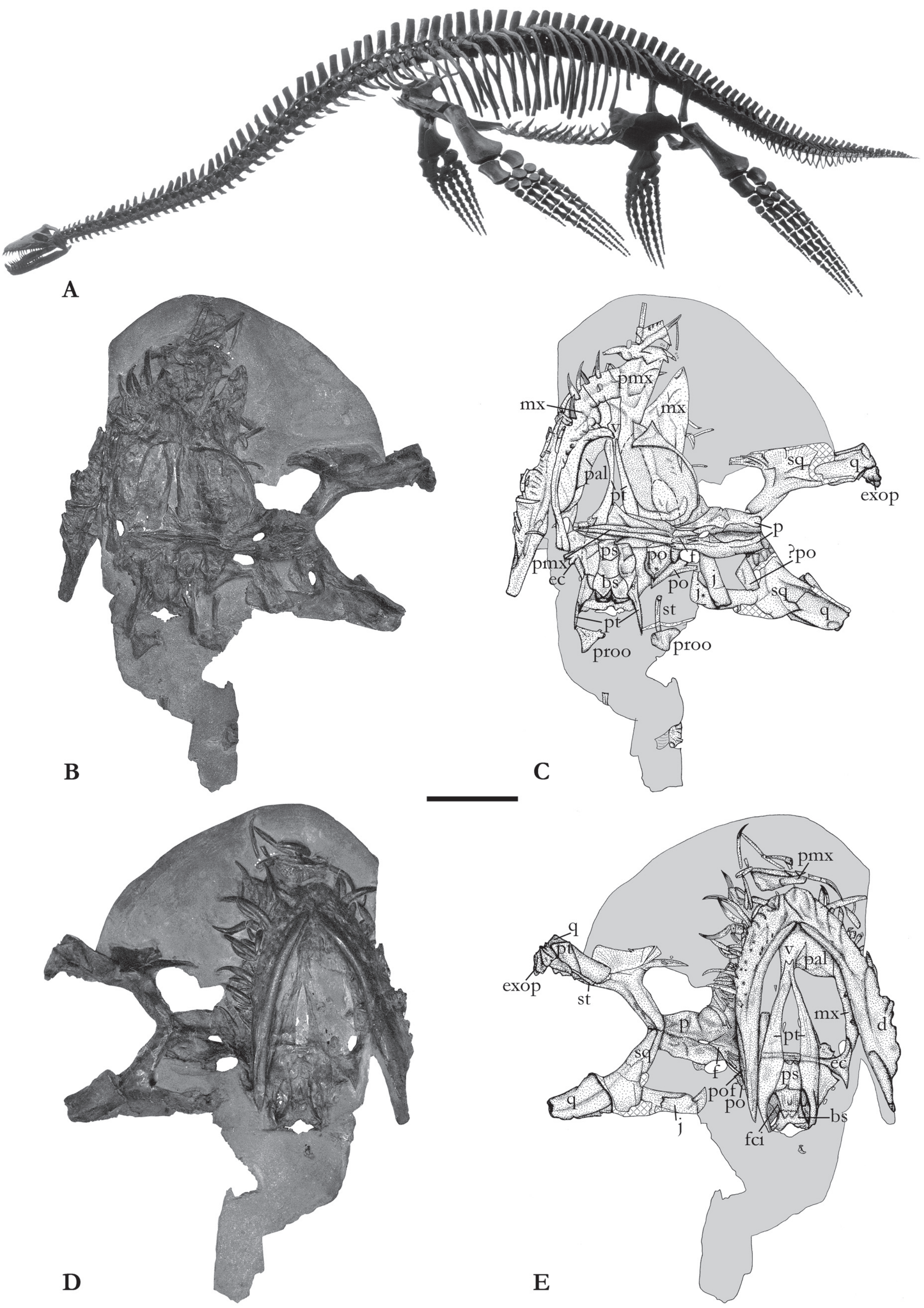


Fig. 2.2: SMNS 16812, the type specimen of *Plesiopterys wildii* O‘Keefe, 2004. (A) complete skeleton as on display in the SMNS, (B) photograph of the skull in dorsal view, (C) drawing of the skull in dorsal view, (D) photograph of the skull in ventral view and (E) drawing of the skull in ventral view (scale bar represents 50 mm); for abbrviations, see appendix A.

The snout of the specimen in dorsal view is distorted (Fig. 2.2 A, B). Both premaxillae and maxillae are visible, they are covered by small pits in the anterior part of the snout. Several teeth are still in their sockets or lying next to the skull. The teeth are slender and recurved. The have fine striations on the lingual side of the tooth crown only, the buccal side is smooth. The exact number of teeth can not be given, there were probably four or five teeth in the premaxilla and around twenty in the maxilla. Several distinctly enlarged teeth lie near the anterior part of the snout. The posterior process of the premaxilla is still attached to the dorsal skull roof and lying further posteriorly. The exact position of the external nares can therefore not be determined with certainty, although it can be assumed that they were only slightly anteriorly of the orbits, as in most plesiosauroids (Andrews 1910, Brown, D. S. 1981, Storrs 1997). Only the anterior and lateral borders of the orbits remain. The left prefrontal only is preserved, it is part of the detached and overturned skull roof and therefore visible in ventral view. The suture between premaxilla and frontal cannot be determined with certainty. The frontals form the anterior part of the parietal foramen. A triangular bone, most probably the right postfrontal, is still in contact with the frontal. The ventral side of the parietals shows some shallow depressions (Fig. 2.2 B, C), which might indicate cavities of the braincase. The dorsal sides of the parietals, squamosals, quadrates and the posterior part of the frontals are also visible on the lower side of the slab (Fig. 2.2 D, E). The squamosal-quadrate suture is difficult to detect, especially on the right side where this area was covered by filler during preparation. The right jugal is still in contact with the squamosal, their suture can be traced on the lower side of the slab. Several bones of the skull roof are lying disarticulated on the upper side of the slab: the left jugal, identifiable by the jugular foramen, covers part of the right jugal and extends from there to the lateral margins of the parietals. Another bone, partly covered by the postfrontal, is presumably the right postorbital in ventral view. A second roughly triangular bone situated in the angle formed by the dorsal and lateral rami of the squamosal and partly covering the latter might be the left postorbital.

Posterior of the detached skull roof the dorsal side of the palate is visible (Fig. 2.2 B, C). The quadrate rami of the pterygoids are visible, their posterior ends are missing. The basisphenoid still exhibits the *sella turcica*, which has been compressed during fossilisation. Anteriorly the dorsal side of the parasphenoid is partly visible. Basisphenoid and parasphenoid are bordered laterally by raised bones, either the pterygoids or epipterygoids. A small part of the right ectopterygoid is visible lateral of this raised area. Dorsally of the posterior endings of the pterygoids lie three disarticulated bones.

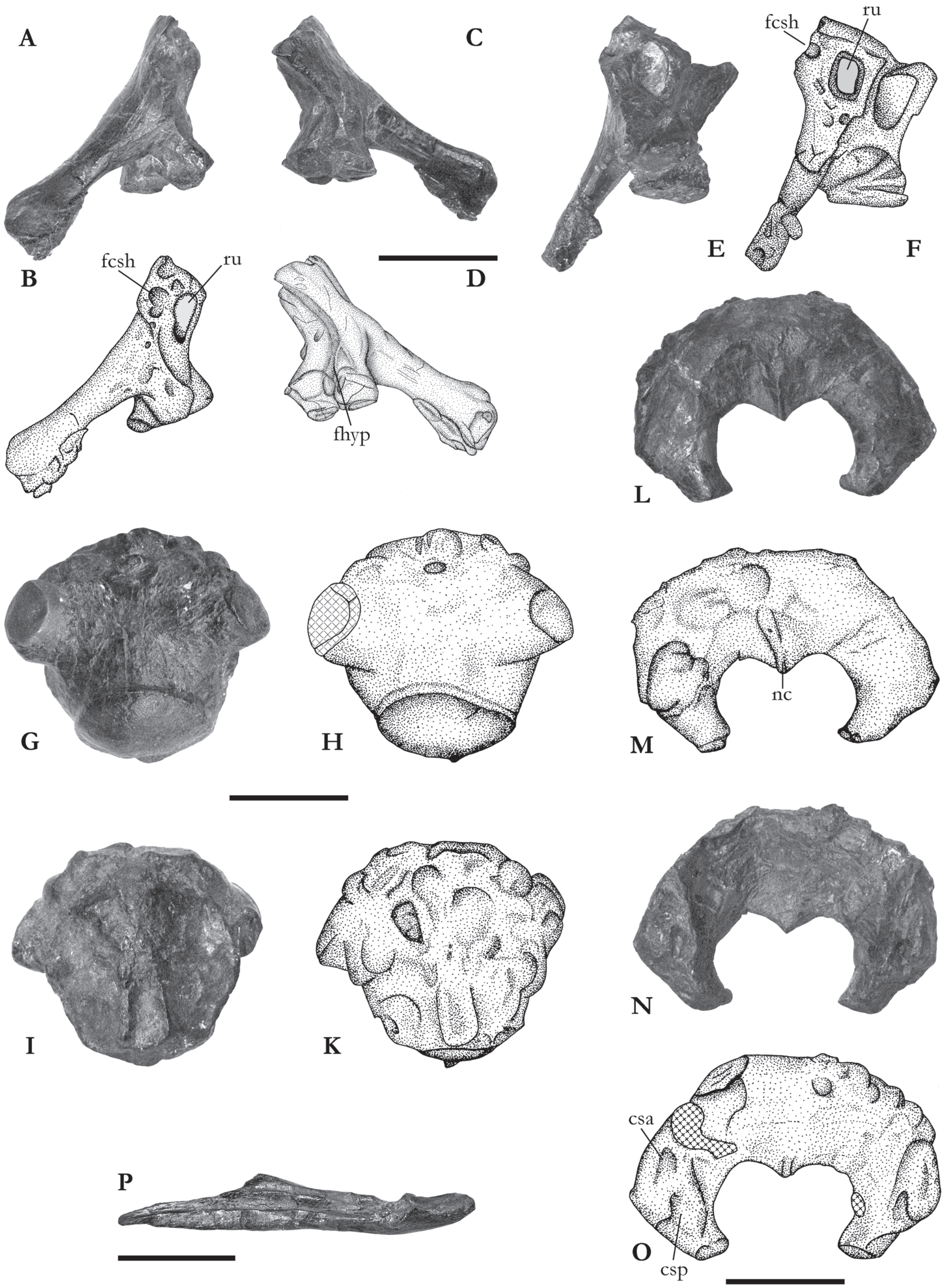


Fig. 2.3: SMNS 16812. Right exopisthotic, (A) photograph in anterior view, (B) drawing in anterior view, (C) photograph in posterior view, (D) drawing in posterior view, (E) photograph in medial view and (F) drawing in medial view (scale bar represents 10 mm); basioccipital, (G) photograph in ventral view, (H) drawing in ventral view, (I) photograph in dorsal view and (K) drawing in dorsal view (scale bar represents 10 mm); supraoccipital, (L) photograph in posterior view, (M) drawing in posterior view, (N) photograph in anterior view and (O) drawing in anterior view (scale bar represents 10 mm); (P) posterior portion of the right lower jaw in medial view (scale bar represents10 mm); for abbreviations, see appendix A.

One is rod like and slender and is most probably a stapes. The other two are the prootics, which are recognisable by their rounded triangular form with a small process. Both are only visible in lateral view.

On the lower side of the slab (Fig. 2.2 D, E) the left quadrate is partly covered by several disarticulated bones. These are the left exoccipital-opisthotic and presumably the ending of the quadrate ramus of the pterygoid and an incomplete stapes.

The ventral side of the skull (Fig. 2.2 D, E) shows the dentaries and parts of the palate. The dentary has a distinct rounded ventral margin and is covered by small pits in its anterior portion. Several teeth are still in their sockets or nearby. The dentaries cover most of the premaxillae and maxillae, and only the inner part of the palate is visible. The choana are also covered by the dentaries. The vomer-pterygoid suture is visible, but the vomer-palatine suture can only be traced along its posterior course. The palatines are mostly missing, except for a part in the left anterior portion of the palate, bordering the vomer and the maxilla, as well as in the right posterior part laterally of the pterygoids and the left posterior part, next to pterygoid and ectopterygoid. The pterygoids meet in an anterior median suture but are separated posteriorly by the anterior interpterygoid vacuity and the parasphenoid. They do not meet again posterior of the posterior interpterygoid vacuities. The rounded posterior border of the anterior interpterygoid vacuity is formed by the parasphenoid, which does not exhibit a cultriform process. The parasphenoid-basisphenoid suture is clearly visible in the posterior part of the palate, situated between the posterior interpterygoid vacuities. The left ectopterygoid is visible, where it contacts the maxilla.

Several of the occipital bones were completely prepared, they are all well preserved and only slightly deformed. They include the right exoccipital-opisthotic (Fig. 2.3 A – F), the basisphenoid (Fig. 2.3 G – H) and the supraoccipital (Fig. 2.3 L – O). The posterior parts of both rami of the lower jaw were also completely prepared (Fig. 2.3 P); unfortunately most of their sutures are not well visible. The splenials are apparently missing and the Mecklian canal is uncovered.

The number of cervical vertebrae includes the atlas and axis which have been reconstructed. There are 38 cervical, five pectoral, 19 dorsal, three sacral and 41 caudal vertebrae present. All vertebrae are amphicoelous and slightly constricted. The cervical vertebrae are all elongated, their length always exceeds their height.

The shoulder girdle is complete (Fig. 2.4 C, D), but the clavicular-interclavicular complex has been

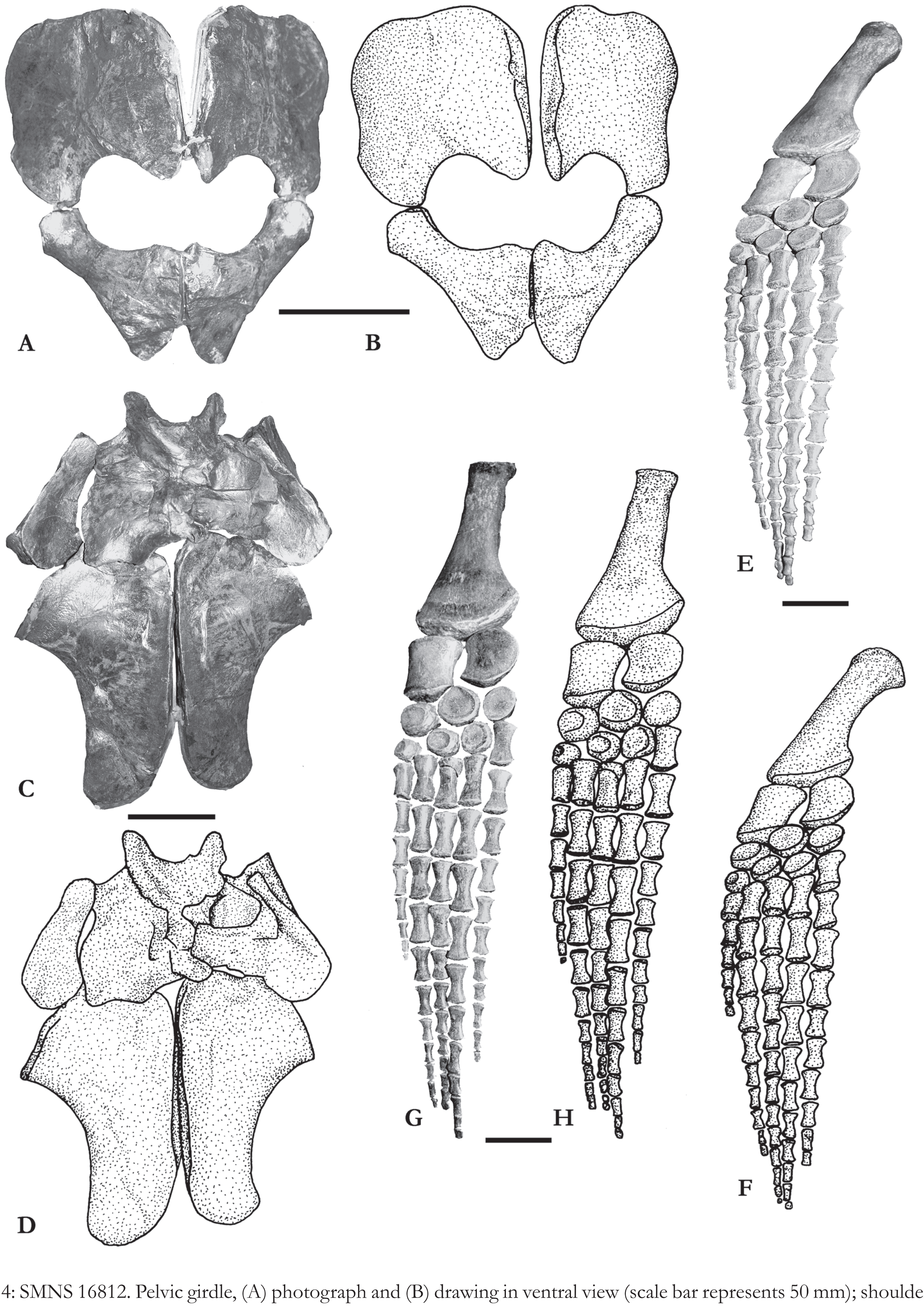


Fig. 2.4: SMNS 16812. Pelvic girdle, (A) photograph and (B) drawing in ventral view (scale bar represents 50 mm); shoulder girdle, (C) photograph and (D) drawing in ventral view (scale bar represents 50 mm); hindlimb, (E) photograph and (F) drawing (scale bar represents 50 mm); forelimb, (G) photograph and (H) drawing (scale bar represents 50 mm).

deformed, and few details are visible. Judging by the form of the coracoids a pectoral bar was absent.

The posterolateral corners of the coracoids are slightly expanded.

The pelvic girdle is complete and well preserved (Fig. 2.4 A, B). The corners of the pubes are rounded and the posteromedial corner is only slightly expanded, similar to the anteromedial corners of the ischia. A pelvic bar was therefore not present.

Both fore limbs are present and complete (Fig. 2.4 G, H). The anterior margin of the humerus is only very slightly convex. The distal end is expanded, especially the posterodistal corner. The facets for the radius and ulna are visible, but not well developed. The radius is of rod-like form and slightly constricted, the ulna is lunate, and they border a elongated oval *spatium interosseum*. There are three proximal and three distal carpals presents. The carpals are all rounded, especially distally, and have distinctly rugose corners which were probably covered by cartilage in life. Metacarpal V has an expanded posteromedial corner, the other metacarpals resemble the phalanges. The number of phalanges is most probably complete (see Table 3.2). All bones were mounted with only small gaps between them. Comparison with articulated juvenile specimens (SMNS 51945 and SMNS 51141) suggest that the actual size of the limbs, especially the length, was greater than reconstructed in the mounted specimen, as there is a large space between these bones in juvenile plesiosaurs. This also affects the measurements, which were directly taken from the mounted skeleton (see appendix B).

The hind limbs closely resemble the fore limbs in the arrangement, form and size of the bones (Fig. 2.4 E, F). The anterior margin of the femur is straight and its posterodistal corner is expanded. The facets for tibia and fibular are not well developed. Tibia and fibula themselves resemble radius and ulna, except they are slightly smaller. The three proximal and three distal tarsals are rounded and have broad rugose margins. The number of phalanges is most probably complete.

SMNS 51141 (Lias εII4, Holzmaden). (Fig. 2.5)

Figured in Urlichs *et al.* (1994, fig. 105) as ?*Microcleidus*.

A nearly complete juvenile specimen in dorsal view. The left lateral side of the complete skull is visible (Fig. 2.5 A, B), it is articulated except for the right maxilla, which is lying next to the skull. Most sutures are not well preserved so that few details are observable. The premaxilla shows weak ornamentation on the anterior end. Part of the mandible can be seen through the left orbit. The occiput is completely obscured.

The lower jaw is disarticulated and dislocated, and the individual bones are lying next to the skull. The dentaries are still connected at the symphysis. A definite identification of the individual bones is

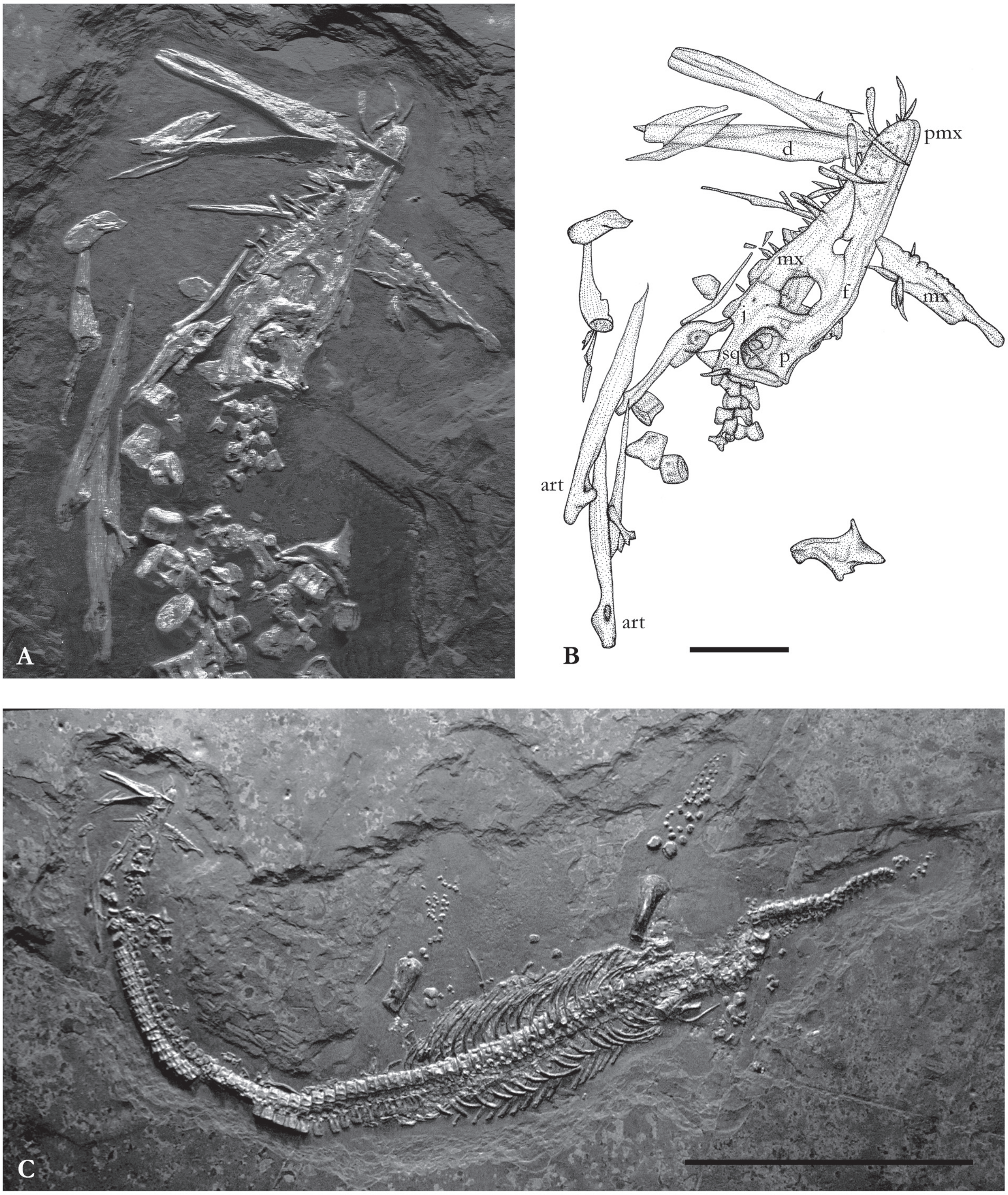


Fig. 2.5: SMNS 51141. Photograph (A) and drawing (B) of the skull (scale bar represents 50 mm); (C) photograph of the specimen (scale bar represents 500 mm); for abbreviations, see appendix A.

not possible, however, the remaining bones are of elongated, rod-like form and probably represent the splenials. The number of premaxillary teeth is unclear, presumably five were present. Fifteen teeth are preserved in the maxilla. In the anterior part of the skull several teeth are distinctly enlarged. The teeth are slightly recurved and show no, or only very faint, striations.

There are 29 cervical, three pectoral, 20 dorsal, two to three sacral and approximately 36 caudal vertebrae present, which are all amphicoelous. Both the pectoral and the pelvic girdle are obscured by the overlying body, and few details can be seen (Fig. 2.5 C). From the pectoral girdle only the dorsal portion of the scapula and the median suture of the coracoids is visible, but the general shape of the girdle cannot be determined.

The limbs clearly show the juvenile status of the specimen, as most bones are only poorly developed (Fig. 2.5 C) Only the right forelimb is present, but the left probably lies beneath the body. The right humerus is rod-like in form and only slightly expanded on its postero-distal corner. All remaining bones of the limb are rounded and distinguishable only by their size and relative position. Both radius and ulna are in situ as well as three carpals, but the metacarpals and phalanges are dislocated.

Only the femur, tibia, fibula and tarsals and phalanges of the right hind limb remain, all dislocated. The femur is lying beneath the sacrum and anterior caudal vertebrae. The left hind limb is better preserved and the bones remain near their original positions. All bones except the femur are rounded, and five tarsals are present.

SMNS 51143 (Lias εII4, Ohmden near Holzmaden). (Fig. 2.6)

Figured in Urlichs *et al.* (1994, fig. 104) as ?*Microcleidus*.

A nearly complete adult specimen exposed in ventral view. The skull is disarticulated and dislocated (Fig. 2.6 A, B). Both dentaries are present but separated at the symphysis. Their anterior portion is covered with elongated grooves and ridges. The posterior bones of the lower jaw appear to be missing. Few bones of the skull can be determined. The incomplete remnant of the premaxilla, which exhibits four alveoli, is covered with elongated furrows externally. The greater part of the right maxilla is present, but the posterior process and the dorsal margin are missing. Part of the posterior palate is still in articulation, it consists of the parasphenoid, the posterior portion of the pterygoids and parts of their quadrate process, and the basioccipital including the condyle. The basisphenoid is probably present, but not visible as it is covered by the pterygoids. The remaining bones of the skull cannot be identified with certainty.

The number of vertebrae in the pectoral and dorsal area is difficult to determine, as most of the vertebral column is covered by the pectoral and pelvic girdles and the gastral ribs (Fig 2.6 C). There are 33 cervical vertebrae preserved in ventral view, which probably include the atlas and axis. Four pectoral vertebrae can be recognised with certainty, one more may have been present. The number of

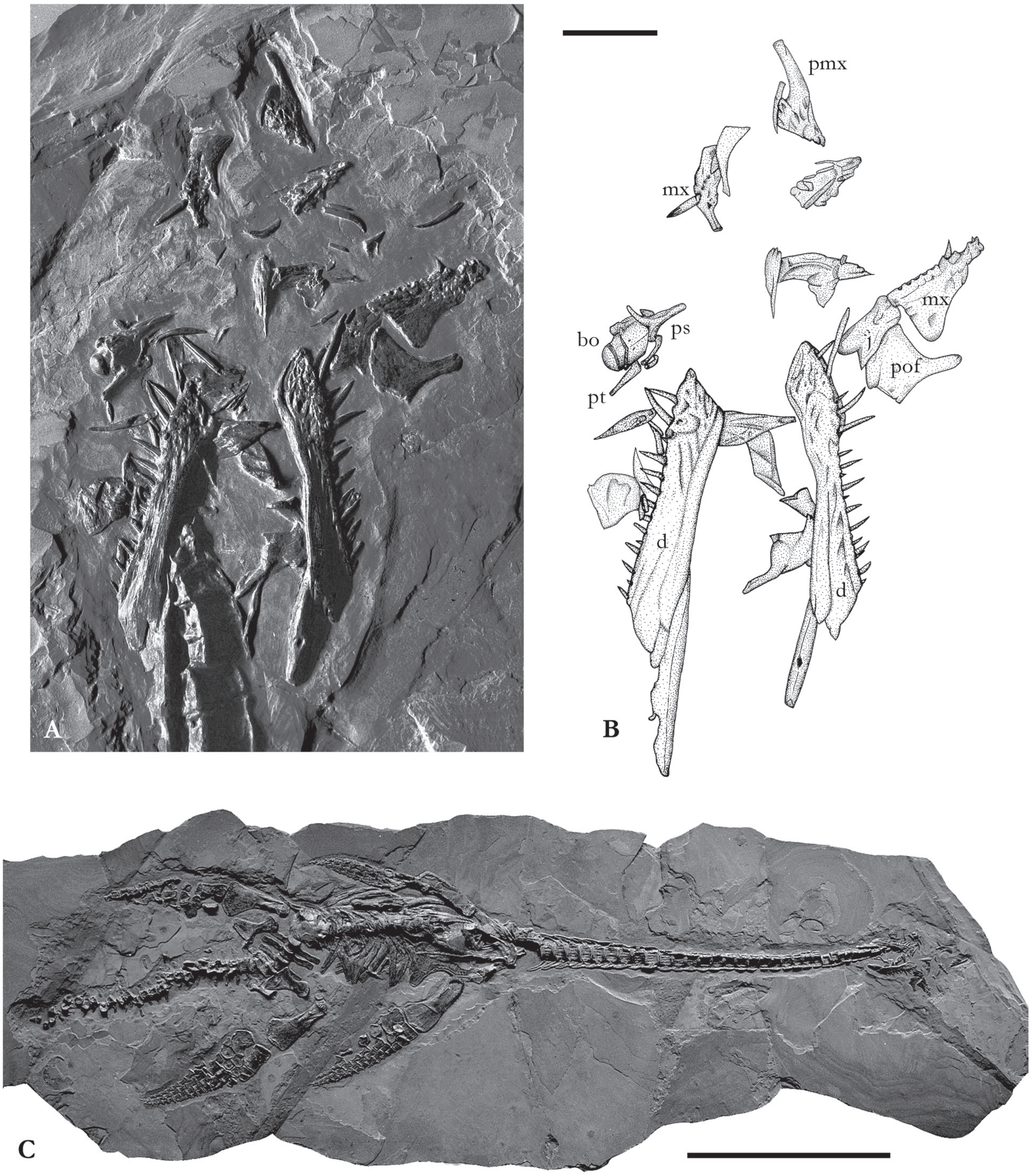


Fig. 2.6: SMNS 51143. Photograph (A) and drawing (B) of the skull (scale bar represents 50 mm); (C) photograph of the specimen (scale bar represent 500 mm); for abbreviations, see appendix A.

dorsal vertebrae is estimated at 17, and two to three sacral vertebrae were present. The three vertebrae directly anterior to the anteriormost sacral vertebra are reconstructed. The line of the 28 caudal vertebrae is interrupted several times, and starting with the 15th the caudal vertebrae are dislocated.

The pectoral girdle is complete and only the portion anterior of the two coracoid fenestrae is deformed, and no details are visible in this area. The coracoids are large and their posterolateral corner is distinctly expanded.

In the pelvic girdle the pubes are dislocated and now lying one on top of the other. Both ischia are dislocated; judging by their anterior margin a pelvic bar was probably absent. Only the right ischium is preserved.

Both fore limbs are present, but the right one is compressed laterally (Fig. 2.6 C). The anterior margin of the humerus is straight, and the posterodorsal corner is expanded. The ulna does not exhibit the lunate form usual for plesiosaurs (Andrews 1910 & 1913, Brown, D. S. 1981, Storrs 1997), but has a concave posterior margin instead of a convex one. Four proximal and three distal carpals were present. The anterior proximal carpals and their following digits are slightly dislocated and displaced proximally, obscuring the posterior half of the radius. The ulnare and the pisiforme are in their normal positions, as well as the digits I and II.

The right hind limb is compressed laterally, similar to the condition in the right fore limb and the digits are partly overlapping each other. The left hind limb is distorted at the level of the metatarsals/ first phalanges, and the posterior part of the hind limb is slightly overlapping the anterior one. The anterior margin of the femur is straight and its posterolateral corner is expanded. The fibula is of lunate form and there are four proximal and three distal tarsals present.

SMNS 51747 (Lias εII_9, Ohmden near Holzmaden). (Fig. 2.7)

An incomplete adult specimen in ventral view, still embedded in sediment, the skull is incomplete and deformed. The specimen was excavated from the residues of a quarry in 1979 and 1980, and unfortunately only part of the fossil could be found. It was later prepared and the missing parts were reconstructed. As it was thought that the specimen would belong to the pliosauroid taxon *Rhomaleosaurus victor*, the proportions and form of the girdles and the limbs were reconstructed accordingly (Wild *pers. com.*). However, the number and form of the cervical vertebrae indicate clearly that this specimen is a plesiosauroid and not a pliosauroid.

The skull is incomplete and disarticulated (Fig. 2.7 A, B). Identifiable are a postorbital and a postfrontal lying isolated on the right side of the skull. A highly deformed bone which is partly covered by the right anterior part of the dentary most probably represents parts of the premaxilla and maxilla. At the posterior part of the skull several other highly deformed bones can be found, which are not identifiable. The lower jaw is incomplete, only the anterior part of the dentary with the symphysis and the posterior part of the lower jaw with the jaw articulation are present. The anterior portion is

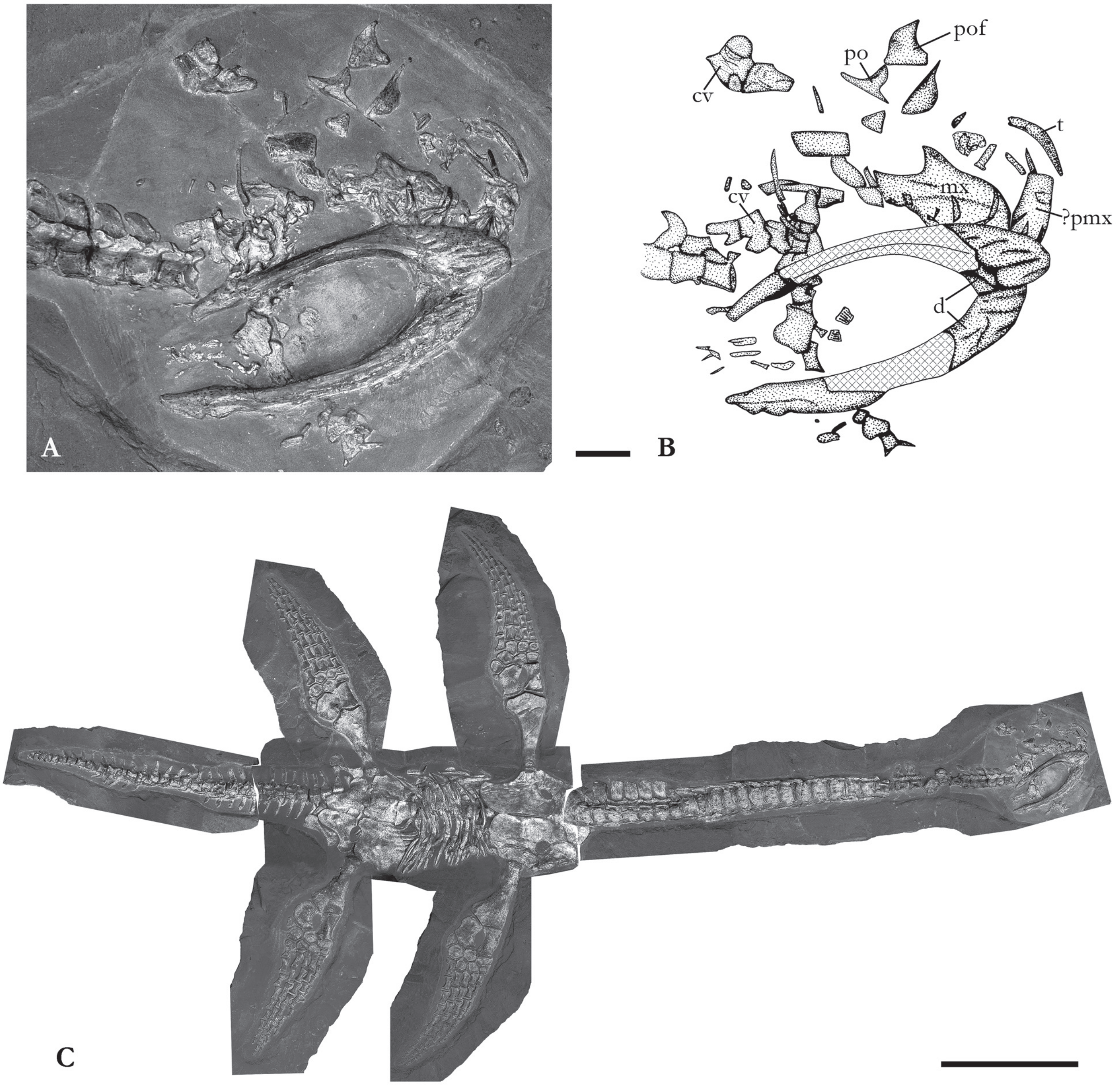


Fig. 2.7: SMNS 51747. Photograph (A) and drawing (B) of the skull (scale bar represents 50 mm); (C) photograph of the specimen (scale bar represents 500 mm); for abbreviations, see appendix A.

covered with distinct grooves. The middle portion has been reconstructed; the total number of teeth can therefore not be given. Ten teeth are preserved both in the dentary and in or next to maxilla and premaxilla. The teeth are large, slender and slightly recurved. Under close examination fine striations are visible, but it is unclear if they are present all around the tooth crown.

The exact number of cervical vertebrae is unclear, as some are isolated and some are reconstructed. The vertebral column has been reconstructed in the incorrect order. There must have been at least 37 vertebrae, of which three are reconstructed completely and of another two the missing half is reconstructed. The cervical vertebrae are slightly elongated and amphicoelous. Whereas the anteriormost 11 vertebrae are in the correct position, the following 14 belong directly anterior to the shoulder girdle, where the middle portion consisting of seven vertebrae is now positioned (Fig. 2.7 C). The misplaced vertebrae are bordered anteriorly and posteriorly by reconstructed vertebrae. The misplacement is determinably by the size of the vertebrae and the length of the cervical ribs, which are small in the anteriormost vertebrae, then very long in the now middle part of the neck and then shorten again directly anteriorly of the shoulder girdle. Usual for plesiosaurs is a continuous increase in length of the cervical vertebrae along the neck (ANDREWS 1910 & 1913, BROWN, D. S. 1981).

The vertebral column of the trunk is mainly covered by the reconstructed pectoral girdle, the gastral ribs and the pelvic girdle (Fig. 2.7 C). The estimated number lies between 17 and 20. Two sacral vertebrae are visible. There are 31 caudal vertebrae present, which slowly diminish in size. Chevrons were present between the third and the 25th caudal vertebra.

The shoulder girdle is mostly missing. Only a small part of the left glenoid formed by the scapula and coracoid is present, the rest has been reconstructed.

The pelvic girdle is mostly complete, with only the lateral part of the left pubis being reconstructed. The right pubis is broken into two parts, which still contact each other. The thyroid fenestra is divided into three portions by an incompletely closed contact between the pubis and ischium. On the left and right side of the pelvic girdle an oval opening is present, whereas in the middle of the pelvic bar a rhomboid space remains open (Fig. 2.7 C).

All of the extremities are incomplete, only the proximal parts are preserved. Of the right forelimb only the distal part of the ulna and the proximal part of the proximal carpals is present. The left forelimb is complete till the middle of the anterior proximal carpals.

In the left hind limb, the anterior femur is reconstructed and only the distal part of the femur, the tibiale, intermedium, the anterior part of the fibulare, the distal tarsal 1 and the proximal halves of the distal tarsals 2 and 3 are present, the rest of the limb is reconstructed. The right hind limb is present up to the metatarsals and the anterior half of the first phalange of the fifth digit.

SMNS 51945 (Lias εII_1, Holzmaden). (Figs 2.8 & 2.9)

A juvenile, nearly complete specimen in lateral view. Of the skull only the posterior part is preserved in ventral view, but extremely deformed so that no details are visible (Fig. 2.8). Only the right retroarticular process of the lower jaw is distinguishable. The vertebral column is lying on the remains of the skull. The vertebrae present at the preserved anterior ending of the skull

Fig. 2.9: SMNS 51945. Photograph of the skull (scale bar represents 50 mm).

are too large to represent either atlas, axis or one of the anteriormost vertebrae. It has therefore to be assumed that the anterior part of the vertebral column is incomplete. There are 35 cervical, five pectoral, 23 to 24 dorsal, two to three sacral and 39 caudal vertebrae preserved. The whole vertebral column is well developed. The sacral vertebrae are not distinguishable from the dorsal vertebrae, and the sacral ribs are not clearly recognisable.

Few details of the pectoral girdle are visible (Fig. 2.9). The interclavicular-clavicular complex is isolated, it consists of a central rod-like bone and two rounded extensions on each side. The scapula is deformed and only partly visible. A raised and darkened, kidney-shaped area posterior of the scapula might represent the remnants of a coracoid.

The pelvic girdle is slightly dislocated but all bones are distinguishable. Both pubes are partly obscured by overlying bones, but the rounded form is still recognisable. The ischia are lying on the right femur and under the left ilium and the vertebral column, they overlap slightly. One ilium is complete, and of the other one only the proximal ending is visible.

The left fore limb is complete and articulated (Fig. 2.9). Of the right one only the radius, one carpal and 29 metatarsals and phalanges are present, which are lying disarticulated in an area next to the left fore limb. The posterodistal corner of the humerus is slightly expanded and its anterior margin

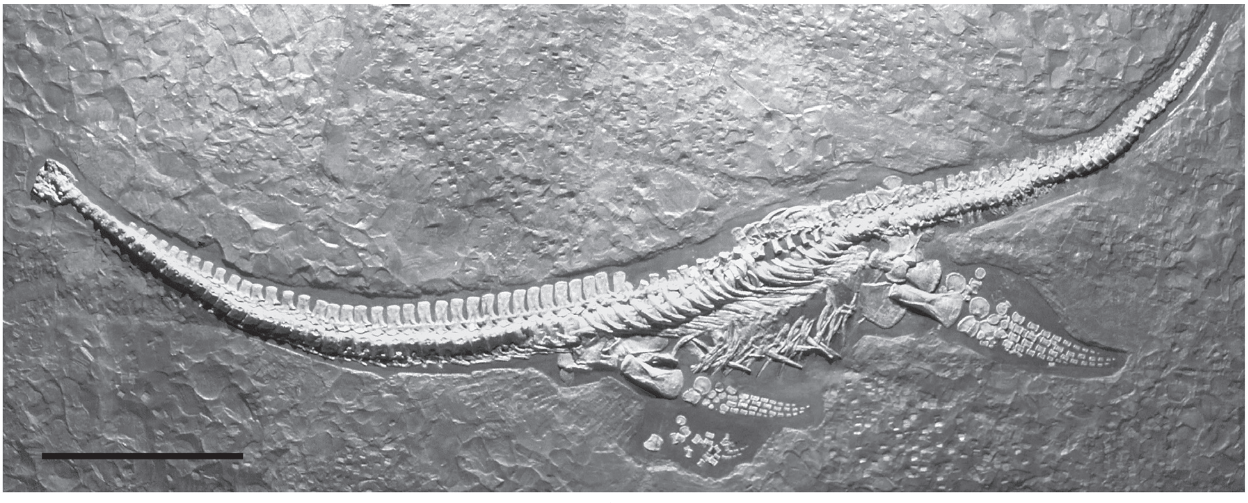


Fig. 2.8: SMNS 51945. Photograph of the specimen (scale bar represents 500 mm).

is straight. Both radius and ulna have the form usually found in plesiosaurs (Andrews 1910 & 1913, Brown, D. S. 1981, Storrs 1997), whereas the carpals are rounded. There are three proximal and three distal carpals present, which have distinctly rugose corners, indicating a cartilaginous covering. Whereas the digits II to V are well developed, only one elongated bone represents the digit I. With a maximum of 10 phalanges in the third digit of the left hind limb, the number of phalanges is rather low compared to adult specimens (SMNS 51143, SMNS 12039, MB.R.1991, MB.R.1992, GPIT/RE/3185; see Table 3.2 for phalangeal counts).

The left hind limb is lying on top of the right one (Fig. 2.9), but most bones are distinguishable. The right hind limb is dislocated and only the femur, tibia, fibula and isolated tarsals are recognisable. The left hind limb is complete and articulated. The femur is straight and distally only slightly expanded. Tibia and fibula resemble strongly radius and ulna, but are slightly larger. The position, number and form of the tarsals are similar to the condition in the fore limb, but they are all slightly larger. No metatarsals or phalanges can be allocated with certainty to the first digit, either there were no bones developed or they cannot be differentiated from the bones of the right hind limb.

MB.R.1991 (Lias εII4, Holzmaden). (Fig. 2.10)

A complete adult specimen in right lateral view. The skull is badly deformed and incomplete, only the ventral side is visible (Fig. 2.10 A, B). The dentaries are recognisable in ventral view and the left posterior part of the lower jaw is separated from the dentary and slightly dislocated. Overall 13 teeth are present, which are slender, slightly recurved and bear very fine striation all around the tooth crown. Several teeth at the anterior part of the skull are distinctly enlarged. Dorsal to the right dentary, part of the premaxilla and maxilla are still in place, but no suture between these two is distinguishable and their dorsal margins are not visible. The posterior and dorsal portions of the skull are not visible, and it is unclear if they are missing or just lying on the unprepared side of the skull.

The postcranium is mostly complete and articulated (Fig. 2.10 C). The specimen on display only exhibits its right fore- and hind limbs, the left ones are stored in the collection. There are 29 cervical, 20 pectoral and dorsal, three sacral and 37 caudal vertebrae present. The distinction between pectoral and dorsal vertebrae is not easily recognisable, there were presumably three to four pectoral vertebrae present. The neural spines of the cervical vertebrae are small anteriorly but rapidly increase in height posteriorly, and from the 21st vertebra on have approximately the same height as the dorsal

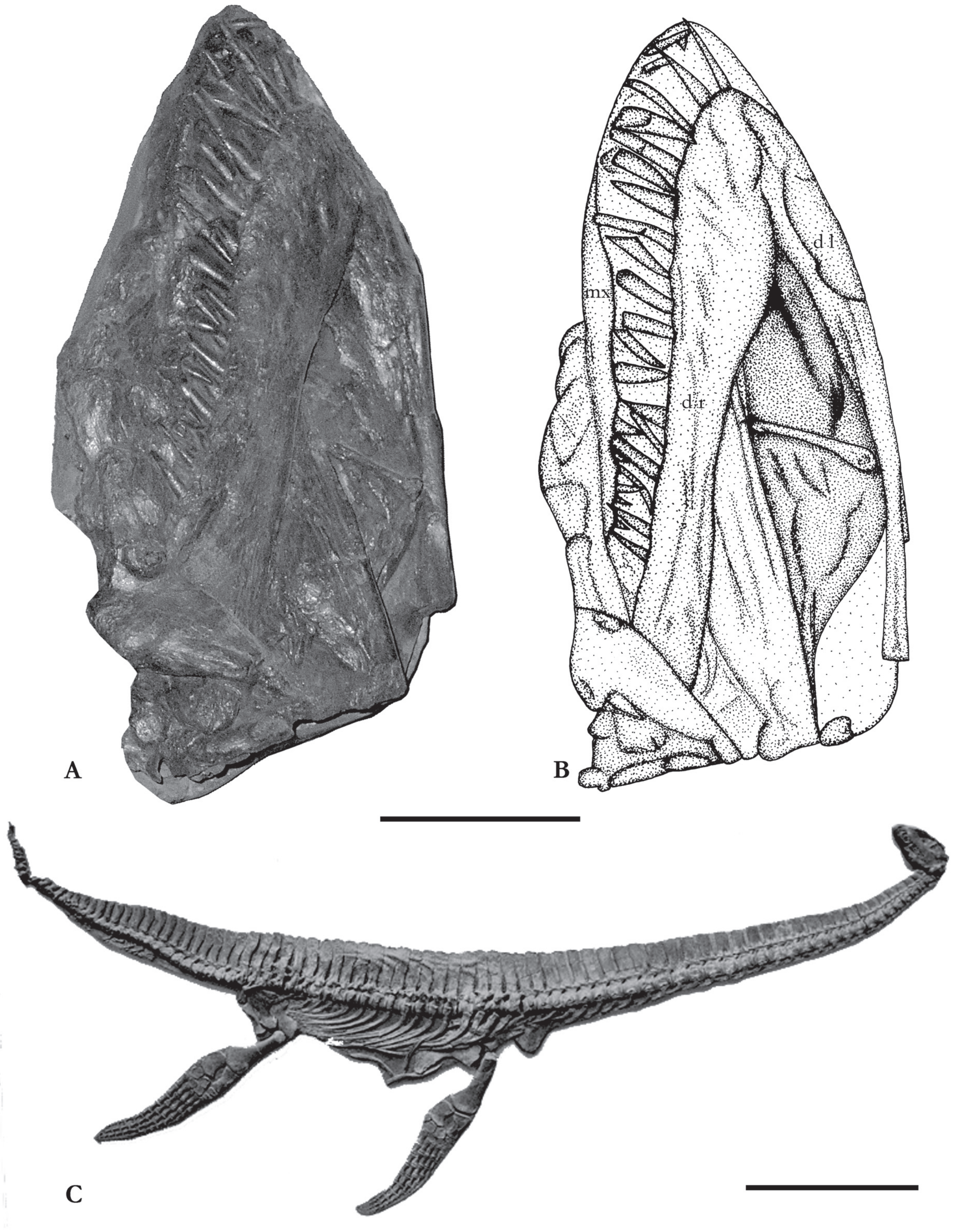


Fig. 2.10: MB.R.1991. Photograph (A) and dawing (B) of the skull (scale bar represents 50 mm); (C) photograph of the specimen (scale bar represents 500 mm); for abbreviations, see appendix A.

vertebrae.

The pectoral girdle is mostly covered by the overlying ribs, and only parts of the scapula and the coracoid are visible. The dorsal process of the scapula is apparently missing and only its ventral part is visible. The lateral margin of the coracoid is distinctly concave and the posterolateral corner is expanded.

The right side of the pelvic girdle is visible, here the ischium and ilium overlie the pubis. Since the anteromedial part of the ischium is expanded anteriorly it can be assumed that it met with a posterolateral process of the pubis, forming a pelvic bar.

Both forelimbs are articulated and complete except the most distal phalanges of the digits III and IV. The humerus is slightly curved posteriorly and the posterodistal margin is expanded. There are four proximal as well as four distal carpals present, the latter being unusual for plesiosaurs. The fourth distal carpal is a small triangular bone, which intercalates between the posterior margins of the carpals 2 and 3 and is bordered by the metacarpal of the third digit.

The hind limbs are also articulated and nearly complete. On the displayed specimen the tibiale, intermedium and fibulare are reconstructed. There are four proximal and three distal tarsals present.

MB.R.1992 (Lias εII4, Holzmaden). (Fig. 2.11)

This is the type specimen of *Plesiosaurus guilelmiimperatoris*, described 1895 by Dames.

It is a nearly complete specimen in dorsal view, with the vertebral column and skull in ventral view. Of the skull, the complete left side, parts of the occiput, and the left lower jaw are visible (Fig. 2.11 A, B). The right and ventral side of the skull is also described by Dames (1895), but was not accessible to the author.

Both maxillae have been dislocated and are lying next to the sides of the skull, displaying their medial side. The jugal has also been dislocated and lies now on the lower jaw. The postorbital bar is broken apart and only the triangular postorbital can be identified, which has been slightly dislocated. Both prefrontal and postfrontal are missing. The parietal foramen is not visible. The parietal and squamosal are separated at the suture, and the roughened sutural facet of the parietal is visible. The suture between the squamosal and quadrate is not detectable. The basioccipital, supraoccipital and the exoccipital-ophistotics are not visible as they are covered by the lateral part of the squamosal. The atlas and axis are still attached to the skull and protrude from its posterior end, uniting with the rest of the vertebral column.

The left lower jaw is articulated but sutures between the dentary and the posterior bones are either not visible or obscured by the jugal. There are several teeth lying next to the skull or still situated in their sockets. A minimum of 16 teeth were present in the lower jaw, however, this probably does not represent the complete number of teeth. The teeth are slender and recurved, they show fine and sometimes weak striation, which is always absent on the buccal side.

Parts of the palate can be seen through the orbital (Fig. 2.11 A, B), the aperture of which is enlarged by the dislocated left maxilla. It is probably the dorsal view of the palate but the bone is too damaged to show any details.

There are 37 cervical, four pectoral, 16 dorsal, two or three sacral and 37 caudal vertebrae present. The anterior cervical vertebrae are slightly elongated.

The pectoral girdle is dislocated, only the coracoids seem to remain in or near their original position

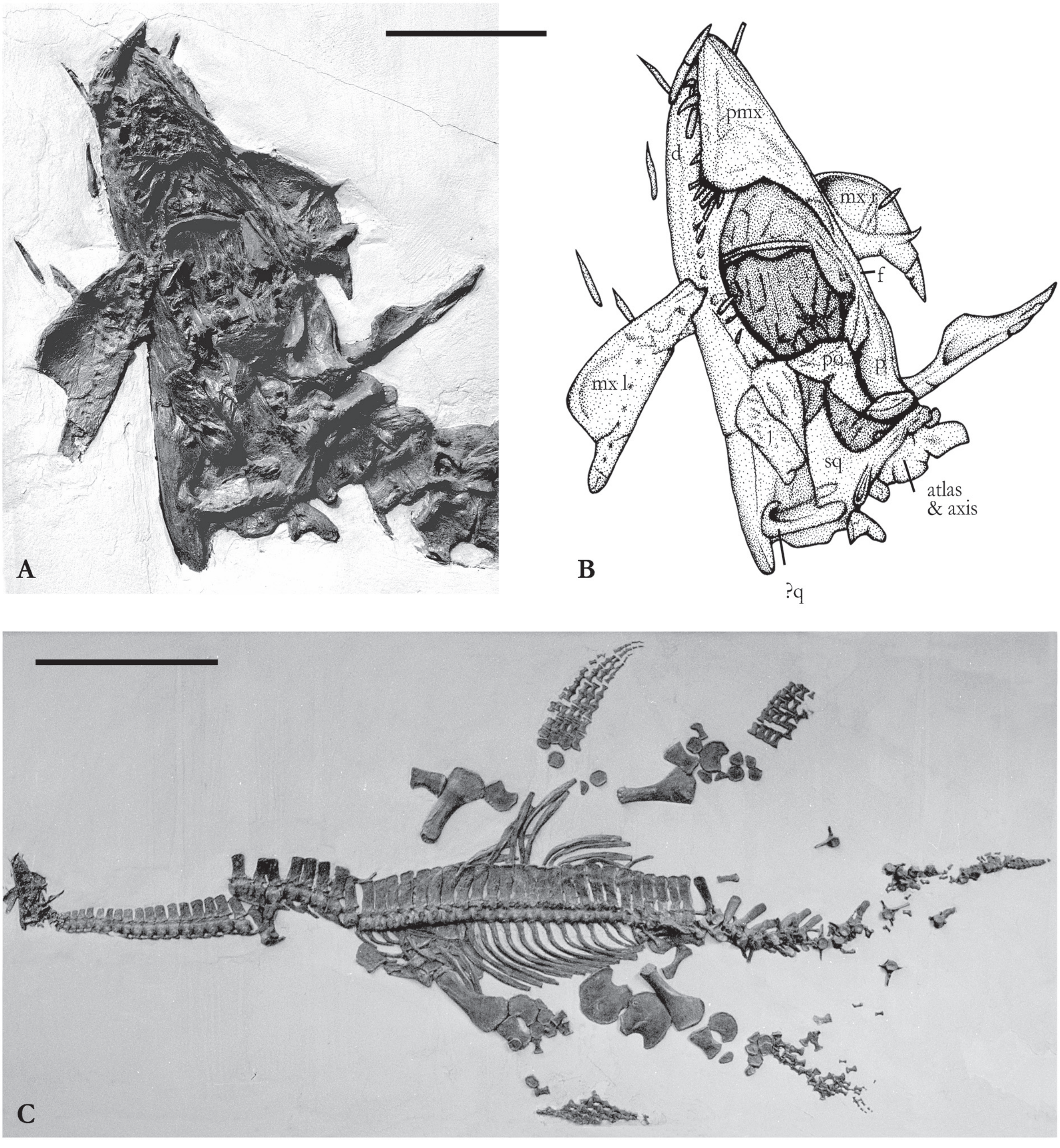


Fig. 2.11: MB.R.1992, the type specimen of *Plesiosaurus guilelmiimperatoris* DAMES, 1895. Photograph (A) and drawing (B) of the skull (scale bar represents 50 mm); (C) photograph of the specimen (scale bar represents 500 mm); for abbreviations, see appendix A.

although they are partly covered by the vertebral column (Fig. 2.11 C). Their expanded posterolateral corner is still visible. Anterior to the coracoids is a rounded flat bone, probably representing the remainder of the left clavicle, a posterior extension is perhaps part of the interclavicle. Of the left scapula only the lateral portion and the dorsal extension is visible.

The pelvic girdle is also disarticulated. Both pubes lie next to the left femur and they have been rotated. Only one ischium is visible, whose distal part is covered by the vertebral column. Both ilia are preserved but one is lying under the vertebral column.

Both fore limbs are disarticulated (Fig. 2.11 C). The right humerus lies slightly separated from the rest of the body, it is slightly curved and has an expanded posterodistal corner. The radius and ulna are situated at the distal end of the humerus, but rotated. A short distance from the epipodials lie the remaining posterior parts of the fore limb, which is apparently complete except for the last phalange of the first digit. The radiale is still in articulation with the articulated metacarpals and phalanges, but the other carpals are dislocated. There were four proximal and three distal carpals present. The left humerus is still in contact with the remainder of the pectoral girdle, followed distally by the radius and ulna. The latter is in contact with the ulnare, intermedium and pisiforme. The radiale is lying on the radius. Two distal carpals and a metacarpal are dislocated and lying distally of the posterior proximal carpals. Separated by a gap lie the third distal carpal and one metacarpal, and again in a distance the remainders of the limb, consisting of some articulated phalanges, whose number is not complete.

Both hind limbs are, again, dislocated. The right femur, tibia, fibula, the tarsals and the metatarsal V are lying unordered in an area next to the body. There were four proximal and three distal tarsals present. The remaining metatarsals and phalanges are in articulation but incomplete. The right femur is isolated, at a short distance lie the articulated tibia and fibula and a dislocated posterior tarsal. The remaining tarsals, metatarsals and an incomplete amount of phalanges follow in an unordered row.

Dames (1895) reported soft-tissue preservation in this specimen, at the posterior ending of the caudal vertebrae. Unfortunately the whole sediment surrounding the bones is now covered with grey paint, and therefore Dames' (1895) observation cannot be verified.

GPIT/RE/3185 (Lias εII4, Holzmaden). (Fig. 2.12)

This is the type specimen of *Plesiosaurus brachypterygius*, described by v. Huene (1923). A modern description of the skull was provided by Maisch & Rücklin (2000).

It is a complete specimen, mostly exposed in dorsal view, with the right lateral side of the vertebral column visible. The skull is complete and three-dimensionally prepared (Fig. 2.12 A - D). It has been flattened substantially but the bones are still in articulation. The snout is rounded and constricted at the level of the third to fourth maxillary tooth. It is densely covered with radially running furrows and ridges on premaxilla and maxilla (Fig. 2.12 A, B). The premaxilla-maxilla suture is not visible but it is inferred that there are five teeth in the premaxilla and 16 in the maxilla. The middle teeth in the premaxilla and several teeth near the premaxilla-maxilla suture in the maxilla are distinctly enlarged, although the teeth directly next to the suture are small. The teeth are slender, slightly recurved and have fine longitudinal striations all around the tooth crown.

The external nares are situated slightly anterior of the orbits and each is bordered by the premaxilla medially, the maxilla laterally, and the prefrontal posteriorly. The raised ascending processes of the premaxilla extends posteriorly well past the anterior margin of the orbits. The frontals are excluded from the orbital margin by a contact between the prefrontals and postfrontals. The anterior margin of the parietal foramen is formed by the frontals. An anterior contact of the postorbital with the maxilla prevents the jugal from contributing to the orbit margin. The postorbital contacts the squamosal posteriorly. Contra MAISCH & RÜCKLIN (2000) the squamosals meet in a median midline suture, and the supraoccipital is not visible in the specimen. Two small rounded bones are exposed just ventrally of the squamosals. These rest on the exposed dorsal surface of the basioccipital and are identified as the ventral portions of the exoccipital-opisthotic. The quadrates form the ventral part of the suspensoria, but the sutures to the squamosals are poorly visible.

In ventral view the closed palate is fully exposed, an anterior interpterygoid vacuity does not exist (Fig. 2.12 C, D). In the anterior part of the snout, between the premaxilla and the vomer a *foramen incissivum* is visible on both sides. The borders of the choana are formed by the maxilla laterally and dorsally, the vomer medially and the pterygoids posteriorly. Both premaxilla and maxilla have a raised shelf along the lateral margin of the skull, upon which the teeth are situated. The pterygoids are large bones with an anterior median suture as well as a posterior one situated posteriorly of the posterior interpterygoid vacuities and underlying the *basis cranii*. The parasphenoid is a lanceolate bone, which intercalates between the pterygoids. The basisphenoid is only exposed through the posterior interpterygoid vacuities, here the foramina for the internal carotid arteries are clearly visible. The ectopterygoids are large as far as can be determined, but their sutures with the jugals are not

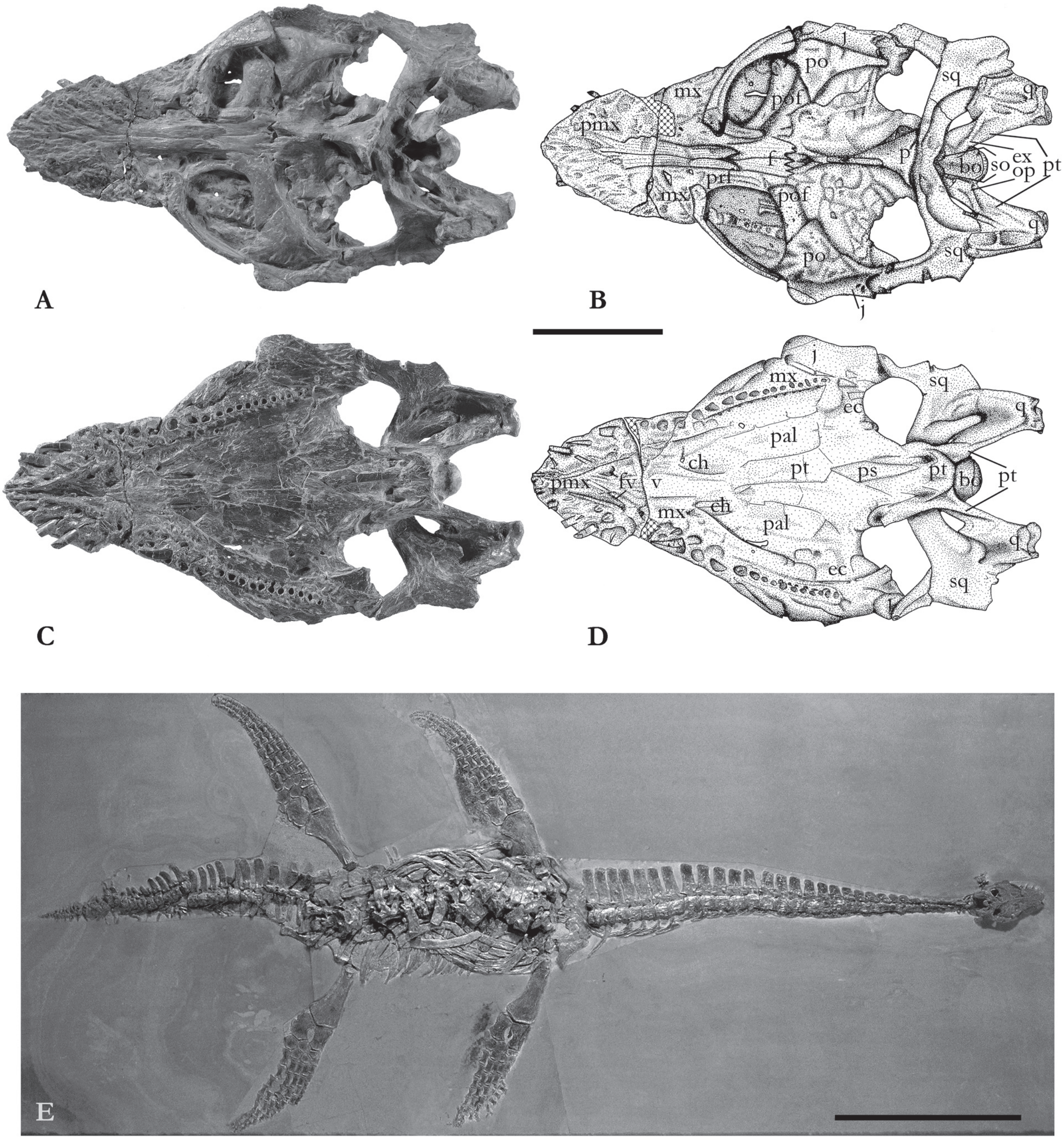


Fig. 2.12: GPIT/RE/3185, the type specimen of *Plesiosaurus brachypterygius* v. Huene, 1923. (A) photograph and (B) drawing of the skull in dorsal view, (C) photograph and (D) drawing of the skull in ventral view (scale bar represents 50 mm); (E) photograph of the specimen (scale bar represents 500 mm); for abbreviations, see appendix A.

obvious.

The lower jaw is still in the sediment and visible as the skull has been prepared separately. The left posterior part of the lower jaw is separated from the dentary, but the right one is still in position. The jaw symphysis and anterior part of the dentary are covered by furrows and ridges similar to those of premaxilla and maxilla. Several teeth are still in their sockets, but the exact number of teeth cannot be given, as some of the alveoli are obscured.

The anterior cervical vertebrae are situated between the two rami of the lower jaw. They are distinctly elongated and amphicoelous. There are 33 cervical vertebrae, four pectoral (one is probably missing), 16 dorsal, two or three sacral (the first one is probably missing) and 42 caudal vertebrae preserved. The vertebrae in the dorsal region are not articulated, most are slightly rotated and the neural arches have been flattened due to taphonomic compression, obscuring many details of the underlying pectoral and pelvic girdles.

The anterior part of the pectoral girdle is visible through a gap in the vertebral column (Fig. 2.12 E). It consists of the interclavicular-clavicular complex, whose sutures are difficult to determine. The scapulae are also visible but their dorsal processes are either missing or covered by other bones. Two scapulo-coracoid fenestrae were present, separated by a midline pectoral bar. Of the coracoid only the distinctly extended right posterolateral corner is visible under some ribs.

Only the lateral margins of the pelvic girdle are visible. The left pubis is nearly completely covered, but the right one is mostly visible. In contrast, the right ischium is better exposed than the left one. The ilia are dislocated and are now lying parallel to the longitudinal axis of the specimen.

The left fore limb is better preserved than the right one, although the proximal part of the left humerus is covered by overlying bones (Fig. 2.12 C). The anterior margin of the humerus is only slightly recurved, and its posterodistal corner is expanded. The ulna has not the lunate form usual for plesiosaurs but is rod-like and constricted in the middle, similar to the radius. There are four proximal and three distal carpals present. The distal phalanges of the right fore limb are slightly disarticulated, but on the left side they are in articulation and complete. Some skin is preserved on the dorsal side of both fore limbs, between the level of the radius and the second row of phalanges. It extends posteriorly for about half the width of the limb itself. This is one of the few known examples of soft tissue preservation in plesiosaurs from the Posidonia shale.

Both hind limbs are present, the left one being the better preserved. The anterior margin of the femur is straight and its posterodistal corner expanded. The fibula is of lunate form and has a distinct notch in its posterior margin. This character, unknown from any other plesiosaur, was already noted by v. Huene (1923) in his description and compared to the *scissae* often found in the anterior metapodials and phalanges of ichthyosaurs. There are four proximal tarsals preserved in the left hind limb and only three in the right, the pisiforme is missing. Both hind limbs have three distal tarsals. The distal phalanges of the right side are slightly dislocated, but the left side is articulated and complete.

MH Nr. 8 (Lias ε, uppermost II$_4$ directly below II$_5$, Holzmaden). (Fig. 2.13)

Remark: Due to light reflections on the glass covering of this specimen, only the skull could be photographed, as it is prepared and stored separately.

A nearly complete adult specimen in lateral view. The skull has been prepared three dimensionally, but due to its high deformation few details can be recognised (Fig. 2.13 A – D). The lower jaw, consisting mostly of the dentary, is visible on the right side of the skull (Fig. 2.13 C, D), together with several dislocated teeth. The teeth are slender, slightly recurved and show fine striation all around the tooth crown. Other bones on this side of the skull cannot be determined with certainty. The bones dorsal of the dentary are presumably the maxilla and perhaps part of the premaxilla and jugal but unfortunately no sutures are visible.

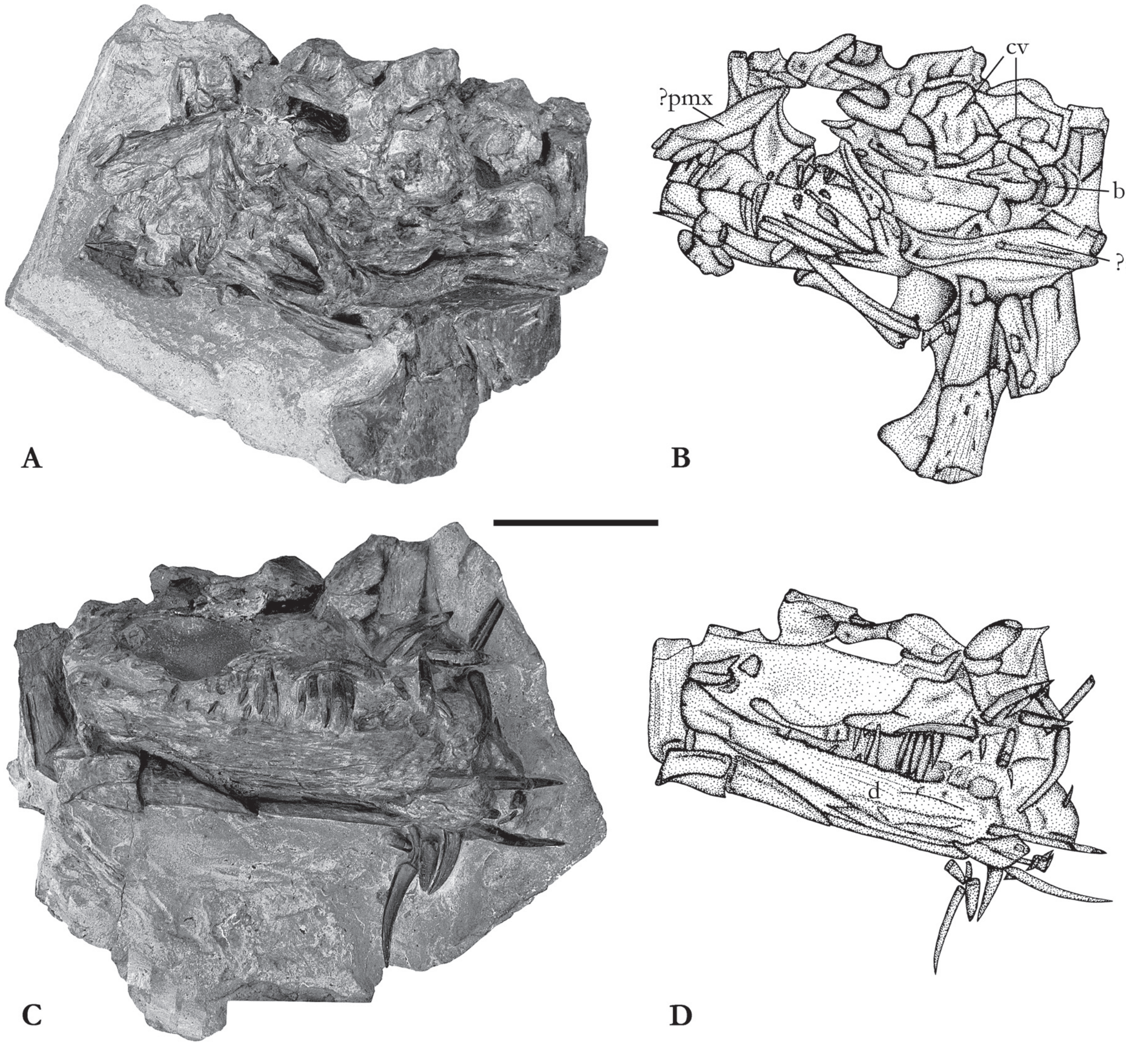


Fig. 2.13: MH Nr. 8. (A) photograph and (B) drawing in right lateral view, (C) photograph and (D) drawing in left lateral view (scale bar represents 50 mm); for abbreviations, see appendix A.

On the left side of the skull all of the bones are dislocated and only few can be determined (Fig. 2.13 A, B). Two cervical vertebrae and their associated neural arches lie on the dorsal part of the skull. A highly deformed bone at the anterior part of the skull probably represents part of the premaxilla, as it still bears some teeth. The basioccipital is recognisable by its condyle and it is presumably still attached to the exoccipital-opisthotic, but again details are not visible due to deformation and covering by other bones.

The postcranial is far better preserved, in full articulation and nearly complete. There are 35 cervical, five pectoral, 14 dorsal, three sacral and 28 caudal vertebrae present, which are all slightly amphicoelous. Of the pectoral girdle only a part of the scapula is present, the rest is missing. The right pelvic girdle is complete, but the ilium overlies the ischium and pubis and thus obscures parts of them.

Both fore limbs are articulated and complete. The proximal end of the left humerus is situated beneath the vertebral column, both humeri are slightly recurved and the posterodistal corner is expanded, there are four proximal and three distal tarsals present.

The situation in the hind limbs is similar - the proximal half of the left femur is covered by the vertebral column whereas the right one is completely visible. In the right hind limb the fibula, fibulare, pisiforme, metacarpal V and several phalanges are reconstructed. The left hind limb is complete and shows four proximal and three distal carpals.

Classification

Two approaches were taken to assign the studied specimens to already existing species or to determine them as new taxa. On the one hand the osteological characters of the specimens were studied and compared. On the other hand, the measurements taken were used for a statistical analysis using the programme SPSS (Statistical Product and Service Solution, Version 12, SPSS Inc.).

The osteological comparison showed that most distinguishing characters are found in the skull, and that the postcranial skeleton is very similar in all specimens, apart from differences due to the ontogenetic stage of the specimen, e.g. the number of phalanges and the form of the pelvic and pectoral girdles. The distinguishing characters include the ornamentation of the teeth, ornamentation and form of the snout, position of jugal and prefrontal in relation to the orbit, presence or absence of an anterior interpterygoid vacuity, form of the parasphenoid and presence or absence of an cultriform process, the presence or absence of a median pterygoid suture posterior of the posterior interpterygoid fenestrae and the length of the limbs in relation to the overall body length. At least one of these characters is visible in all specimens, and allows most specimens to be assigned to one of the following taxa, "*P.*" *guilelmiimperatoris* and "*P.*" *brachypterygius*.

For the second approach, the measurements of different body lengths and their ratios to the overall body length were entered in the statistical analysis program SPSS (see appendix B). Since this was done at an early stage of the project, only the specimens in the SMNS and GPIT were entered in the analysis. For the holotype of "*P*". *guilelmiimperatoris* the published measurements (Dames 1895) were used. This specimen and the other remaining two specimens in the MB and MH were studied later in detail. The program analyses the similarity of entered data by calculating regression factors.

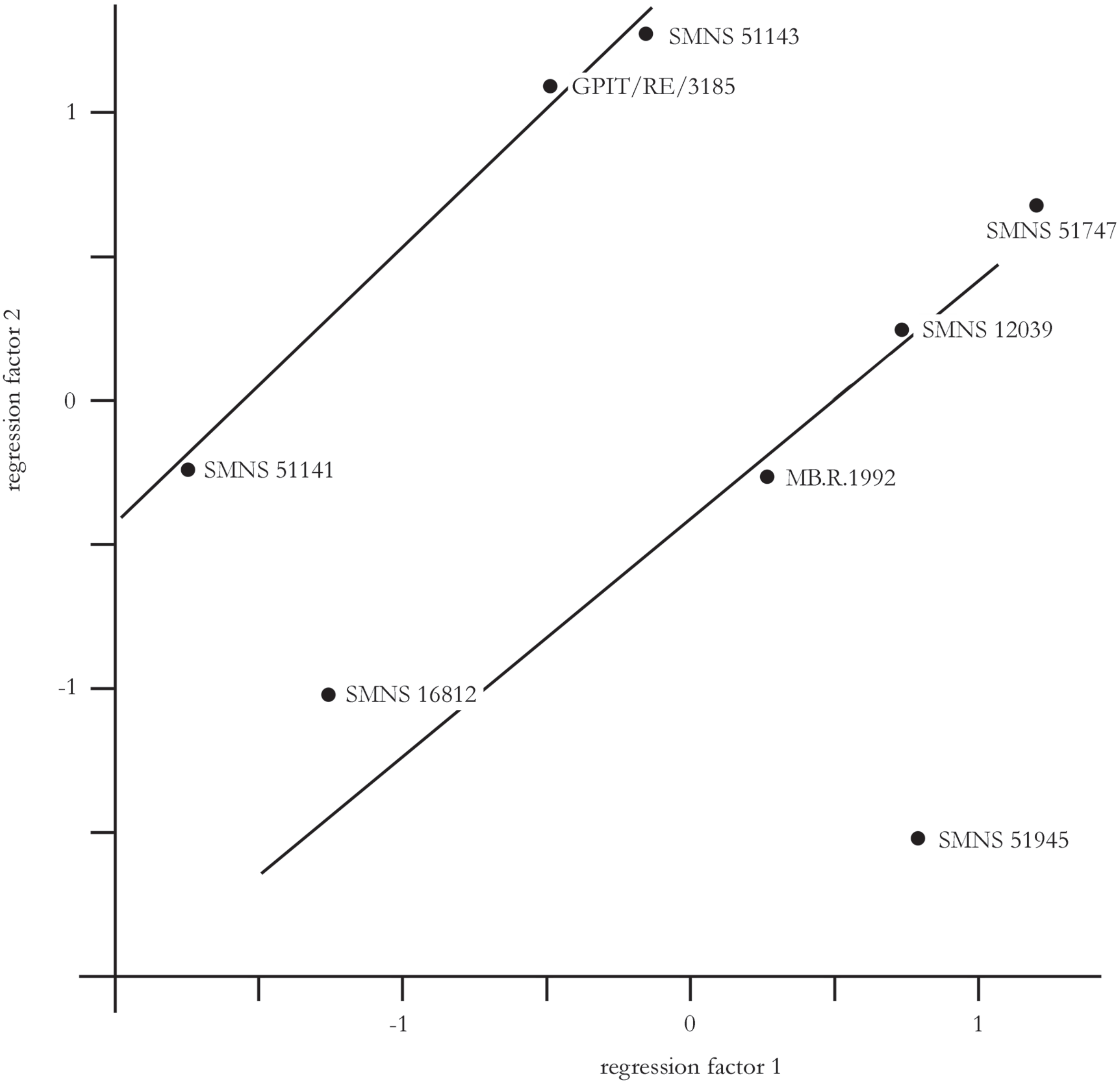


Fig. 2.14: Results of the statistical analysis with SPSS. Specimens belonging to the species "*P.*" *brachypterygius* lie on or near the upper, those belonging to "*P.*" *guilelmiimperatoris* on the lower line. SMNS 51045 plots in some distance from both lines, which indicates that it forms a different taxon.

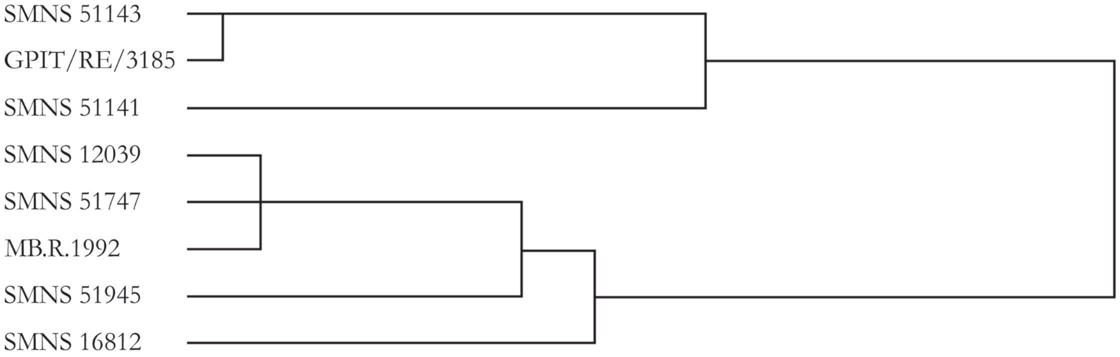


Fig. 2.15: Results of the statistical analysis with SPSS in form of a dendogramm, showing the morphological likeliness of the specimens.

The regression factor with the highest significance was correlated to the relative limb-length. Fig. 2.14 shows two regression factors (including the limb-length related one) plotted against each other. The plotted specimens can be arranged on two lines, one including the holotype of "*P.*" *guilelmiimperatoris* (MB.R.1992) and the second described specimen of this species (SMNS 12039) and the other one the holotype of "*P.*" *brachypterygius* (GPIT/RE/3185). SMNS 51945 does not lie on any of these lines.

SPSS also gave a dendogramm showing the relative morphological likeliness of the different analysed specimens (Fig. 2.15). This shows a clear division between one group including the type specimen of "*P.*" *brachypterygius*, SMNS 51141 and 51143 on the one hand and the remaining specimens on the other hand, which include the type specimen of "*P.*" *guilelmiimperatoris*.

Results

The results from both approaches to assign the studied specimens coincide. Therefore the following assignments can be made:

MB.R. 1992 (type specimen), SMNS 12039 and SMNS 16812 are referred to "*P.*" *guilelmiimperatoris*. In the resulting diagram of the statistical analysis SMNS 16812 plots in some distance from the line formed by MB.R. 1992 and SMNS 12039. This is probably due to the measurements of the limbs, which were taken from the mounted specimen where they are probably reconstructed too small. However, SMNS 16812 shares several osteological characters with the other two specimens, and is therefore referred to "*P.*" *guilelmiimperatoris*.

GPIT/RE/3185 (type specimen), SMNS 51141, SMNS 51143, MB.R.1991 and MH Nr. 8 are referred to "*P.*" *brachypterygius*.

SMNS 51747 is very incomplete, and its measurements of the limbs (and its resulting position in

Figs 2.14 and 2.15) are based on the reconstructions made during preparation. These reconstructions were based on the assumption that the specimen belongs to the pliosauroid species *Rhomaleosaurus victor* (Wild, *pers. comm.*). However, the cervical vertebrae of this specimen are approximately as long as high and their number exceeds 33, which are both characters of plesiosauroids and not of pliosauroids (Brown, D. S. 1981, Bardet *et al.* 1999, O'Keefe 2001a). The reconstructions are probably incorrect, and any assignment based on the reconstructed limb proportions is highly questionable. Of the skull, mainly the lower jaw is preserved (see description) and only few morphological characters are visible. Therefore it is not possible to accurately or confidently classify SMNS 51747. However, the anterior part of the dentaries seems to be covered by furrows, and the specimen is therefore referred to as *cf.* "*P.*" *brachypterygius*, since one of the morphological characters of this species is the possession of an ornamented snout and lower jaw.

SMNS 51945 most probably belongs to a novel species. The specimen is certainly a juvenile (see description), but with a body length of 3.5 m it is already longer than adult specimens of both "*P.*" *guilelmiimperatoris* and "*P.*" *brachypterygius*, which usually reach about 3.0 m (see appendix B). Unfortunately the skull is incomplete and the remains are extremely badly preserved. The erection of a new species based on a juvenile specimen with virtually no head is not advisable, since the diagnosis would not be valid for adult specimens and thus later findings could not be referred to this species. The erection of a new taxon including SMNS 51945 must await new plesiosauroid findings from the Posidonia shale.

SYSTEMATIC PALAEONTOLOGY

Order SAUROPTERYGIA Owen, 1860

Suborder PLESIOSAURIA de Blainville, 1835

Family ELASMOSAURIDAE Cope, 1869

Genus SEELEYOSAURUS White, 1940

Type species. Seeleyosaurus guilelmiimperatoris Dames, 1895 (Fig. 3.1)

Range and distribution. Only known from the Posidonia shale, Lias ε, Lower Toarcian of Holzmaden near Kirchheim-Teck, Baden-Württemberg, southwest Germany

Diagnosis. As for type and only species.

Seeleyosaurus guilelmiimperatoris (Dames, 1895) (comb. nov.)

Figs 2.1 – 2.4, 2.11

v* 1895 *Plesiosaurus Guilelmi imperatoris* Dames, pp. 16 – 64, pls 1–3
v. 1910 *Plesiosaurus Guilelmi imperatoris* Fraas, pp. 105 – 123 , pls 6 – 7; pl. 10, figs 4 – 6; figs 1 – 6
v. 1940 *Seeleyosaurus holzmadensis* White, pp. 461 – 462, fig. 9b
v. *1985 Plesiosaurus guilelmi imperatoris* Jäger, fig. 17
v. *1994* ?*Microcleidus* Urlichs *et al.*, fig 105
v. 2004 *Plesiopterys wildii* O'Keefe, pp. 973–982, figs 1 – 7

Type specimen. MB.R.1992 (Fig. 2.11), described by Dames (1895).

Type locality and horizon. Holzmaden, Baden-Württemberg, southwest Germany; Posidonia shale, Lias εII$_4$ (Unterer Schiefer), *Harpoceras falcifer* zone, Lower Toarcian

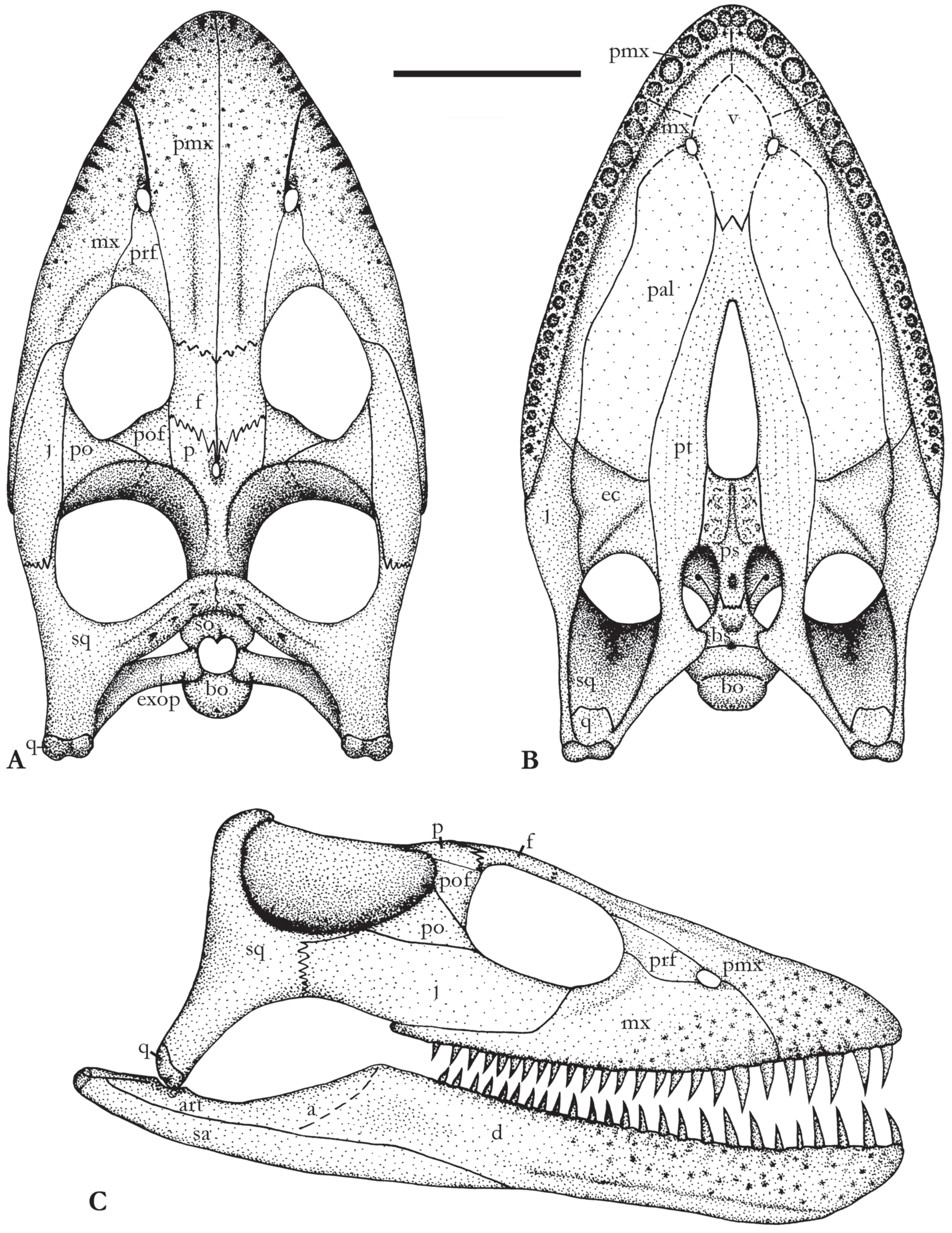


Fig. 3.1: Reconstruction of the skull of *Seeleyosaurus guilelmiimperatoris* in dorsal (A), ventral (B) and lateral (C) view (scale bar represents 50 mm); for abbreviations, see appendix A.

Referred specimens.

SMNS 12039 (from the Lias εII$_4$ of Holzmaden) (Fig. 2.1): A complete specimen, described by Fraas (1910) as *P. guilelmiimperatoris*. White (1940) made this the type specimen of the genus and species *Seeleyosaurus holzmadensis*. Most of the specimen was destroyed during World War II, and only the skull and several fragments of the ribcage, the vertebral column and the limbs were found in the ruins of the old museum. Nevertheless a cast of the complete specimen exists in the collections of the SMNS. Figured in Jäger (1985, fig. 17) as *Plesiosaurus guilelmi imperatoris*.

SMNS 16812 (from the Lias εII$_4$ of Holzmaden) (Figs 2.2 – 2.4): a complete skeleton of a subadult individual described as *Plesiopterys wildii* (O'Keefe 2004). Figured in Urlichs *et al.* (1994, fig. 105) as ?*Microcleidus*.

Emended diagnosis: Moderately sized plesiosauroid, adults up to 3.5 m in length with a skull-length of approximately 170 mm, temporal openings have approximately the same size as the orbits; five premaxillary teeth, a maximum of 20 maxillary teeth, smaller teeth directly around the premaxillary-maxillary suture and four to five enlarged teeth in both premaxilla and maxilla near the premaxillary-maxillary suture, teeth with fine striae on the lingual side and distinctly less pronounced or absent striae on the buccal side; maxilla with a long posteroventral process reaching approximately to the middle of the jugal, small parietal foramen situated at the frontal-parietal suture, parasphenoid of oblong form without cultriform process and anterior interpterygoid vacuity with rounded posterior margin, straight pterygoid-ectopterygoid suture; four proximal carpals and tarsals, maximum number of phalanges more than ten in the third digit, limbs long, approximately 25 per cent of the overall body length in adults.

Range and distribution. Only known from the Posidonia shale, Lias εII$_4$, Lower Toarcian of Holzmaden, Baden-Württemberg, southwest Germany.

Description

Both the type specimen and the referred specimen SMNS 12039 are described and figured accurately in Dames (1895) and Fraas (1910) respectively, and a short description is given in the first chapter. A short revised description of SMNS 16812 is given here, as the original description (O'Keefe 2004) is partly incorrect. In the present paper, alternative interpretations are given together with additional observations.

It should be noted that the "upper side" of the slab (Fig. 2.2 B, C) exposes the dorsal side of the snout, the dorsal part of the palate and the ventral part of the skull roof. The "lower side" (Fig. 2.2 D, E) shows the palate, the dentary and the dorsal side of the posterior skull roof.

The general outlines of the skull were correctly interpreted, apart from the position of the skull roof. It is not only rotated as stated by O'KEEFE (2004), but also flipped over and is now displaying its ventral side. An indicator for the upturned position is the position of the parietals and the squamosals. On the lower side of the slab, the squamosals form the posterior margin of the skull and overlap the parietals, whereas on the upper side the parietals reach the posterior margin of the skull. This arrangement can also be seen in occipital view, although the specimen is strongly flattened. In all plesiosaurs the squamosals meet in a median suture, lying directly dorsal to and in contact with the parietals. Therefore the side where the squamosals form the posterior margin of the skull is the dorsal skull side, i.e. in this specimen the side exposed on the lower side of the slab. Consequently O'KEEFE (2004) described the ventral part of the skull roof as being the dorsal, which led to some misinterpretations. As seen on the dorsal side of the skull roof, the frontal-parietal suture passes through the parietal foramen, so that the frontal contributes to a small part of the foramen margin. O'KEEFE (2004) interpreted the triangular prefrontals, visible on the upper side of the slab and exposing their ventral surfaces, as lateral extension of the frontals. The premaxillary-frontal suture lies just anterior to the prefrontals. However, as the bones are in ventral view, no conclusion about the extent of the premaxilla on the skull roof can be drawn.

The tooth crowns have fine longitudinal striations, which are clearly more pronounced on the lingual side of the tooth, and less pronounced or even absent on the buccal side.

Several features of the posterior part of the skull roof can also be interpreted differently to O'KEEFE (2004), principally the element he described as postorbital. A close examination of this part of the skull shows that it is not a single bone but comprises two separate bones. The first lies in articulation with the anterior process of the squamosal, and represents the posterior part of the right jugal. The jugal-squamosal suture is visible on the right dorsal side of the skull. It runs vertically to the longitudinal axis of the skull in its ventral part, and turns anteriorly, so that the squamosal has a small anterodorsal process. The anterior margin of the right jugal is broken and incomplete, so that the anterior extent of this bone remains unknown. Nevertheless, a small foramen can be seen in the preserved anterior part of the right jugal. The second element overlies the right jugal approximately at a right angle, and has been crushed into the right jugal during compaction. The form of the bone and the presence of a small foramen makes it most likely that it represents the left jugal, which was dislocated during the distortion of the skull. Under close examination this bone does not have a suture with the parietal, as a small amount of sediment lies between these two elements. The postfrontal is still in articulation with the frontal and parietal. In ventral view, it has a triangular form with a small process on its posterior part. Two small pits can be seen in the lateral part of the bone. Next to the postfrontal lies the right postorbital, which is partly covered by the postfrontal. The exposed part is rod-like with a small rounded process. Another element of similar form lying next to the squamosal and parietal probably represents the left postorbital. As a consequence of his interpretation of the cheek, O'Keefe (2004) described the temporal opening as being very small. In the new interpretation presented here, the temporal openings have approximately the size of the orbits.

The squamosal-quadrate suture is clearly visible on the right internal side of the skull. The suture runs in a weak curvature from the lateral to the medial margin of the suspensorium. Furthermore, the deformed and dislocated, but distinguishable, left opisthotic-exoccipital is attached to the left quadrate (Fig. 2.3). Two other fragmentary bones lying on top of the left quadrate may represent the quadrate process of the left pterygoid and the posterior part of the left stapes, in which case these bones are still near their original position for articulation with the quadrate.

On the palate the intercalating vomer-pterygoid suture is present just anterior to the anterior interpterygoid vacuity. The choanae were not found on the palate. Both left and right margins of the anteriormost part of the pterygoids next to the position of O'Keefe's (2004) choana do not form a smooth margin but are broken. Furthermore the position of the choanae as described by O'Keefe (2004) would be distinctly posterior to the vomer-pterygoid suture, which is not the case in any known plesiosaur (pers. obs.). The actual position of the choanae was probably more anteriorly and is now not visible as the dentary covers this area of the palate. The left anterior part of the palate as preserved is formed mainly by the palatine. The posterior part of the palatine-vomer suture is visible, whereas the anterior part cannot be traced. On the left side of the palatine, the maxillary suture is visible. The maxilla forms the left part of the preserved palate, just visible next to the underlying dentary.

The anterior interpterygoid vacuity has a rounded posterior margin. The structure O'Keefe (2004) interprets as a cultriform process, which does not enter the anterior interpterygoid vacuity, is clearly visible in the specimen. It is slightly elevated, forming a low and narrow ridge, but distinct sutures surrounding this ridge could not be detected. The actual pterygoid-parasphenoid sutures are straight and run from the posterolateral margin of the anterior interpterygoid vacuity to the anterior ending of the posterior interpterygoid vacuities. The bone surface next to the ridge, which was interpreted as flanges of the pterygoid by O'Keefe (2004), is distinctly rugose and belongs to the parasphenoid. The weakly interdigitating parasphenoid-basisphenoid suture could also be identified, originating at approximately the middle of the median margin of the posterior interpterygoid vacuities and running first posteromedially before turning and running transverse to the longitudinal axis of the skull. The rounded structure O'Keefe (2004) interpreted as the ventro-posterior process of the basisphenoid seems to be only an elevation of the palate on the basisphenoid.

The existence of a passage for the internal carotid arteries in the ventral surfaces of the pterygoids cannot be confirmed with confidence (contra O'Keefe 2004). The bone in this part of the skull is very thin and fragile, and parts of it have been broken and filled during preparation, so that the structures probably represent preparational artefacts.

In the ventral part of the palate, the bones lateral to the sella turcica should be regarded as part of the pterygoids or epipterygoids rather than prootics. Both prootics are found lying disarticulated posterior to the palate and are only exposed in lateral view. The right prootic is easily recognisable by its characteristic, roughly triangular form with a small process. A small elongated bone lies anterior to the left opisthotic, which covers its posterior end. This bone most probably represents the right stapes, due to its form and position. The visible end is rounded and slightly broader than the rest of the bone and is triangular in cross-section. The middle part of the bone is reconstructed.

Of the lower jaw, only the dentary is located on the slab. However, both posterior parts of the lower jaw are disarticulated and prepared in three dimensions. They have a thin anterior part, which is formed by the angular. The suture with the surangular runs posteriorly until it reaches a point just anterior to the glenoid fossa where it turns dorsally. The articular and angular are completely fused, and the suture is not distinguishable. The lateral part of the retroarticular process was probably formed by the angular and the dorsal and posterior part by the articular.

vertebra nr.	length	heigth	width	cervical index
1	1.15	0.94	1.51	1.22
2	1.35	1.00	1.51	1.35
3	1.39	1.13	1.70	1.23
4	1.43	1.05	1.70	1.36
5	1.55	1.14	1.90	1.36
6	1.54	1.11	1.94	1.39
7	1.63	1.33	1.99	1.23
8	1.73	1.33	2.14	1.30
9	1.94	1.30	2.20	1.49
10	1.95	1.40	2.22	1.39
15	2.16	2.70	2.64	0.80
20	2.40	1.87	3.05	1.28
25	2.68	2.33	3.30	1.15
30	2.79	2.57	3.40	1.08
35	2.83	2.51	3.62	1.17

Table 3.1: *Seeleyosaurus guilelmiimperatoris*: measurements in mm of the anterior cervical vertebrae of SMNS 16812 and relation of length to height.

The surangular forms the dorsal part of the posterior jaw, including the coronoid eminence. The glenoid fossa is divided into two concavities, a slightly larger lateral one and a medial one, which are separated by a low ridge. The splenial is missing, leaving the Mecklian canal uncovered. The mediolateral thickness increases suddenly in the middle of the posterior part of the lower jaw. This probably represents the posterior margin of the splenial and the former aperture of the Mecklian canal.

The postcranial skeleton was generally correctly described by DAMES (1895), FRAAS (1910) and O'KEEFE (2004). However, contra O'KEEFE (2004) the length of the cervical centra always exceeds their height by up to 1.5 times (Table 3.1). The ratio of the cervical length to height lies around an average of 1.33.

Genus HYDRORION gen. nov.

Type species. Plesiosaurus brachypterygius v. HUENE, 1923

Derivation of name. from *hydro* (Greek: water) and *Orion*, the hunter of the Greek mythology

Range and distribution. Only known from the Posidonia shale, Lias ε, Lower Toarcian of Holzmaden near Kirchheim-Teck, Baden-Württemberg, southwest Germany.

Diagnosis. As for type and only species.

Hydrorion brachypterygius (v. HUENE, 1923)

Fig. 3.2

v* 1923 *Plesiosaurus brachypterygius* v. HUENE, pp. 3 – 22, pls 1 – 2
v. *1994 ?Microcleidus* URLICHS *et al.*, fig. 104
v. 2000 *Plesiosaurus brachypterygius* MAISCH & RÜCKLIN 2000, pp. 29 – 40, figs 1 – 5

Type specimen. GPIT/RE/3185 (Fig. 2.12)

Type locality and horizon. Quarry 29, Ohmden near Holzmaden, Baden-Württemberg, southwest Germany; Posidonia shale, Lias εII_4 (Unterer Schiefer), *Harpoceras falcifer* zone, Lower Toarcian.

Referred specimens.

MB.R.1991 (Lias εII$_4$, Holzmaden): a complete specimen in lateral view; only the anterior part of the skull is preserved (Fig. 2.10).

SMNS 51143 (Lias εII$_4$, Ohmden near Holzmaden): a nearly complete specimen exposed in ventral view; the skull is incomplete and disarticulated; the lower jaw is complete and lying in situ at the end of the vertebral column (Fig. 2.6). Figured in Urlichs *et al.* (1994, fig. 104) as ?*Microcleidus*.

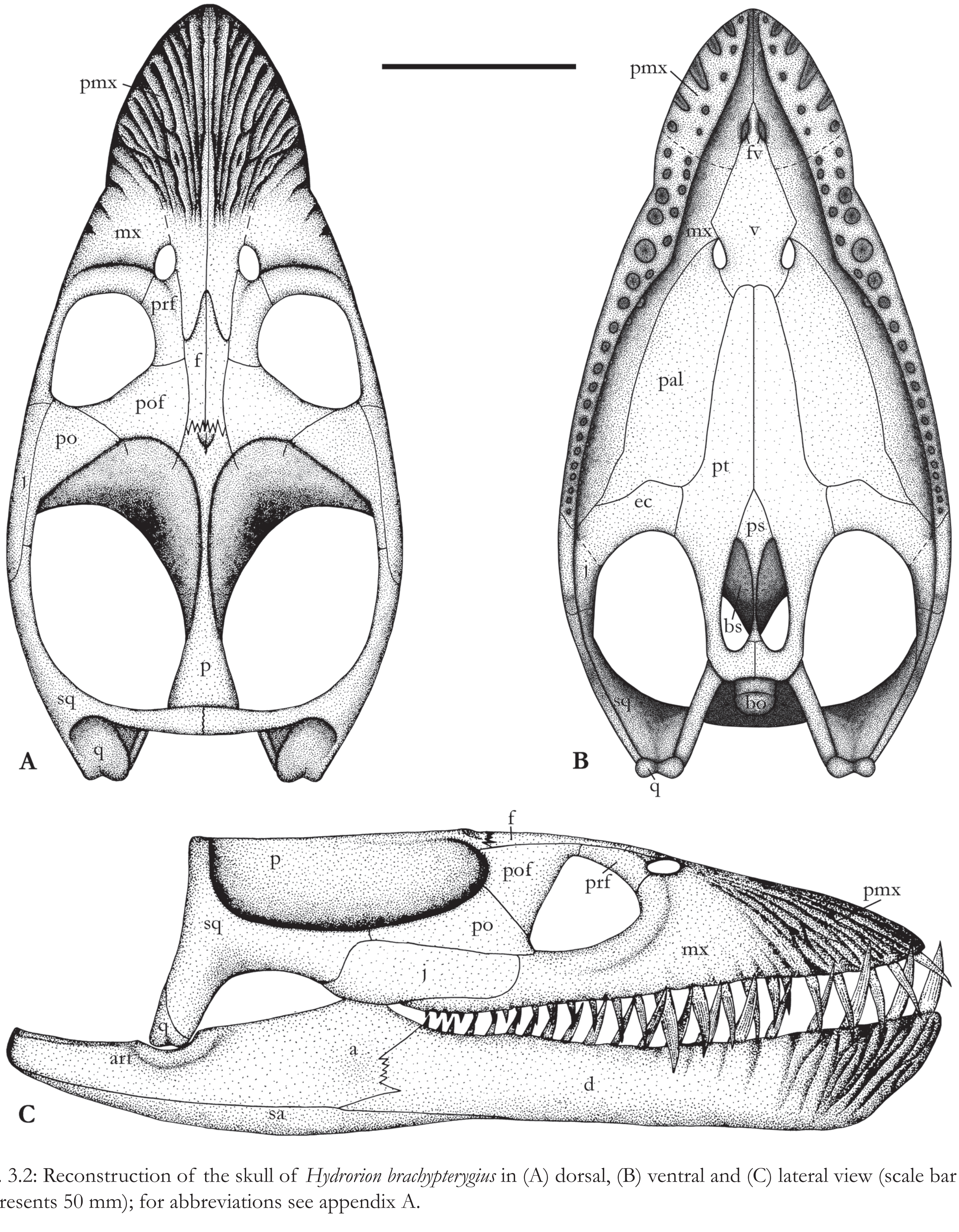


Fig. 3.2: Reconstruction of the skull of *Hydrorion brachypterygius* in (A) dorsal, (B) ventral and (C) lateral view (scale bar represents 50 mm); for abbreviations see appendix A.

SMNS 51141 (Lias εII$_4$, Holzmaden): a nearly complete juvenile specimen in dorsal view; skull in lateral view and nearly complete, with the right maxilla lying next to the skull; the mandible is dislocated; the metapodials of the fore- and hind limbs are very small and rounded and the first digit is scarcely developed, therefore it is a juvenile specimen (Fig. 2.5). Figured in Urlichs *et al.* (1994, fig. 105) as ?*Microcleidus*.

MH Nr. 8 (Lias ε, uppermost II$_4$ directly below II$_5$, Holzmaden): a nearly complete specimen in lateral view; the skull is incomplete and highly deformed so that no details are observable (Fig. 2.13).

Emended diagnosis. Moderately sized plesiosauroid, adults with an overall length of up to 3.0 m and a skull-length of approximately 180 to 200 mm, snout rounded and constricted, with elongated sculpturing, temporal openings larger than orbits; small teeth at the premaxillary-maxillary suture and four to five larger teeth in the maxilla and premaxilla near the premaxillary-maxillary suture; parietal foramen situated at the parietal-frontal suture, no jugal-orbit contact, no postorbital-parietal contact, squamosal with a lateral process extending ventrally; vomeronasal opening present, anterior interpterygoid vacuity absent, pterygoids meet in a dorsal median suture ventral to the basis cranii; 29 to 36 elongated cervical vertebrae, two to three sacral vertebrae, four proximal propodials in adults, maximum number of phalanges more than ten in the third finger, rather short limbs of approximately 20 per cent of the overall length in adults.

Range and distribution. Only known from the Posidonia shale, Lias εII$_4$, Lower Toarcian of Holzmaden, Baden-Württemberg, southwest Germany.

Description

In addition to the original description by v. Huene (1923), the skull of the type specimen of *H. brachypterygius* was described in detail by Maisch & Rücklin (2000). The descriptions are correct but for one point. Maisch & Rücklin (2000) described the supraoccipital as a “wide, delicate plate of bone sutured to the occipital rami of the squamosals laterally, the parietals dorsally and the otoccipitals ventrally” (Maisch & Rücklin 2000, p. 34). A close examination of the skull could not reveal any supraoccipital-squamosal sutures in the position indicated by the reconstruction of Maisch & Rücklin (2000). As in all plesiosaurs the squamosals in *Hydrorion* meet in a midline suture, and the supraoccipital

	Seeleyosaurus guilelmiimperatoris			*Hydrorion brachypterygius*				
	MB.R. 1992	SMNS 12039	SMNS 16812	GPIT/ RE/3185	MB.R. 1991	MH. Nr. 8	SMNS 51143	SMNS 51141
body lengths								
overall	2.88	3.40	2.44	3.00	3.09	2.88	2.88	1.73
skull	160	170	130	180	200	230	180	174
neck	1.23	1.30	0.84	0.80	1.18	1.10	1.26	0.73
trunk	0.75	0.90	0.77	0.74	0.89	0.80	0.77	0.54
fore limb	778 (0.27)	810 (0.23)	489 (0.20)	625 (0.21)	602 (0.20)	610 (0.21)	678 (0.23)	?
hind limb	681 (0.24)	890 (0.26)	495 (0.20)	640 (0.21)	636 (0.21)	630 (0.22)	691 (0.23)	330 (0.19)
number of vertebrae								
cervical	27	35	38	36	29	35	33	29
pectoral	4	4	5	5	2–3	5	4	3
dorsal	16	16	19	14	17–18	14	17	20
sacral	2	2	3	2	3	3	2	3
caudal	37	43	41	42	37	28	28	36
presacral	57	55	62	55	49	54	54	52
number of phalanges								
fore limb	(6.9.13.11.9)	(4.9.8.5.5)	5.9.12.10.9	4.8.12.11.10	4.9.12.12.11	4.8.13.11.11	4.9.11.10.?	?
hind limb	(4.5.5.4.2)	6.10.14.11.11	7.10.11.10.10	4.8.12.11.10	6.10.12.12.10	4.8.13.12.11	(5.8.11.10.10)	?

Tab. 3.2: Postcranial characters of specimens of *Seeleyosaurus guilelmiimperatoris* and *Hydrorion brachypterygius*. Measurements are in m, but skull lengths in mm; numbers in brackets after the limb lengths are the ratios of limb length to overall body length; phalangeal counts in brackets are from incomplete limbs.

is situated ventral to the squamosals. Due to the deformation of the skull the supraoccipital is now covered by the squamosals, and only the ventral extensions which contact the opisthotic-exoccipitals are visible (Fig. 2.12 C, D).

The postcranial has been correctly described for the holotype (v. Huene 1923). The assigned and undescribed specimen show considerable size variation (Table 3.2). The smallest individual (SMNS 52241) is a juvenile, as the neural arches are not fused to the centra and the metapodials are all rounded. The vertebral count for the five specimens assigned to the genus differ slightly (Table 3.2). The number of presacral vertebrae varies between 49 and 55, the number of cervical vertebrae between 29 and 36. The juvenile SMNS 51141 has a low number of cervical but a high number of dorsal and pectoral vertebrae. In adult specimens the position of the pectoral vertebrae shift posteriorly, and the number of cervical vertebrae increase. A variance of the position of the transitional pectoral vertebrae was also noted for *Cryptoclidus eurymerus* (Brown 1981), although in this species the number of cervical vertebrae was lower in the old adult specimen than in the juvenile one.

The pectoral bar which is seen in the type specimen (v. Huene 1923) is not found in any other specimen, which is due to incomplete, obscured of deformed pectoral girdles. If visible, the coracoid shows an expanded posterolateral corner. A pelvic bar probably existed in MB.R.1991, but its presence can not be confirmed for any other specimen.

The main differences between the specimens are found in the limbs. The anterior margin of the humerus is usually slightly convex, and its posterodistal corner is distinctly more expanded than the anterodistal. The humerus of the juvenile SMNS 51141 has a straight anterior margin, and only the posterodistal corner is expanded. In all specimens the femur is more straight than the humerus. The ulna is normally of lunate form, as usual in plesiosaurs. However, GPIT/RE/3185 and SMNS 51143 have an ulna which is constricted in the middle. This resembles the condition found in *Pistosaurus* (SUES 1987) and is therefore plesiomorphic. The usual lunate form of the ulna in plesiosaurs is probably due to delayed ossification of the metapodials, as shown for *Cryptoclidus eurymerus* (CALDWELL 1997), and the plesiomorphic form can then be found in old individuals. GPIT/RE/3185 has a fibula with a distinct notch in its posterior margin (V. HUENE 1923), a character not found in any other specimen.

The usual number of proximal carpals and tarsals in adults is four. The juvenile SMNS 51141, whose limbs are all disarticulated, has rounded and not fully ossified metapodials. The exact number of carpals and tarsals can not be given, but it was presumably less than in adult specimen. The usual number of distal carpals and tarsals is three, but MB.R.1991 has a supernumerary fourth distal carpal, which intercalates between the posterior margins of the carpals 2 and 3 and is bordered by the metacarpal V laterally.

The number of phalanges in the limbs differ slightly in the specimens (Table 3.2). The fourth digit is the longest, although the third one usually has one or two phalanges more. The phalangeal formula for SMNS 51141 can not be given, as the limbs are all disarticulated and incomplete. The best preserved limb is the right hind limb, and here can be deduced that the number of phalanges was distinctly lower than in adult specimens. It is also remarkable that the first digit is not or only very incompletely evolved in this juvenile specimen. This is also the case in another undescribed juvenile plesiosauroid specimen on display in the SMNS (SMNS 51945) (see chapter 2). CALDWELL (1997) noted that the mesopodial ossification spreads from postaxial to preaxial in Lower Jurassic plesiosaurs. This may also be the case for the metapodials, as seen by this delayed development of the first digit.

Comparison.

In order to demonstrate the validity of the new generic name *Hydrorion* and the new combination *Seeleyosaurus guilelmiimperatoris*, several comparisons are given here. It is shown that (1) *Seeleyosaurus holzmadensis* is a junior synonym of "*Plesiosaurus*" *guilelmiimperatoris*; (2) *Plesiopterys wildii* is also a junior synonym of *"P." guilelmiimperatoris* and (3) that *"P." guilelmiimperatoris* and *"P." brachypterygius* differ sufficiently from other taxa, as to be given own generic status.

1. Seeleyosaurus holzmadensis *is a junior synonym of* "P." guilelmiimperatoris. WHITE (1940) based his classification of plesiosaurs to a high degree on differences in the shoulder girdle. He gave three characters that would distinguish *S. holzmadensis* from *"P." guilelmiimperatoris*: (1) an extremely brachycephalic skull; (2) the presence of an interclavicle and (3) the general form of the shoulder girdle. Unfortunately the skull proportions cannot be determined for either the type specimens of *S. holzmadensis* (SMNS 12039) nor *"P." guilelmiimperatoris* (MB.R.1992), as both skulls are severely crushed and only visible in lateral view (Figs 2.1, 2.11), so that the breadth of the skulls can only be estimated. Due to the deformation of the shoulder girdle of MB.R.1992, which is only partially visible, it is also difficult to compare the shoulder girdles of the two specimens. The apparent absence of an interclavicle does not mean that it was never present in the specimen, it might be hidden by other parts of the skeleton; an elongated portion of bone attached to the clavicle might represent the remains of the posterior extension of the interclavicle.

SMNS 12039 and MB.R.1992 have several characters in common which are not shared with other taxa such as for example *Cryptoclidus*, *Muraenosaurus*, *Hydrorion*, *Microcleidus* or *Brancasaurus*. Both skulls are deformed, but the general arrangement of the sutures of the skull roof is similar (especially the form and position of maxilla, jugal, pre- and postfrontal). The teeth of both specimens have asymmetrical ornamentation, where the striation on the buccal part of the crown is less pronounced or absent. Similar tooth ornamentations are known from the Callovian genera *Muraenosaurus* and *Cryptoclidus* but are absent in other Liassic taxa such as *Plesiosaurus dolichodeirus*, *Hydrorion brachypterygius* or *Microcleidus homalospondylus*. Both specimens have a high degree of concordance in the number of vertebrae (FRAAS 1910), which differ only in the number of cervical (SMNS 12039 has two less than MB.R.1992) and caudal vertebrae (SMNS 12039 has six more than the MB.R.1992). The overall body proportions like neck and trunk length in the two specimens are also similar (Table 3.2), especially the proportional length of the paddles, which are approximately 25 per cent of the overall body length.

It is therefore concluded, that *Seeleyosaurus holzmadensis* is a junior synonym of "*Plesiosaurus*" *guilelmiimperatoris*.

2. Plesiopterys wildii *is a junior synonym of* "P." guilelmiimperatoris. O'KEEFE (2004) gives four autapomorphies for *Plesiopterys wildii*. Two of these characters ((1) possession of flanges of the pterygoid dorsal to the plane of the palate at the anterior end of the posterior interpterygoid vacuity; (2) exposure of the cultriform process of the parasphenoid almost to the margin of anterior interpterygoid vacuity) result from his misinterpretation of the parasphenoid (see above). The third character (large anterior interpterygoid vacuity with round posterior margin and pointed anterior margin) can be found in both *Muraenosaurus* (Andrews 1910, p. 89) and *Tricleidus* (Andrews 1910, p. 152) and is therefore not a generic autapomorphy. The fourth character (quadrate flange of the pterygoid is straight and narrow and expands into a wide boss at its terminus) could not be determined in the specimen, as the posterior end of the quadrate process of the pterygoid is not preserved (see also O'Keefe 2004, p. 981).

SMNS 16812 shows several similarities to *Seeleyosaurus guilelmiimperatoris*. The asymmetrical tooth ornamentation with more prominent longitudinal striae on the lingual side and weaker or absence of striae on the buccal side can be found in all three specimens assigned to this genus.

Furthermore SMNS 16812 and *Seeleyosaurus guilelmiimperatoris* share a combination of characters in the cheek which is not found in any other plesiosauroid taxon. This includes a horizontally orientated, elongated rectangular jugal which forms part of the orbits; a maxillary-jugal suture with a right angle between its nearly vertical dorsal part and the horizontal ventral part; and a squamosal with an anterodorsal process for contact with the postorbital, thus excluding the jugal from the temporal opening. This arrangement of sutures in the cheek is quite different to the condition found in *Plesiosaurus* and *Thalassiodracon*. *Muraenosaurus*, *Hydrorion* or *Brancasaurus* each show a partial combination of these characters, but only *Seeleyosaurus guilelmiimperatoris*, SMNS 12039 and SMNS 16812 possess all of them. The postcranial skeleton of the specimens is very plesiomorphic, and there are few distinguishing features. The number of cervical vertebrae is nearly the same in SMNS 16812 and the type specimen of *Seeleyosaurus guilelmiimperatoris* (Table 3.2), but SMNS 16812 has more dorsal vertebrae. However, this difference lies within the range of variation as seen in the different specimens of *Hydrorion brachypterygius* (Table 3.2). The absence of a pelvic bar in SMNS 16812 (present in SMNS 12039) is a ontogenetic feature, as is also the absence of a fourth proximal tarsal and carpal (present in MB.R.1992 and SMNS 12039). SMNS 16812 has slightly less phalanges than the other two specimen, but this is to be expected in a juvenile specimen. SMNS 16812 is therefore assigned to *Seeleyosaurus guilelmiimperatoris*.

The relative length of the paddle compared to the body length lies around 0.25 in *Seeleyosaurus* and is 0.2 for SMNS 16812 (Table 3.2). The relative paddle in juveniles is slightly smaller than in adults, as seen for *Hydrorion* (Table 3.2), but the difference between *Seeleyosaurus* and SMNS 16812 is too high as to be completely due to ontogentic growth. The measurements for the paddle length of SMNS 16812 were taken from the mounted skeleton. They are not yet fully ossified and rounded, but the bones are nearly in contact with one another, leaving nearly no interspace, unlike the situation in other juvenile specimens (SMNS 51141 and 51945). It has to be assumed that the paddles were mounted rather to tight and that the actual size of the paddle in the living animal was longer.

3. The validity of the genera Seeleyosaurus *and* Hydrorion. To show that *Seeleyosaurus* and *Hydrorion* differ sufficiently from other genera, they are compared with similar taxa. These include *Plesiosaurus*, the genus to which the two German species were originally ascribed, the Upper Jurassic genus *Muraenosaurus*, which resembles *Seeleyosaurus*, and the Liassic genera *Microcleidus* and *Occitanosaurus*, which are similar to *Hydrorion*. The main results of this comparison are summarized in Table 3.3.

	Plesiosaurus	*Seeleyosaurus*	*Muraenosaurus*	*Hydrorion*	*Microcleidus*	*Occitanosaurus*
snout ornamentation	no ornamentation	small pits	no ornamentation	prominent ridges and furrows	prominent ridges and furrows	prominent ridges and furrows
snout form	not constricted	not constricted	not constricted	constricted	constricted	constricted
posterior extent of the premaxilla	up to middle of the orbits	up to middle of the orbits	up to middle of the orbits	up to middle of the orbits	up to middle of the orbits	shortly posterior of nares
prefrontal	broad, forms anterior margin of the orbits	forms anterodorsal margin of the orbits	forms dorsal margin of the orbits	forms dorsal margin of the orbits	forms anterodorsal margin of the orbits	forms anterior margin of the orbits
parietal foramen	large, completely in parietals, at the middle of the postorbital bar	with frontal participation, at the posterior margin of the postorbital bar	with frontal participation, at the posterior margin of the postorbital bar	with frontal participation, at the posterior margin of the postorbital bar	completely in parietals, at the posterior margin of the postorbital bar	parietal foramen lost
jugal	participates in orbits	participates in orbits	participates in orbits	excluded from orbits	excluded from orbits	excluded from orbits
anterior interpterygoid vacuity	present, slit–like	present, rounded posterior margin	present, rounded posterior margin	absent	absent	absent
parasphenoid	lanceolate	without cultriform process	without cultriform process	lanceolate	lanceolate	lanceolate
posterior ending of the pterygoid	no posterior median suture	no posterior median suture	no posterior median suture	with posterior median suture	with posterior median suture	no posterior median suture
dentition	homodont	larger teeth in maxilla and premaxilla	larger teeth in maxilla and premaxilla	larger teeth in maxilla and premaxilla	larger teeth in maxilla and premaxilla	larger teeth in maxilla and premaxilla
tooth ornamentation	symmetrical	asymmetrical	asymmetrical	symmetrical	symmetrical	symmetrical
number of cervical vertebrae	38 – 42	35 – 38	44	29 – 36	38	44
form of cervical vertebrae	amphicoelous, not elongated	amphicoelous, elongated	amphicoelous, elongated	amphicoelous, elongated	amphicoelous, elongated	platycoelous, elongated
number of proximal metapodials	3	4	3–4	4	4	unknown
maximal number of phalanges	10	13 – 14	14 – 15	12 – 13	7	unknown

Table 3.3: Distinguishing characters of the genera *Plesiosaurus*, *Seeleyosaurus*, *Muraenosaurus*, *Hydrorion*, *Microcleidus* and *Occitanosaurus*.

However, some additional information has to be given, and some remarks to be made.

Hydrorion and *Seeleyosaurus* differ in the length of their limbs. In *Seeleyosaurus* the limbs of adults are approximately 25 per cent of the overall body length, whereas in adult specimens of *Hydrorion* they are distinctly shorter and only about 20 per cent of the overall body length (Table 3.2).

Seeleyosaurus resembles *Muraenosaurus*, especially in the construction of the palate. The form of the parasphenoid, which has a rounded anterior ending lacking a cultriform process, is only found in these two genera and in *Tricleidus* from the Upper Jurassic of England. Further differences exist in the course of the maxillary-jugal suture, which has a distinct angle in *Seeleyosaurus* and is more continually in *Muraenosaurus*. *Muraenosaurus* also lacks the anterodorsal process of the squamosal which is present in *Seeleyosaurus*. In the palate the vomer of *Muraenosaurus* extends further posteriorly than in *Seeleyosaurus*. In *Muraenosaurus* the pterygoids have a lateral extension anterior of the posterior interpterygoid vacuities and the ectopterygoids are small, whereas the ectopterygoids in *Seeleyosaurus* are larger and the pterygoids lack a lateral extension.

Unfortunately no detailed modern reconstruction of *Muraenosaurus* is available, and the most recent preliminary reconstruction (Evans 1999) shows significant differences in shape and bone arrangement from the first reconstruction by Andrews (1910). Therefore a comparison of the cranial morphology of these two genera is rather difficult. However, the taxa differ also in their postcranial morphology (Table 3.3). Additionally it has to be noted that the epipodials have a columnar form in *Seeleyosaurus*, and are longer than broad, which is not the case in *Muraenosaurus*.

PHYLOGENETIC ANALYSIS

Introduction and methods

A phylogenetic analysis of 13 ingroup taxa and one outgroup (Fig. 4.1, Table 4.1) was carried out to specify the position of the German taxa within a phylogeny of the Lower Jurassic plesiosauroids. Therefore the Liassic plesiosauroid genera *Thalassiodracon*, *Plesiosaurus* and *Microcleidus* from England and *Occitanosaurus* from south France as well as the two German taxa *Hydrorion brachypterygius* and *Seeleyosaurus guilelmiimperatoris* were included. In order to test O'Keefe's (2004) hypothesis that *Plesiopterys wildii* is a valid genus and a very basal plesiosauroid, SMNS 16812 (the holotype of *Plesiopterys wildii*) was coded independently from *Seeleyosaurus*. These seven taxa comprise all known plesiosauroids from the Lower

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Pistosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassiodracon	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	?	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0
Plesiosaurus	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cryptoclidus	0	0	1	1	0	0	2	0	0	0	1	0	0	1	1	?	0	?	?	1	1	0	1	0	1	1	0	0	0	0	1	1	0
Kimmerosaurus	?	0	1	1	0	0	2	?	0	?	1	?	0	1	1	?	?	?	0	1	1	0	1	?	?	1	?	0	0	0	?	?	0
SMNS 16812	0	0	0	1	1	?	?	0	1	0	0	1	0	0	1	?	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0
Seeleyosaurus	0	0	0	1	1	1	?	0	1	0	0	1	0	0	?	?	?	?	0	0	?	?	0	1	1	0	1	1	0	0	1	1	0
Muraenosaurus	?	0	0	1	1	1	1	1	1	0	0	1	0	1	1	1	0	1	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0
Occitanosaurus	1	1	0	0	2	0	1	1	1	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0
Hydrorion	1	1	0	0	1	1	1	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	0	1	1	0
Microcleidus	1	1	0	0	1	1	1	1	1	1	0	1	?	1	0	?	?	0	1	0	0	0	0	1	?	?	1	1	0	1	1	?	0
Brancasaurus	0	0	0	1	1	1	1	1	1	0	0	1	1	1	?	0	1	0	?	0	0	1	0	1	1	0	1	1	1	1	1	0	1
Libonectes	0	0	0	0	2	1	1	?	?	?	0	1	1	?	0	0	1	0	1	0	0	1	0	1	0	0	1	1	1	1	1	?	1

Table 4.1: Data matrix with the character states used in the phylogenetic analysis.

Liassic. To clarify their position within the different plesiosauroid families, the British Upper Jurassic genera *Muraenosaurus*, the cryptoclidids *Kimmerosaurus* and *Cryptoclidus* and the Cretaceous elasmosaur genera *Brancasaurus* from Germany and *Libonectes* from North America, were added. These genera were chosen because they are representative for their families as well as well described and figured in literature. The genus *Pistosaurus* was chosen as an outgroup, as it is considered by several authors to be the sister taxon to all plesiosaurs (Sues 1987, Rieppel 1999, O'Keefe 2001a).

The taxa were scored for 33 morphological characters, all unordered and unweighted, 26 of them refer to the skull and dentition and seven to postcranial anatomy. Character coding was based on first hand observations for the German genera. *Microcleidus* is inadequately described, and all skull characters were determined using the newly prepared and well preserved skull of the holotype (BMNH 36184). All other information was taken from literature. The characters were scored zero for the basal state and the polarity was determined by comparison with the outgroup, *Pistosaurus*. Most of the characters were taken from Bardet *et al.* (1999); O'Keefe (2001a); Gasparini *et al.* (2002) and from an unpublished analysis of the Plesiosauria undertaken by Dr M. W. Maisch.

Results and discussion.

The data matrix (Table 4.1) was analysed using PAUP*4b10 (Swofford 2001), which resulted in three most parsimonious trees. The consensus tree has a length of 53 steps, the consistency index (CI) is 0.64, the rescaled consistency index (RC) is 0.49 and the retention index (RI) is 0.77.

In this tree (Fig. 4.1), *Thalassiodracon* and *Plesiosaurus* represent the basal members of the plesiosauroids. *Cryptoclidus* and *Kimmerosaurus* together form the family Cryptoclididae, whose monophyly is well established by several synapomorphies, such as the shape and orientation of the jugal and the shortened paroccipital process. All other taxa belong to the family Elasmosauridae. At its base the exact position of SMNS 16812 and *Seeleyosaurus* in relation to all other elasmosaurs remains unresolved. Here the three most parsimonious trees differ, one showing SMNS 16812 and *Seeleyosaurus* as a monophyletic clade, one placing *Seeleyosaurus* at the base of the elasmosaurs, and in the third SMNS 16812 appears as the most basal elasmosaur. As can be seen in the matrix (Table 4.1) the character coding for SMNS 16812 and *Seeleyosaurus* mostly coincides, apart from those characters whose states are unknown for one or the other taxon. This favours the inclusion of SMNS 16812 into the genus *Seeleyosaurus*, as proposed in chapter 3.

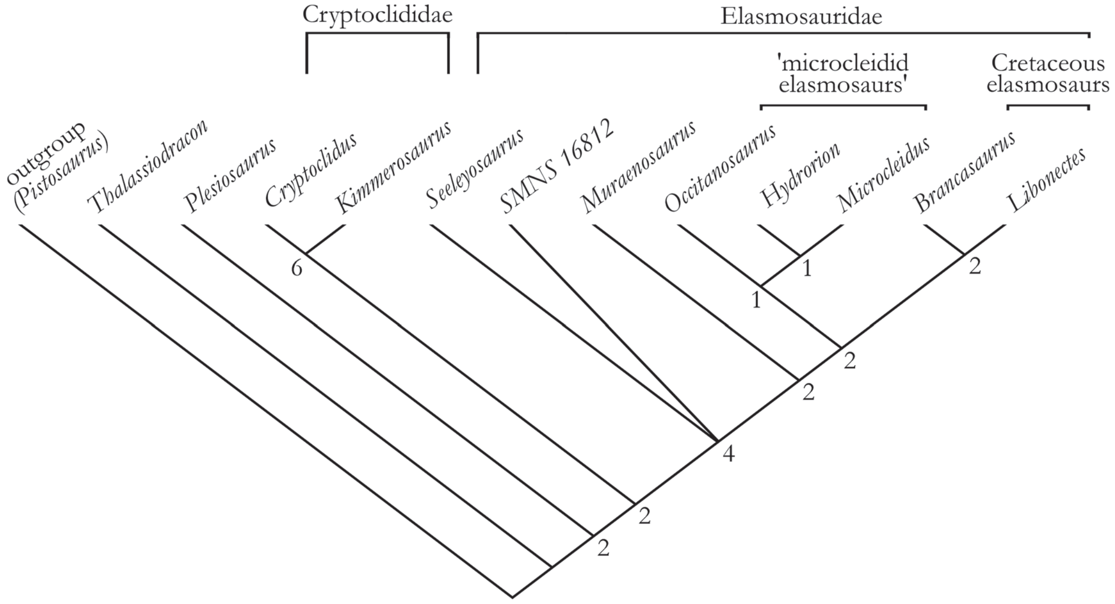


Fig. 4.1: Most parsimonious tree resulting from the phylogenetic analysis. Numbers next to nodes indicate Bremer support.

Whatever the actual positions might be, both *Seeleyosaurus* and SMNS 16812 are, together with *Muraenosaurus*, basal elasmosaurs. The genera *Microcleidus, Occitanosaurus* and *Hydrorion* form a monophyletic clade, here called the 'microcleidid elasmosaurs'. This is the sister taxon of the more derived Cretaceous elasmosaurs *Brancasaurus* and *Libonectes*, which also form a monophyletic clade in this study. The 'microcleidid elasmosaurs' exhibit basal plesiosauroid characters, for example the long and slender paroccipital process and absence of a large intercoracoid fenestra, but also share derived characters with the Cretaceous elasmosaurs, such as the closed palate. The 'microcleidid elasmosaurs' are characterised by a deeply sculptured and constricted snout and the exclusion of the jugal from both orbit and temporal opening.

Three main groups can be distinguished from this phylogeny: (1) the basal plesiosauroids *Thalassiodracon* and *Plesiosaurus*; (2) the cryptoclidids *Cryptoclidus* and *Kimmerosaurus*; and (3) the Elasmosauridae, including *Muraenosaurus* and *Seeleyosaurus* as basal members, the 'microcleidid elasmosaurs' and the Cretaceous elasmosaurs *Brancasaurus* and *Libonectes*.

The presented result is similar to the published phylogenies of Bardet *et al.* (1999) and Gasparini *et al.* (2003). The analysis of Gasparini *et al.* (2003) uses mainly characters taken from Bardet *et al.* (1999) and only three characters differ. A comparison with Gasparini *et al.* (2002), from which several characters were taken, is not necessary, since this phylogeny is based exclusively on cryptoclidids. Only Bardet *et al.* (1999) included *Hydrorion brachypterygius* (as *P. brachypterygius*) and *Seeleyosaurus guilelmiimperatoris* (as *P.*

guilelmiimperatoris). Both studies regarded *Occitanosaurus*, *Microcleidus* and *Muraenosaurus* as closely related and included them into the Elasmosauridae. *Hydrorion* and *Seeleyosaurus* are more basal in BARDET *et al.* (1999), in which *Hydrorion* formed a trichotomy together with the outgroup (*P. dolichodeirus*) and all other plesiosauroids, whereas *Seeleyosaurus* was the sister–taxon to all plesiosauroids apart from the outgroup and *Hydrorion*. The different positions of *Hydrorion* and *Seeleyosaurus* between the present study and BARDET *et al.* (1999) can be explained by new personal observations and new data, especially on the palate of *Seeleyosaurus*, which differs significantly from that of *P. dolichodeirus*.

O'KEEFE's (2001a) analysis placed *Microcleidus* at the base of the Plesiosauroidea, in a trichotomy with the Elasmosauridae and the Cryptocleidoidea. In this analysis (O'KEEFE 2001a) *Muraenosaurus* is the sister taxon of *Cryptoclidus* and included into the Cryptoclididae, whereas in BARDET *et al.* (1999), GASPARINI *et al.* (2003) and the current analysis *Muraenosaurus* is part of the Elasmosauridae. The construction of the parasphenoid with a smooth anterior margin and no cultriform process supports O'KEEFE's (2001a) theory, but postcranial characters such as the number and elongation of the cervical vertebrae place *Muraenosaurus* within the elasmosaurs in the current study.

A great difference between the analysis presented here and one published by O'KEEFE (2004) lies in the position of '*Plesiopterys wildii*'. In the analysis (O'KEEFE 2004) '*Plesiopterys wildii*' was shown to be the sister taxon of all other plesiosauroids including *Plesiosaurus*, and was placed outside the Plesiosauroidea by O'KEEFE (2004). '*Plesiopterys wildii*' is regarded as a junior synonym of *Seeleyosaurus guilelmiimperatoris* in this study, which is supported by the close relationship of these two taxa in the present study. The differences between the two studies can mainly be ascribed to the different interpretation of the palate (see chapter 2).

Furthermore several problems arise with the character codings for the newly added characters 168 to 170 (O'KEEFE 2004). Character 168 relates to a posterior process of the postorbital, which according to O'KEEFE (2004) can only be found in the pistosauroids, *Plesiopterys*, *Plesiosaurus*, *Thalassiodracon* and *Rhomaleosaurus megacephalus*. A posterior extension of the postorbital which forms part of the ventral margin of the parietal fenestra can also be found in *Muraenosaurus* (ANDREWS 1910), *Hydrorion* (DAMES 1985; MAISCH & RÜCKLIN 2000; this paper), *Microcleidus* (BROWN, D. S. 1993), *Occitanosaurus* (BARDET *et al.* 1999), *Brancasaurus* (WEGNER 1914), *Leptocleidus* (CRUICKSHANK 1997), *Pliosaurus* (TAYLOR & CRUICKSHANK 1993b), *Elasmosaurus* (WELLES 1949) and *Hydrotherosaurus* (WELLES 1943). It is definitely absent in the cryptoclidids (sensu BARDET *et al.* 1999) and the absence of this character seems to be more characteristic for this group, than its presence is for any other. Character 169 refers to a deep notch in the posterior part of the basioccipital body which O'KEEFE (2004) states is found in *Cymatosaurus*, *Plesiopterys*, '*Eurycleidus*' and *Thalassiodracon*. MAISCH (1998) described such a structure as remnants of the embryonic posterior basicranial foramen from specimens of *Muraenosaurus* of different ontogenetic stages, and concluded that the foramen probably persisted as an unossified area between basisphenoid and parasphenoid in adults. The opening of the foramen towards the palate is closed during ontogeny, so that in adults the foramen can only be seen in disarticulated specimens. Therefore it cannot be confirmed in those genera for which only articulated specimens are known and might be present in other taxa than the ones mentioned by O'KEEFE (2004).

Character 170 relates to grooves on the dorsal surface of the pterygoid for the internal carotid artery in *Nothosaurus* and *Cymatosaurus*. These grooves are also described by O'KEEFE (2004) in '*Plesiopterys*', but, as shown in chapter 2, the structures are probably caused by preparation.

Definition of characters

1. Snout with no or with weak sculpture (0), snout distinctly sculptured (1).

   Sculpturing of the snout is usually absent in basal plesiosauroids (*Thalassiodracon*, *Plesiosaurus*) or consists of small pits on premaxilla, maxilla and dentary (*Seeleyosaurus*, *Brancasaurus*, *Libonectes*). Only *Occitanosaurus*, *Hydrorion* and *Microcleidus* show a pronounced sculpturing which is formed by anteriorly and anterolaterally running ridges and furrows on the snout and anterior lower jaw.
2. Snout not constricted (0), snout constricted (1).

   So far, this character has only been described for pliosauroids (O´KEEFE 2001a; MAISCH unpubl.) Among the Plesiosauroidea, the genera *Occitanosaurus*, *Microcleidus* and *Hydrorion* have a slight constriction at the premaxillary-maxillary suture, which is not found in any other plesiosauroid.
3. Cheek emargination weak, ventral surface of jugal and squamosal almost flat (0), deeply emarginated (1) (BARDET *et al.* 1999, character 4; O´KEEFE 2001a, character 10; modified MAISCH unpubl.).

   This is one of the synapomorphies of the Family Cryptoclididae. All other taxa have a weak cheek emargination.
4. Temporal fenestra larger than orbit (0); temporal fenestra approximately the same size as orbit (1) (modified BARDET *et al.* 1999; MAISCH unpubl.)

   The plesiomorphic condition is found in *Pistosaurus* as well as in *Nothosaurus* and in most elasmosaurs with the exception of the basal genera *Seeleyosaurus* and *Muraenosaurus*. The lower Cretaceous genus *Brancasaurus* has also orbits of approximately the same size as the temporal fenestra, but here it seems as if the orbits are enlarged, and have a distinctly elongated shape, as well as the temporal fenestrae. The basal plesiosauroids *Thalassiodracon* and *Plesiosaurus* as well as the cryptoclidids have enlarged temporal openings.

5. Foramen parietale between orbits and temporal openings (0), foramen parietale nearer to temporal openings than to orbits (1).

   The plesiomorphic condition of this character was defined according to its state in *Thalassiodracon* and *Plesiosaurus*. Several basal pliosauroids also have the plesiomorphic condition. All elasmosaurs have a posteriorly shifted parietal foramen. The condition in *Occitanosaurus* and *Libonectes* is unknown, the parietal foramen is absent.

6. Premaxilla reaches posteriorly up to anterior orbital margin (0), reaches above orbit (1) (modified O'Keefe 2001a, character 11; Maisch unpubl.).

   In *Pistosaurus* the dorsomedial process of the premaxilla reaches slightly posterior to the anterior orbital margin. The process is also short in *Thalassiodracon*, *Cryptoclidus*, *Kimmerosaurus* and *Occitanosaurus*. All other plesiosauroids have a dorsomedial premaxillary process that reaches considerably posterior to the anterior orbital margin.

7. Prefrontal separated from external nares (0), forms posterior margin of external nares (1), prefrontal absent (modified Bardet *et al.* 1999, character 6; Maisch unpubl.).

   Only *Thalassiodracon* shows the plesiomorphic condition found in *Pistosaurus*. The cryptoclidids have lost their prefrontal completely. In all other plesiosauroids the prefrontal is anteriorly expanded and contacts the external nares.

8. Form of the postfrontal triangular (0), quadrangular (1) (Bardet *et al.* 1999, character 7).

   Pistosaurus has a triangular postfrontal, as have *Thalassiodracon*, *Plesiosaurus* and the Cryptoclididae. All elasmosaurs with the exception of *Seeleyosaurus* have a quadrangular postfrontal.

9. Jugal-postorbital suture short and/or sigmoidal (0), large and/or straight (1) (Bardet *et al.* 1999, character 2).

   In *Pistosaurus*, *Thalassiodracon*, *Plesiosaurus* and the cryptoclidids the postorbital has a distinctly curved and not very extensive contact with the jugal. In contrast to this the jugal-postorbital suture in the Elasmosauridae is distinctly longer and straight.

10. Jugal participates in the orbital margin (0), does not participate in the orbital margin (1) (BARDET *et al.* 1999, character 3; O'KEEFE 2001a, character 31).

    The jugal forms most of the ventral part of the orbit in *Pistosaurus*, and participates in all plesiosauroids with the exception of *Occitanosaurus*, *Hydrorion* and *Microcleidus*. In these three genera the postorbital gains contact with the maxilla, thus excluding the jugal from the orbit.

11. Long axis of jugal horizontal (0), jugal transformed into narrow vertical strut (1) (modified BARDET *et al.* 1999, character 1; O'KEEFE 2001a, character 33; MAISCH unpubl.).

    This is an autapomorphy of the cryptoclidids. All other taxa have an elongated jugal with a horizontal long axis.

12. Maxilla extends approximately to the posterior margin of the orbit (0), extends considerably beyond orbit (1) (MAISCH unpubl.).

    The posteroventral process of the maxillary is short in *Pistosaurus* as well as in *Plesiosaurus* and *Cryptoclidus*. All other taxa have an enlarged posteroventral maxillary process, which reaches beyond the posterior orbital margin.

13. Maxilla and squamosal separated by jugal (0), in contact along zygomatic arch (1) (MAISCH unpubl.)

    In *Pistosaurus* and *Plesiosaurus* the maxilla does not reach a level posterior to the orbital margin. In all other plesiosaurs the maxilla is extended posteriorly, but only in the Cretaceous elasmosaurs *Brancasaurus* and *Libonectes* the maxilla and squamosal gain contact. The condition in *Microcleidus* is uncertain. In the only published reconstruction of *Microcleidus* (BROWN, D. S. 1993) the maxilla and squamosal do not contact, although the distance between them is very short. Personal observation on BMNH 36183 shows a broken posterior ending of the maxilla, which might well have covered the small remaining distance to the squamosal. The character has therefore been coded as unknown for *Microcleidus*.

14. Squamosal reaches forward to the anterior margin of the temporal opening (0), does not reach the anterior margin of the temporal opening (1) (O'KEEFE 2001a, character 41; MAISCH unpublished)

    In the basal plesiosaurs *Thalassiodracon* and *Plesiosaurus* the zygomatic ramus of the squamosal ends slightly anterior to the anterior margin of the temporal opening. In the Cryptoclididae and Elasmosauridae, the anteriormost end of the squamosal is situated approximately in the middle of the zygomatic arch.

15. Anterior interpterygoid vacuity absent (0), present (1) (Bardet *et al.* 1999, character 13; O'Keefe 2001a, character 60; modified Gasparini *et al.* 2002, character 6; modified Maisch unpubl.).

    Pistosaurus has a closed palate without any opening, as does *Thalassiodracon*. *Plesiosaurus*, the Cryptoclididae, *Seeleyosaurus* and *Muraenosaurus* have an anterior interpterygoid vacuity, whereas the remaining elasmosaurs have none. This character could be linked to cranial kinetics and feeding habits (Bardet *et al.* 1999).

16. Vomeronasal fenestra absent (0), present (1) (modified Maisch unpubl.).

    A vomeronasal fenestra is present in *Pistosaurus*, which represents the plesiomorphic condition. It appears to have been reduced several times independently in the plesiosaurs, and only *Hydrorion* and the Cretaceous elasmosaurs retain the vomeronasal fenestra. The situation in the cryptoclidids remains unknown.

17. Vomer extends considerably posterior to internal nares (0), ends shortly posterior to internal nares (1) (O'Keefe 2001a, character 83; Maisch unpubl.)

    The plesiomorphic condition shown by *Pistosaurus* is a vomer with a posterior extension which reaches considerably posterior to the internal nares. In *Occitanosaurus*, *Hydrorion*, and the Cretaceous elasmosaurs the vomer ends just posterior to the internal nares. The condition in *Microcleidus* is unknown.

18. Parasphenoid oblong with long cultriform process (0), plate-like without cultriform process (1) (modified O'Keefe 2001a, character 70; modified Maisch unpubl.)

    The parasphenoid in plesiosauroids usually has a lanceolate form, and the cultriform process forms the anterior tip. The genera *Seeleyosaurus* and *Muraenosaurus* have a plate-like parasphenoid which lacks a cultriform process. The parasphenoid in *Cryptoclidus* and *Kimmerosaurus* is not known, but the cryptoclidid *Tricleidus*, not included in this analysis, has also a plate-like parasphenoid.

19. Pterygoids without posterior median suture below basis cranii (0), pterygoids meet in a posterior median suture below *basis cranii* (1) (modified Bardet *et al.* 1999, character 12; O'Keefe 2001a, character 62; Maisch unpubl.).

    The basal plesiosaurs have a *basis cranii* which is not completely covered by the pterygoids. These form a medial extension, but do not meet in a posterior median suture. In *Hydrorion*, *Microcleidus* and *Libonectes* the pterygoids contact each other posterior to the posterior pterygoid vacuity.

20. Exoccipital condyle formed by basioccipital only (0), formed by basioccipital and exoccipitals (1) (Bardet *et al.* 1999, character 14; O'Keefe 2001a, character 42; Gasparini *et al.* 2002, character 7; Maisch unpubl.).

    The exoccipital forms a small portion of the exoccipital condyle only in the Cryptoclididae. In all other taxa including *Pistosaurus* the condyle is formed exclusively by the basioccipital.

21. Paroccipital process long and slender (0), shortened (1) (modified O'Keefe 2001a, character 46; Maisch unpubl.)

    The paroccipital process is shortened in the Cryptoclididae, a synapomorphy of the family. All other taxa have long and slender paroccipital process.

22. Paroccipital process extending rather laterally (0), strongly deflected ventrally (1) (Maisch unpubl.)

    The paroccipital process in the Plesiosauria usually extends laterally. A ventrally deflected paroccipital process is only found in the Cretaceous elasmosaurs *Brancasaurus* and *Libonectes*.

23. Number of premaxillary tooth positions 5 (0), more than 5 (1) (Bardet *et al.* 1999, character 15; O'Keefe 2001a, character 106; Gasparini *et al.* 2002, character 8; Maisch unpubl.).

    The primitive number of premaxillary teeth is five (Brown, D. S. 1981), and this number is retained in most taxa. The number increases only in the Cryptoclididae, *Cryptoclidus* has six and *Kimmerosaurus* eight premaxillary teeth.

24. Upper dentition isodont around premaxillary-maxillary suture (0); small teeth around the premaxillary-maxillary suture (1) (modified Bardet *et al.* 1999, character 17; O'Keefe 2001a, character 102; Maisch unpubl.).

    Thalassiodracon, *Plesiosaurus* and the Cryptoclididae have a dentition without obvious changes in the tooth size around the premaxillary-maxillary suture. All elasmosaurs have smaller teeth directly next to the premaxillary-maxillary suture and more pronounced teeth anterior and posterior to these.

25. Tooth ornamentation symmetrical (0), tooth ornamentation asymmetrical (1) (O'Keefe 2001a, character 105; modified Gasparini *et al.* 2002, character 9; Maisch unpubl.)

    In basal plesiosaurs, such as *Thalassiodracon* (Storrs & Taylor 1996) and *Plesiosaurus dolichodeirus* (Storrs 1997), the sculpturing on the teeth is well-developed on both the labial and the lingual side. The sculpturing in *Brancasaurus*, *Seeleyosaurus* and *Muraenosaurus* is asymmetrical and is distinctly weaker on the buccal side of the teeth than on the lingual side. In contrast to this the teeth of the 'microcleidid elasmosaurs' have ornamentation all round the tooth crown. The tooth ornamentation in *Kimmerosaurus* and *Cryptoclidus* is greatly reduced, but in *Cryptoclidus* some faint striae remain on the lingual side of the teeth.

26. Tooth ornamentation well developed (0), strongly reduced (1) (modified Bardet *et al.* 1999, character 18; Maisch unpubl.).

    The teeth of the Plesiosauria are usually ornamented by more or less prominent ridges, which can be very fine in the case of *Plesiosaurus*. The Cryptoclididae are the only family where the tooth ornamentation is drastically reduced or as in *Kimmerosaurus* even absent.

27. Number of cervical vertebrae less than 35 (0), 35 or more (1) (modified Bardet *et al.* 1999, character 19; modified Maisch unpubl.)

    The primitive number of cervical vertebrae (as for example in *Plesiosaurus*) is around 30, and numbers lower than 35 can be found in the pliosaurs. Among the plesiosaurs, only the Cryptoclididae retain a low number of cervical vertebrae, all other taxa have more than 35 cervical vertebrae.

28. Anterior cervical centra short or of moderate length (0), elongate (1) (modified Bardet *et al.* 1999, character 20; O'Keefe 2001a, character 112; Maisch unpubl.).

    Short or moderate length is here defined as a length that is shorter than or approximately equals the height of the cervical centra. This condition is found in *Plesiosaurus*, *Thalassiodracon* and the Cryptoclididae. Elongate means length exceeds the height, and such cervical vertebra are common for all elasmosaurs.

29. Amphicoelous cervical centra (0), platycoelous cervical centra (1) (Bardet *et al.* 1999, character 21; Maisch unpubl.).

    Amphicoelous cervical centra are primitive for the Plesiosauria, and the basal forms *Plesiosaurus*, *Thalassiodracon* and the Cryptoclididae retain this shape. Platycoelous cervical centra are only found in *Occitanosaurus*, *Brancasaurus* and *Libonectes*.

30. Lateral keel on anterior cervical vertebrae absent (0), present (1) (Bardet *et al.* 1999, character 22; O'Keefe 2001a, character 115; Maisch unpubl.).

    A lateral keel on anterior cervical vertebrae is only found among the Elasmosauridae with the exception of *Seeleyosaurus* and *Hydrorion*. *Plesiosaurus*, *Thalassiodracon* and all cryptoclidids have cervical centra with smooth lateral surfaces.

31. Postglenoidal portion of the coracoid short (0), long (1) (MAISCH unpubl.)

A long postglenoidal portion of the coracoid is defined here as being at least 1.5 times longer than the preglenoidal portion. Only *Thalassiodracon* and *Plesiosaurus* have a short postglenoidal portion, in all other plesiosauroids the postglenoidal portion is long.

32. Coracoid cornua absent (0), present, at least in adult, large and distinct (1) (BARDET *et al.* 1999, character 25; O'KEEFE 2001a, character 142; MAISCH unpubl.).

A coracoid cornua is definitely absent in the basal plesiosaurs *Plesiosaurus* and *Thalassiodracon*. The cornua is present in the cryptoclidid *Cryptoclidus* and *Tricleidus*, whereas it is not known for *Kimmerosaurus*. Among the elasmosauroids, a coracoid cornua is only present in the Jurassic taxa *Seeleyosaurus*, *Muraenosaurus*, *Hydrorion*, *Microcleidus* and *Occitanosaurus*, the Cretaceous genera *Brancasaurus* and *Libonectes* do not show any lateral expansion of the posterolateral coracoid corner.

33. Large intercoracoid fenestra absent (0), present (1) (BARDET *et al.* 1999, character 27; MAISCH unpubl.).

The Jurassic plesiosaurs have coracoids which contact along their entire length. They are separated posteriorly by a intercoracoid fenestra in the Cretaceous elasmosaurs.

FUNCTIONAL MORPHOLOGY

The study of functional morphology helps to improve understanding of the physical abilities of an extinct animal. By reconstructing muscles and their properties, conclusions about diet, locomotion and the possible behaviours can be drawn. In this chapter, the first reconstructions of the cranial musculature of plesiosauroids is presented, and their functional morphology is discussed. The limbs, as main propulsive organs, were analysed in respect of the implications for locomotion. The palaeoecological conclusions arising from the results of the functional analyses will be discussed in the next chapter.

Functional morphology of the skull.

Introduction and methods. Reconstructions of the musculature of extinct animals is difficult. Soft part preservation is extremely rare, and muscle scars are not always visible and only indicate possible sites of insertion for muscles and/or tendons. They give little evidence of the actual sizes of muscles (TAYLOR 1992). Usually close living relatives are used as models for muscle architecture, for example varanid lizards for mosasaurs (RUSSEL, D. A. 1967). As plesiosaurs have no living relatives, the reconstructions presented here are based on the general arrangement of muscles in reptiles. A similar approach was chosen by TAYLOR (1992), TAYLOR & CRUICKSHANK (1993b), RIEPPEL (1994 & 2002) and NOÈ (2001) for some pliosauroids and basal sauropterygians. Since the jaw musculature in a wide range of living reptiles is remarkably similar (NOÈ 2001), this method is likely to give reasonable results. The jaw adductor muscles in sauropterygians were probably complex pinnate (RIEPPEL 2002) as they are most likely derived from anapsid ancestors. The anapsid skull is closed and has therefore only limited space for each muscle, and complex pinnate muscles only bulge slightly upon contraction (ALEXANDER 1968). Pinnation therefore maximizes the physiological cross sections of muscles in a closed space. The M. depressor mandibulae is usually parallel-fibred in extant reptiles (RIEPPEL 2002), and since it lies outside of the skull it can bulge without restriction.

Reconstructions of the cranial musculature of plesiosauroids have not been done previously, and the reconstructions presented here are kept relatively simple, following the description of the reptilian musculature by Rieppel (2002). Only the main jaw adductor muscles and the depressor mandibulae were reconstructed and interpreted. Reconstructions of the constrictor internus dorsalis group, which includes eye-lid muscles and muscles related to cranial kinesis, was not attempted, since most of these muscles are probably not present in the akinetic skull of plesiosaurs. The musculature of the pharyngeal floor was also not considered, as information about the arrangement of these muscles was too scarce.

As a basis for the muscle reconstructions the reconstructed skulls of *Seeleyosaurus* and *Hydrorion* presented above were used. The specimens themselves were studied for evidence of attachment of muscles and tendons. The general arrangement of reptilian jaw musculature was then adapted to the studied taxa.

Abbreviations for muscles used. M., Musculus; M.am, Musculus adductor mandibulae (either externus or posterior); M.ame, Musculus adductor mandibulae externus.

Description. The general arrangement of muscles as reconstructed (Figs 5.1, 5.2) is similar for both genera, so that one general description pointing out the differences will suffice.

The M.am externus is here divided into three portions, the M.ame medialis, the M.ame superficialis and the M.ame profundus (Rieppel 2002). The M.am externus fills the temporal fenestra as visible from outside. It probably originated from the rim of the temporal fossa as well as from aponeurotic membranes covering the temporal fenestra (Taylor 1992). The M.am externus inserts onto the coronoid eminence, partly directly and partly over a bodenaponeurosis. As rugosities and slight concavities in the lateral wall of the braincase suggest, the M.ame medialis occupied the anterior half of the temporal fenestra, where it also connected to the distinct edge at the anterior margin of the temporal opening formed by the postfrontal and postorbital and to the bone directly ventrally of this edge. The M.ame superficialis is reconstructed in the posteromedial region of the temporal fenestra, where it originated in the posterolateral wall of the braincase and the anteromedial side of the squamosal. Both the M.ame medialis and superficialis insert onto the coronoid eminence via the bodenaponeurosis. Since the temporal opening of *Hydrorion* is approximately 1.4 times larger than that of *Seeleyosaurus*, these two muscles are distinctly larger in *Hydrorion*. The skull of *Seeleyosaurus* is higher than that of *Hydrorion*, resulting in longer muscles. The orientation of the muscles is similar in both

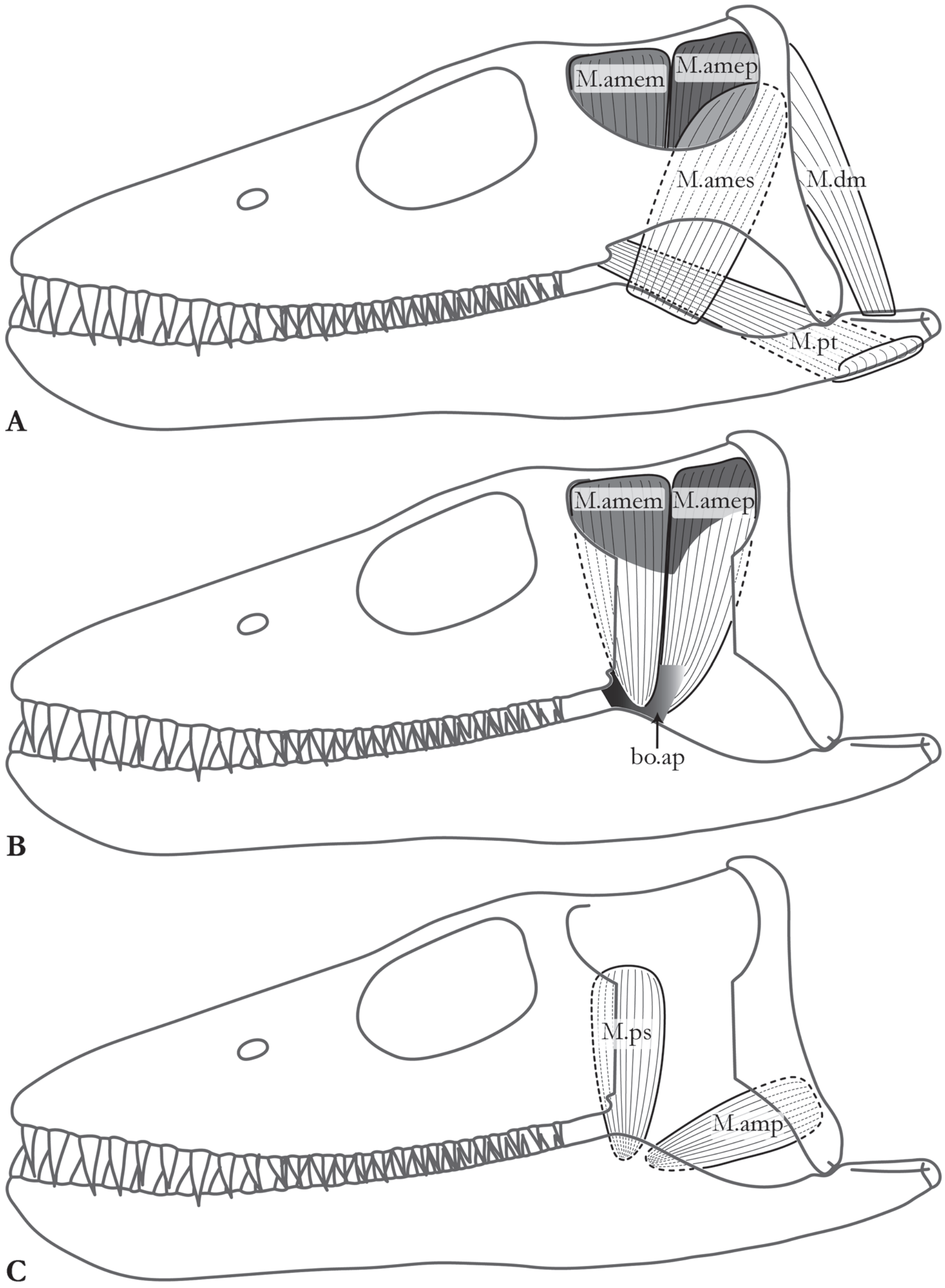


Fig. 5.1: Reconstruction of the cranial musculature of *Seeleyosaurus guilelmiimperatoris*. A-C successively deeper layers of dissection; for abbreviations, see appendix A.

genera, although their alignment is more vertical in *Seeleyosaurus*. The M.ame profundus is situated in the posteroventral region of the temporal opening. Its lateroventral portion inserts directly onto the coronoid eminence (Rieppel 2002). It is reconstructed as attaching only on the dorsal edge of the coronoid eminence and not extending further onto the lateral surface of the lower jaw, since no direct evidence of insertion was found on the lateral surface. Rieppel (2002) reconstructed this muscle in *Pistosaurus* with a larger extent on the lower jaw, and it is possible that this was also the case in *Hydrorion* and *Seeleyosaurus*. Unlike the other two dorsal portions of the M.am externus, the M.ame superficialis has approximately the same size in both studied taxa.

The M. pseudotemporalis inserts at the anterior part of the lateral wall of the braincase, more ventrally than the M.ame medialis and probably at least partly on the epipterygoid. Its onset is on the medial side of the coronoid eminence. In *Seeleyosaurus* this muscle runs almost vertically (Fig. 5.1 C), but in *Hydrorion* it inserts further anteriorly (Fig. 5.2 C) and has an anterodorsal to posteroventral alignment due to the considerably larger temporal opening. The M.am posterior originates on the anterior side of the quadrate and connects directly to the ventral side of the coronoid eminence, slightly more posteriorly than the M. pseudotemporalis. The M. pterygoideus has a more complicated course. Unlike the other muscles it inserts on the palate, probably on the posterior margins of the ectopterygoid. The M. pterygoideus runs from the palate posteriorly and also slightly ventrally and laterally. It curves around the ventral margin of the posterior end of the lower jaw at the level of the articulation and has its onset on the ventrolateral side of the retroarticular process. The actual extent of this muscle on the retroarticular process could not be determined by direct evidence. In *Iguana* this muscle covers nearly the whole retroarticular process, including the ventral ending (RIEPPEL 2002). Since no evidence for a similar extent in plesiosaurs was found, the muscle was reconstructed as smaller, but with the possibility of a more extensive attachment.

The M. depressor mandibulae originates on the posterodorsal areas of the squamosals. Several characteristic pits and rugose areas are found on this part of the bone in all specimens studied. However, not all of them belong to the M. depressor mandibulae, since the epaxial neck musculature and the nuchal ligament also inserted in this area. The attachment of the M. depressor mandibulae is on the dorsal surface of the retroarticular process. Contrary to other reconstructions (TAYLOR 1992, TAYLOR & CRUICKSHANK 1993b, RIEPPEL 2002) this muscle was not attached to the whole dorsal surface of the retroarticular process in the specimens studied, but only to its anterior half, as indicated by a shallow depression in this area of the bone. Since the retroarticular process in *Seeleyosaurus* is comparatively shorter than in *Hydrorion*, the ventral part of the M. depressor mandibulae is accordingly smaller. Apart from this detail, the general arrangement of the cranial musculature of the German taxa resembles the reconstruction of *Rhomaleosaurus zetlandicus* (TAYLOR 1992), *Pliosaurus brachyspondylus* (TAYLOR & CRUICKSHANK 1993b) and *Pistosaurus longaevus* (RIEPPEL 2002). TAYLOR (1992) and TAYLOR & CRUICKSHANK (1993b) did not subdivide the M.am externus into its three portions, as in RIEPPEL (2002) and the present study. Accordingly the M.am externus only occupies the posterior half of the temporal fenestra in the reconstructions of *R. zetlandicus* (Taylor 1992) and *P. brachyspondylus* (Taylor & Cruickshank 1993b), and the M. pseudotemporalis is the only muscle situated in the anterior portion of the temporal fenestra. In these two taxa, the M.am posterior is reconstructed as inserting onto the lower jaw more posteriorly than in this study, and the muscle therefore runs vertically (Taylor 1992, Taylor & Cruickshank 1993b). The main differences between the reconstructions presented here and those of Taylor (1992) and Taylor & Cruickshank (1993b) lies in the different resolution of the M.am externus reconstruction.

The cranial musculature of *Hydrorion* and *Seeleyosaurus* shows many similarities to *Pistosaurus longaevus* (Rieppel 2002). In *P. longaevus* the M.ame superficialis has a broader insertion area on the

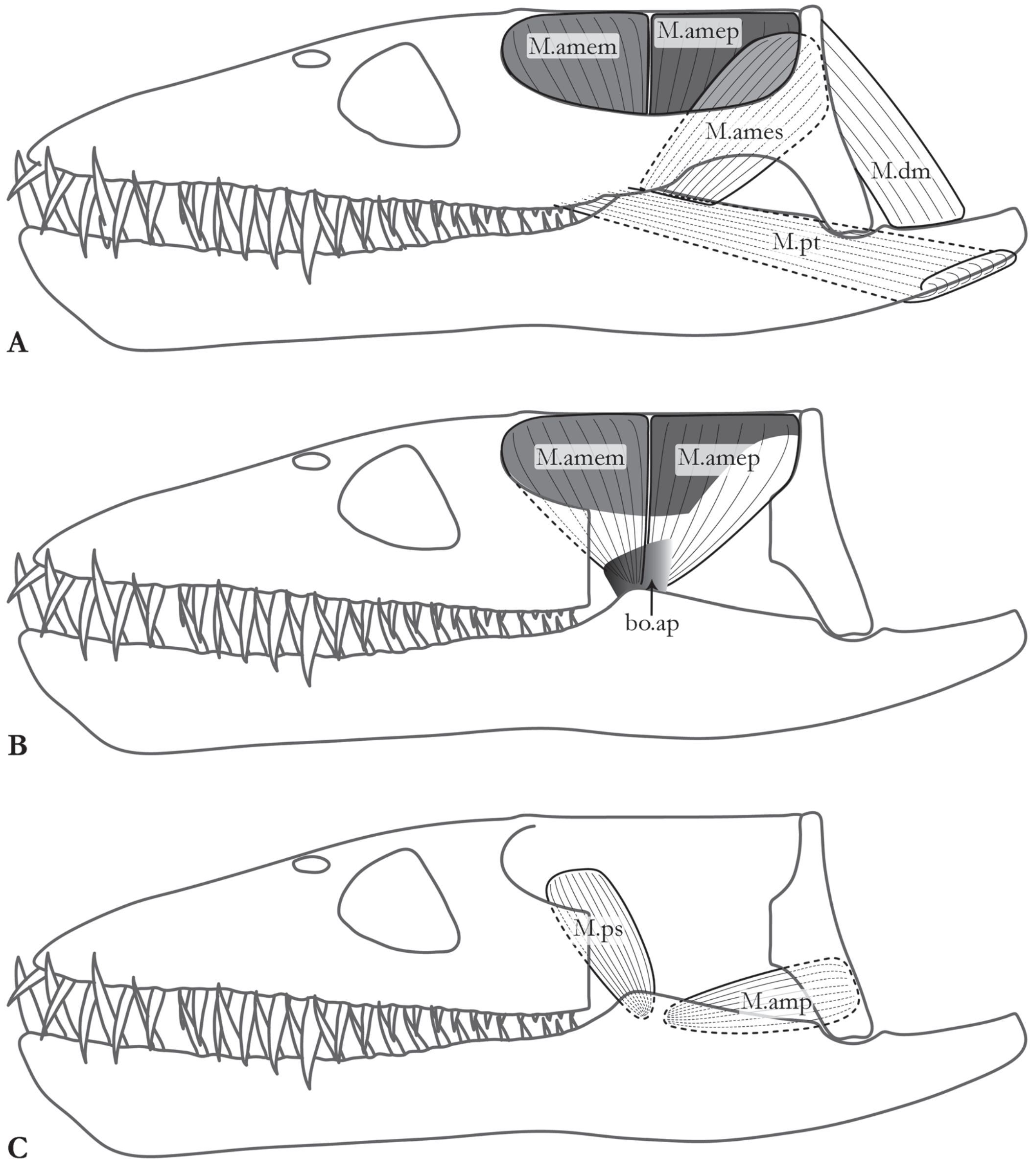


Fig. 5.2: Reconstruction of the cranial musculature of *Hydrorion brachypterygius*. A-C, successively deeper layers of dissection; for abbreviations, see appendix A.

lateral side of the lower jaw. As explained above, the actual extent of this area in the German taxa could not be determined with certainty, and may be larger than reconstructed. In *P. longaevus* (Rieppel 2002) as well as in the German taxa the M.am posterior runs not strictly vertically but dorsoposteriorly to anteroventrally, contrary to the condition as reconstructed for *R. zetlandicus* (Taylor 1992) and *P. brachyspondylus* (Taylor & Cruickshank 1993b). Although the reconstructions of the cranial musculature of *R. zetlandicus* and *P. brachyspondylus* and their subsequent analyses are sufficient to determine the function of the different muscles, a more detailed reconstruction would be desirable for comparison with other plesiosauroid and pliosauroid taxa and with basal sauropterygians, to get a better understanding of the evolution of this character.

Functional analysis. In order to estimate the function of the jaw adductor musculature of *Seeleyosaurus* and *Hydrorion*, the efficiency of each separate muscle was determined. Only the dorsoventral components of the muscle forces have been considered. The lateral components have been ignored since they would be small in relation to the vertical components (Kemp 1969). Three approaches were used to study the muscle efficiency. (1) The different insertion angles of each muscle and/or its insertation tendons relative to the longitudinal axis of the lower jaw were assessed (Rieppel 1994) (Figs 5.3 A, 5.4 A). The more vertical a muscle is orientated relative to the lower jaw, the greater is its mechanical advantage. Although the line of force in complex pinnate muscles as probably present in plesiosaurs is not necessarily along the direct line between the centre of the reconstructed insertion and the centre of the origin (Taylor 1992), such a line of action was used for simplicity (Noè 2001). (2) The relation of force arm to load arm at different angles of jaw opening was estimated for each adductor muscle (Figs 5.3 B, 5.4 B). A long force arm in relation to load arm is advantageous for exerting high forces, whereas a short force arm in relation to load arm is speed-advantageous (Noè 2001). (3) The degree of stretch of each muscle at different angles of jaw opening was measured (Figs 5.3 C, 5.4 C). The force a muscle can generate upon contraction depends on the amount of passive stretching prior to contraction (Rieppel 1994). Since the muscles were probably complex pinnate, a simple length-tension relation as for parallel fibred muscles must not be assumed (Taylor 1992). However, independent of the type of musculature, a muscle is usually damaged if it is stretched to approximately 180 per cent or more of its resting length (Mann 1981). On the other hand a muscle does not develop any tension when stimulated if its length is less than 70 per cent of its resting length (Mann 1981). Contraction of

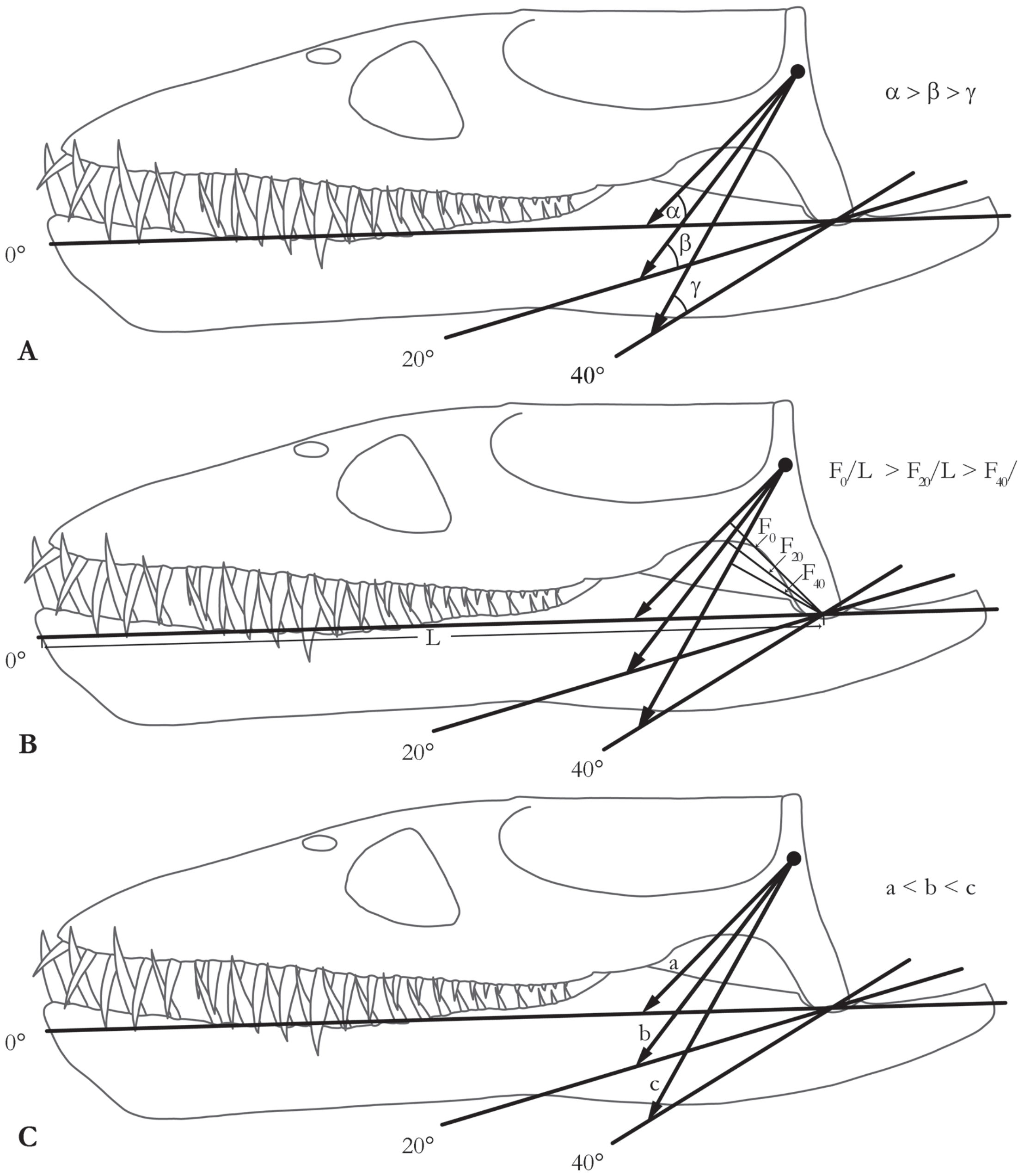


Fig. 5.3: Sketch to illustrate the methods used to analyse the cranial musculature. (A) Change of the insertational angle (α, β and γ) of the M.ames with increasing jaw gape. (B) Change of the relation of force arm (F_0 - F_{40}) to load arm (L) of the M.ames with increasing jaw gape. (C) Change of the length of the M.ames (a, b and c) with increasing jaw gape.

a muscle is achieved by the thick and the thin filaments of which a muscle is formed sliding past each other. The movement is caused by actively moving actin- and myosin-molecules, a process requiring ATP, the body's energy form. The force a muscle can produce is proportional to the number of actin-myosin bridges it has. The more the muscle is stretched, the less the thick and thin muscles overlap and the less actin-myosin bridges exist. The degree of stretch of a muscle therefore gives an estimate about the amount of force it can exert. Stretching of more than 150 per cent of the resting length is here regarded as possible, but not economic.

There are no previous studies regarding the jaw gape plesiosaurs could achieve. Therefore arbitrary

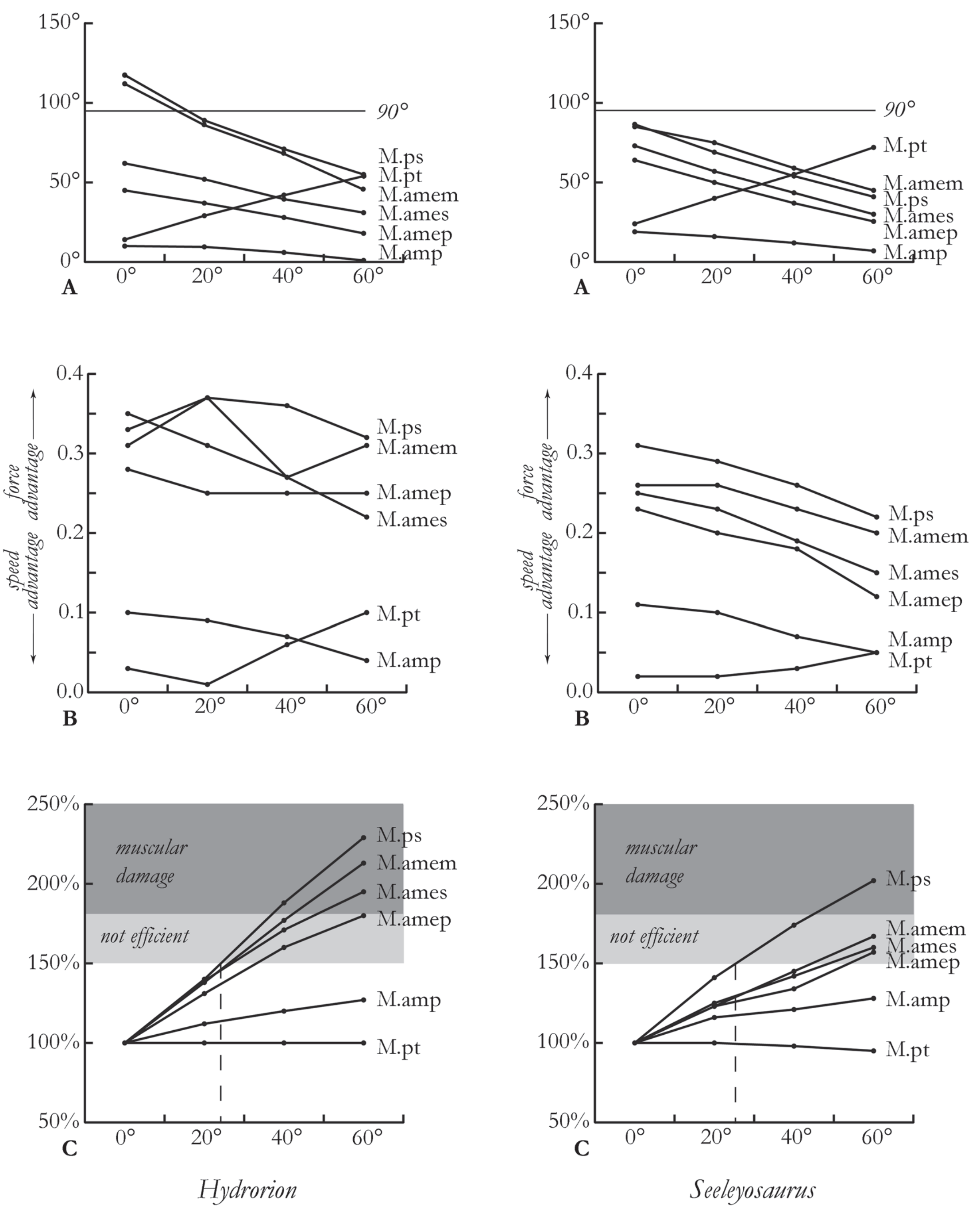


Fig. 5.4: Functional analysis of muscle properties of *Hydrorion* (left) and *Seeleyosaurus* (right). A: changes in the angle of insertion of the muscles with increasing jaw gape, muscles work most efficiently when the insertational angle is 90°; B: changes in the relation of force arm to load arm with increasing jaw gape, high values are advantageous for generating forces, low values are advantageous for speed; C: changes in the length of the muscles (in per cent of the resting length) with increasing jaw gape, lengths higher than 150 per cent resting lengths are no efficient, above 180 per cent the muscle is damaged, the dashed line indicates maximum jaw gape; for abbreviations, see appendix A.

angles of 0°, 20°, 40° and 60° were considered. It is improbable that plesiosaurs could really open their jaw that far, but the wide range helps to determine trends for muscle efficiency.

The values used for the functional analysis were determined emprirically. In reconstructions of the skull of both genera the line of effort (approximated as the centre line of the muscle) was drawn for different angles of jaw gape (see Fig. 5.3) and the insertational angles, the length of the force arm and the length of the muscle were measured (see appendix C for tables of measured values).

Because of the problems of reconstructing muscle systems discussed above and the problems of reconstructing the actual force a muscle can develop no quantitative analysis of the reconstructed muscles are attempted. Only qualitative remarks about the efficiency of the individual muscles are made (TAYLOR 1992). As the method of reconstruction and functional analysis for both taxa studied is the same, a comparison of the genera is possible.

Results. A dual system of muscle function seems to be in action in both *Hydrorion* and *Seeleyosaurus*. Similar systems were found in the pliosaurs *Rhomaleosaurus zetlandicus* (TAYLOR 1992) and *Pliosaurus brachyspondylus* (TAYLOR & CRUICKSHANK 1993b) as well as for the basal sauropterygian *Simosaurus* (RIEPPEL 1994). This seems to be primitive for sauropterygians. However, the actual assignment of the muscles in *Hydrorion* and *Seeleyosaurus* differs slightly from previous reconstructions.

In both genera the angle of muscle insertion and the relation of force to load arm is more favourable at low angles of jaw opening for all three portions of the M.am externus and the M. pseudotemporalis (Fig. 5.4 A). Therefore these muscles could exert higher forces when the mouth was nearly or completely shut than when it was wide open. The relation of force to load arm is distinctly higher in this muscle group than for all other muscles (Fig. 5.4 B), being highest in the M. pseudotemporalis, which is advantageous for generating forces. This indicates that these muscles exerted relatively high forces when the mouth was nearly or completely shut. This muscle group was probably responsible for producing the biting forces needed to hold and kill the prey. This function was called "static pressure" by RIEPPEL (1994).

In contrast to this, in the M. pterygoideus both the angle of insertion (Fig. 5.4 A) and the force to load arm relation (Fig. 5.4 B) are more favourable for exerting forces when the jaw is wide open. The relation of force to load arm is the lowest for the muscles studied in both genera, indicating a speed advantage. This muscle was probably used to apply the initial power to shut the jaw. RIEPPEL (1994) named this function unit "kinetic inertial".

The function of the M.am posterior is more difficult to determine. It is oriented nearly anteroposteriorly and its angle of insertion in relation to the longitudinal axis remain constantly low throughout the opening of the jaw (Fig. 5.4 A). The relation of load to force arm is always relatively low, but tends to decrease towards high angles of jaw opening (Fig. 5.4 B). This muscle probably did not play a great role in the closing of the jaw, but rather pulled the lower jaw posteriorly into the joint, maybe to stabilize it.

The amount of stretching reconstructed for the muscles supports this division into two main acting units. The M.am externus and the M. pseudotemporalis reach levels of stretching of 120 per cent to 140 per cent resting length at 20° jaw opening, and of 135 per cent to 170 per cent at 40° jaw opening (Fig. 5.4 C). This means, that at jaw openings of distinctly more than 20°, the length of the muscles soon exceeds the maximum length for efficient contraction. Generally the amount of stretching is higher in *Hydrorion* than in *Seeleyosaurus*, due to the more vertical orientation of the muscles in the latter genus. The stretching of the M. pterygoideus does not increase as fast as for other muscles. It lies at about 130 per cent for 60° of jaw opening in both taxa (Fig. 5.4 C), which is still within the range for efficient working. This again indicates that the M.am externus and M. pseudotemporalis could work more efficiently at low angles of jaw opening, whereas the M. pterygoideus was also powerful at higher angles of jaw opening. The M.am posterior shows no stretching in *Hydrorion* and even a slight shortening for high angles of jaw opening in *Seeleyosaurus* (Fig. 5.4 C), which suggests that the efficiency of the M.am posterior was not coupled to the opening of the mouth.

In previous studies (Taylor 1992, Taylor & Cruickshank 1993b, Rieppel 1994) the M.am posterior was integrated into the "static pressure" unit, which exerts high forces when the mouth is nearly or completely shut. The M. pterygoideus was always assigned to the "kinetic inertial" group, whose function is the rapid closure of the open jaws. However, in *R. zetlandicu*s the M. pseudotemporalis, (Taylor 1992) and in *Simosaurus* the M.ame superficialis (Rieppel 1994) are also included into this group. These differences between the reconstructions might either be caused by taxonomic differences, or by different methods of reconstruction. Taylor (1992) and Taylor & Cruickshank (1993b) did not subdivide the M.am externus into its three portions, which obscures a possible differentiation of function within the muscle. More detailed studies are needed based on the same methods before a reliable comparison of different taxa can be made.

The amount of stretching of the muscles also restricts the maximum angle of jaw opening. The M. pseudotemporalis is stretched to about 180 per cent at jaw opening angles of 40° in both taxa (Fig. 5.4 C). This is equal to the maximum amount a muscle can be stretched without damage (see above), and is surely beyond the range for efficient operation. Jaw opening angles of 60° are not possible as some muscles are stretched to more than double their resting size (Fig. 5.4 C). The amount of

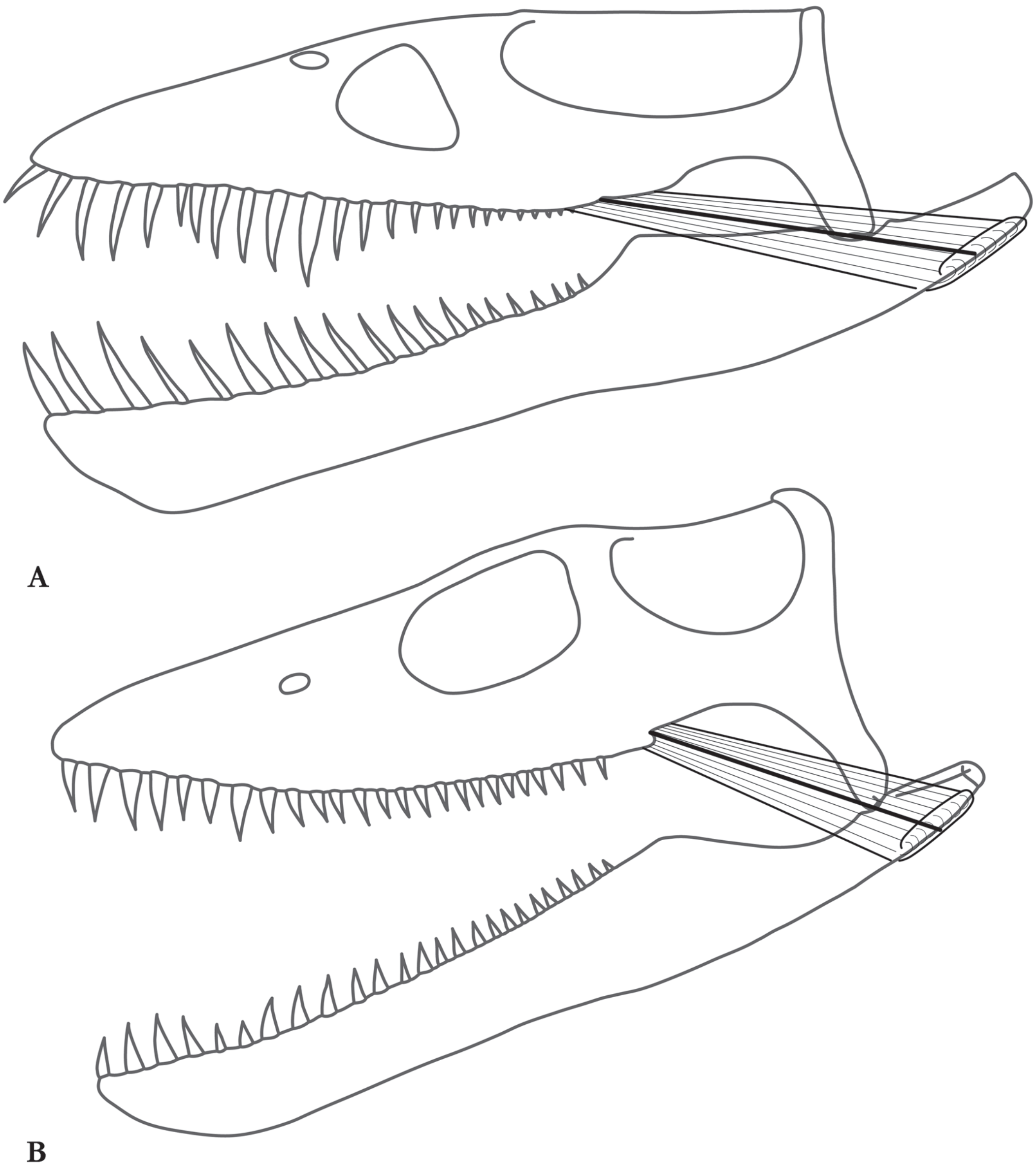


Fig. 5.5: Maximum jaw gape for *Hydrorion brachypterygius* (A) and *Seeleyosaurus guilelmiimperatoris* (B), as limited by the course of the M. pterygoideus. The line of action of the muscle (thick line) runs through the jaw joint at 13° of jaw opening for *Hydrorion* and at 17° for *Seeleyosaurus*.

stretching for all muscles lies within the range of efficient operation at a jaw opening angle of 20° (Fig. 5.4 C). Therefore it can be concluded that the maximum angle of jaw opening probably did not exceed 30°.

A special situation not considered before arises because of the insertion point of the M. pterygoideus on the ventrolateral side of the retroarticular process. Even when the jaws are closed the centre line of the muscle, which is here considered to approximate to the line of effort for the muscle passes only slightly ventrally of the jaw joint (Figs 5.1, 5.2). If the mouth is opened, the retroarticular process rotates posteriorly and dorsally, and the centreline of the M. pterygoideus approaches the jaw joint. It runs directly through the joint at 13° of gape in *Hydrorion* and 17° of jaw opening in *Seeleyosaurus* (Fig. 5.5). If the jaw is opened further, any contraction of the M. pterygoideus would result in the retroarticular process being pulled towards the occiput and opening the mouth. The M. pterygoideus would then work as a depressor mandibulae. It can be assumed that the angle of gape in the living animal did not exceed the angle at which the centreline of the M. pterygoideus runs through the jaw joint. This restricts the maximum angle of gape further to 15° to 20°. However, as said above the actual extent of the insertion of the M. pterygoideus onto the retroarticular process could not be determined with certainty and may reach further posteriorly than reconstructed. Any extension of the insertion of the M. pterygoideus further posteriorly results in a posterior shift of the line of action of this muscle, which would then pass the joint at even lower angles of gape.

Discussion. On the basis of the reconstructions, the following sequence of muscle function during prey capture is reasonable.

1. The jaw is opened by the M. depressor mandibulae, which acts on the lower jaw, and probably also by elevation of the upper jaw by contraction of the epaxial jaw musculature (RIEPPEL 2002). It has been argued that the M. depressor mandibulae must be powerful to open the jaw against the water pressure and that the long retroarticular process of the lower jaw was used as lever (TAYLOR 1992, TAYLOR & CRUICKSHANK 1993b). However, as described above the M. depressor mandibulae in the two plesiosauroids studied only uses the anterior half of the retroarticular process for insertion. The retroarticular process of plesiosauroids is distinctly longer in relation to the length of the lower jaw than in pliosauroids (pers. obs.), and therefore in the plesiosauroids the whole extension of the retroarticular process may not have been needed to ensure an efficient opening of the jaw. When in motion, the pressure of the water rushing into the jaws also helped to open them.
2. At about 15° gape the centreline of the M. pterygoideus runs directly through the jaw joint. Any contraction of the muscle at this point presses the lower jaw into the joint and immobilises it.
3. When suitable prey is between the jaws, a slight contraction of any of the other jaw adductor muscles moves the line of action of the M. pterygoideus anteriorly to the jaw joint. The M. pterygoideus, still contracted, would then act very quickly and shut the jaws with the prey between them. A similar pre-tensioning of a muscle and its sudden release to catch prey (although by a completely different mechanism) is known from the deep-sea fish *Malacosteus* (GÜNTHER &

Deckert 1959).

4. When the jaws are nearly closed the M.am externus and the M. pseudotemporalis could exert enough force to pierce and subsequently hold the prey till its death.
5. During this stage the M.am posterior would retract the lower jaw and secure it in its joint, to avoid dislocation of the lower jaw by struggling prey. When the catch was dead it could be swallowed.

Although the general arrangement of muscles in both taxa studied is similar, several differences have been noted. One of the most striking is the size of the muscles. Since the temporal fenestra of *Hydrorion* is approximately 1.4 times larger than that of *Seeleyosaurus*, the M.ame medialis and M.ame superficialis are approximately 1.5 times broader in *Hydrorion* than in *Seeleyosaurus*. The remaining muscles are reconstructed as having a similar size in both genera. These differences result in a higher physiological cross-section of the M.ame medialis and the M.ame superficialis in *Hydrorion*, which were therefore able to exert higher forces. This is also mirrored in the load to force arm ratios, which are generally higher in *Hydrorion* than in *Seeleyosaurus* (Fig. 5.4 B). In contrast, all muscles except the M.am posterior are distinctly longer in *Seeleyosaurus* than in *Hydrorion*. As the ratio of load to force arm is lower, the muscles have a speed advantage.

Therefore it can be concluded that *Seeleyosaurus* could close its jaws quickly, whereas the bite of *Hydrorion* was distinctly stronger. This is also supported by osteological characters. Generally the skull of *Hydrorion* is more robustly built than that of *Seeleyosaurus*. The palate of *Seeleyosaurus* has an anterior interpterygoid vacuity, which was probably covered by skin and closed by cartilage in the living animal. The palate of *Hydrorion* is completely ossified and could probably withstand higher stresses than that of *Seeleyosaurus*. However, this is only an assumption based on skull morphology. A complete and detailed analysis of the static of the skulls would be necessary to determine the actual kinetic qualities. Such an analysis is difficult in specimens that are not preserved three-dimensionally, and is thus beyond the scope of this thesis.

As shown above, two muscles insert onto the retroarticular process: the M. pterygoideus on its ventrolateral side, and the M. depressor mandibulae on its dorsal surface. Both muscles probably did not use the complete extent of the retroarticular process, but were probably restricted to its anterior portion. Unfortunately the present study does not establish a reasonable function for the posterior portion of this process. The retroarticular process of plesiosauroids is usually longer than that of pliosauroids (pers. obs.), and is unlikely that such a distinctive character would have no function. Further studies and more detailed reconstructions of the cranial musculature of additional plesiosauroid and pliosauroid taxa are needed to solve this problem. In addition to the analyses of the muscles, studies of the structure of the cranial osteology regarding the reaction of the skull to the implied forces are desirable. These, in combination with the analysis of the musculature will lead to a more detailed picture of the functional morphology of the plesiosaurian skull. This will improve our understanding of the diversity and evolution of the plesiosaurian cranial musculature as well as their feeding mechanisms.

Functional morphology of the limbs

Introduction. The locomotion of plesiosaurs has been a matter of interest since the very first published description of a plesiosaur (De la Beche & Conybeare 1821). Conybeare (1824) remarks that "In its motion this animal must have resembled the turtles more than any other." (p. 388), thus suggesting a locomotion which today is called underwater-flight. This interpretation was generally accepted and further elaborated by many authors (Owen 1851, Parker 1880, Fraas 1905, Abel 1912). In 1924 Watson studied the limb musculature and stroke of plesiosaurs and was the first to suggest a rowing motion. He deduced that plesiosauroids were more manoeuvrable, and that pliosaurs were capable of powerful swimming in a straight line. This concept was soon generally established. Robinson (1975) made the first detailed functional analysis of plesiosaur limbs and compared the hydrofoil shaped flippers of plesiosaurs to those of penguins, sea-turtles and sea-lions. She differentiated between rowing, a form of locomotion involving the posterior displacement of water-masses, and underwater-flight, which creates lift and propulsive force with hydrofoil-shaped limbs on the same physical principles as that for birds in aerial flight. Underwater flight was considered to be a more efficient form of locomotion than rowing, and therefore suggested for plesiosaurs. The stroke had the form of a narrow figure-of-eight, and the shape and angle of the limbs in relation to the flow of the surrounding water produced both lift and forward thrust. She envisaged pliosauroids as ambush predators, which were capable of short but powerful bursts of speed to capture large prey, whereas plesiosauroids were endurance swimmers, relying on smaller prey caught more frequently.

While the general idea of plesiosaurs relying on lift and propulsion using hydrofoil-shaped limbs for locomotion has since then not been seriously questioned, several details have been discussed extensively and some are still open to debate. Tarsitano & Riess (1982) found several problems in Robinson's (1975) publication, mainly in the reconstruction of the musculature and the movement of the limbs, which were not capable of elevating the limbs dorsally to the shoulder girdle or exert the forces needed for a powerful upstroke. Frey & Riess (1982) concluded that the upstroke must have been passive, creating no thrust, and that fore- and hind-limbs were used alternately to produce continuous forward motion. Godfrey (1984) compared plesiosaur locomotion with that of sea-lions rather than with that of penguins or sea-turtles. In this stroke pattern the limbs start in the horizontal plane extending laterally from the body and are first brought ventrally and then dorsally and laterally, until resting parallel to the body. This motion produces forward thrust both by "flight" and by displacement of water masses posteriorly. For the recovery stroke the limb is pronated and brought anteriorly with minimal drag, which may be to some degree propulsive. As plesiosaurs have a high body mass, the non-propulsive recovery stroke would not have reduced their forward speed significantly. This concept is nowadays generally accepted, although discussion about the details of limb movement continues. It has been argued that plesiosaurs had to use fore- and hind-limbs alternately, as the up-stroke may have been passive (Frey & Riess 1982; Riess & Frey 1991), but also that a simultaneous movement could have increased the efficiency of the hind-limb (Lingham-Soliar 2000). Lingham-Soliar (2000) suggested that the fore- and hind-limbs had different strokes and functions in locomotion. The fore-limb would act in a stroke similar to the one described by Godfrey (1984) but the hind-limbs had a more restricted movement and could predominantly move anteroposteriorly, so that they had only a short flight phase and a long rowing phase. The hind-limbs were mainly responsible for steering and rotating the body.

Massare & Sperber (2001) studied the changes in centrum shape along the vertebral column in several cretaceous plesiosaur taxa, which indicate how the various parts of the vertebral column were used for locomotion. They found three different swimming styles ((1) fore- and hind-limb working together in one powerful stroke; (2) both limb pairs used independently to produce continuous thrust and (3) only the front-limbs used to generate thrust, the hind-limbs being passive, maybe for steering) in different taxa and concluded that plesiosaurs may well have had a greater diversity in swimming capability than previously assumed.

Long *et al.* (2006) used an aquatic robot to simulate certain aspects of underwater flight. The robot had four flippers similar to those used by under water fliers. Several stroke patterns were studied and the amount of energy used and the acceleration were logged. They found that for long, steady cruising the use of two flippers consumed distinctly less energy than the use of four flippers. However, acceleration was substantially higher when all four flippers were used.

The present work does not aim to study the locomotion of plesiosaurs in general. It is assumed that plesiosaur locomotion was as described by GODFREY (1984) and LINGHAM-SOLIAR (2000). Equally the differences between plesiosauroid and pliosauroid locomotion are not discussed, since only plesiosauroids were studied. It is rather attempted to determine differences in the locomotion of the two German plesiosauroid taxa. For this, three publications are of major interest. MASSARE (1988) estimated the maximum swimming speed of several Mesozoic marine reptiles. Her calculations are based on the total drag created by an animal, whose form was approximated as an ellipsoid, and the available energy output as a function of the metabolic rate. The method was tested by calculating the swimming speed of cetaceans and comparing them to observed swimming speeds. The calculated results are about 1.5 to 2.0 times larger than observed. She concluded that for fossil reptiles the calculated speeds represent the upper limit for sustained swimming speed. Concerning plesiosaurs, she argued that pliosauroids were able to sustain relatively high swimming speeds over a long time, and thus pursued their prey over some distance. In contrast to this plesiosauroids had lower continuous swimming speeds and could only catch slower prey, probably using an ambush strategy or specialising in sessile prey. In this study, the form of the limbs has not been considered, and MASSARE (1988) herself said that the low swimming speeds calculated for plesiosaurs were a result of their long neck, which contributes to the body length without having a great mass. The maximum swimming speed of "*Plesiosaurus*" *brachypterygius* as given in this publication (MASSARE 1988) is 2.3 m/s. By comparison, this approximates the fastest short distance swimming speeds of human athletes. (The current world record holder is Alexander POPOV, who swam 50 m freestyle in 21.64 s, which equals 2.31 m/s.)

MASSARE's (1988) calculations were optimized by MOTANI (2002) by eliminating some calculation errors, and using more accurate body shapes as well as updated metabolic rate models. MOTANI (2002) also calculated optimal rather than maximum swimming speeds. The new calculations were again tested against extant animals, but not only for cetaceans, which use a thunniform swimming style, but also for otariids (which use subaqueous flight) and seals (with an axial swimming style). MOTANI (2002) also used three different metabolic rates, one average reptilian metabolism, one slightly raised as observed in the Leatherback turtle or the tuna, and one of cetaceans and pinnipeds. MOTANI (2002) argued that obligate marine reptiles had no opportunity to raise their body temperature by basking on land, and probably did not need this as their large body sizes allowed them to maintain body temperature at least to some degree.

The resulting optimal swimming speed of extinct marine reptiles as calculated by Motani (2002) are significantly lower than those of Massare (1988). Swimming speeds were calculated for two plesiosauroids ("*Plesiosaurus*" *brachypterygius* and *Cryptoclidus*) and one pliosauroid (*Rhomaleosaurus victor*). In contrast to the results of Massare (1988), the calculated speed of the pliosauroid is very similar to that of the two plesiosauroids, at about 1 m/s for all three taxa with an assumed raised metabolic rate comparable to that of the Leatherback turtle.

O'Keefe (2001b) approached the differences in the locomotion within the plesiosaurs from a different point of view. He estimated the aspect ratio (AR) for several pliosauroid and plesiosauroid taxa. The AR is a dimensionless measure of wing span, defined as span over mean chord. A long tapering wing form has a high AR and produces fewer vortices at the wing tip and is therefore more efficient than a short wing. In contrast to this a short broad wing with a low AR is able to function at slower speeds and enables better manoeuvrability. O'Keefe (2001b) found higher ARs in plesiosauroids than in pliosauroids. He coupled these results with Massare's (1988) calculation of the maximal swimming speed and concluded that pliosauroids were pursuit-predators able to reach high speeds and good manoeuvrability. In contrast plesiosauroids used lower speeds, were less manoeuvrable but had a very efficient locomotion. They were therefore cruising specialists which covered long distances.

Functional analysis. The work of O'Keefe (2001b) shows how important the shape of the main propulsive organs, i.e. the limbs, is in relation to efficiency and manoeuvrability. The two German plesiosauroid genera studied, *Seeleyosaurus guilelmiimperatoris* and *Hydrorion brachypterygius*, are of similar size (about three meters length in adults) and similar proportions of head, neck and trunk. The major postcranial difference is the size of the limbs (see previous chapters). *Seeleyosaurus* has limbs which reach about 25 per cent of the overall body length, whereas the limbs of *Hydrorion* (as the species name *brachypterygius*, meaning "short wing", already indicates) are distinctly shorter and are only about 20 per cent of the body length (Fig. 5.6). It can be assumed that this significant difference leads to diverging swimming abilities.

In order to quantify the difference between the two studied taxa, the AR was calculated according to O'Keefe (2001b) and compared to the published results of other taxa in this work. Some critical remarks concerning O'Keefe's (2001b) method have to be made. The AR is defined as span over mean chord, and can also be calculated by the square of the span over the surface area or surface area over mean chord square (Storrs 1993; Lingham-Soliar 2000; O'Keefe 2001b) (Fig. 5.7). Since information about the form of the flipper can not be obtained for most specimens O'Keefe (2001b) calculated the wing area of several well preserved specimens, and used these measurements to calculate a geometrical correction factor. This factor was then used to estimate the AR of other flippers with only two measurements: the maximum diameter of the distal propodial (which he assumed to be equivalent to the root chord) and the length of the limb distal of the propodial, thought to be equivalent to the span of the flipper. It is not easily comprehensible why the surface of the propodials does not contribute to the wing span. Additionally, O'Keefe (2001b) apparently only used the preserved bony part of the limbs to calculate the surface area of the wings, and did not allow for any fleshy tissue. Soft-tissue preservation on the posterior margin of the limbs is known from the well-preserved type specimen of *Hydrorion brachypterygius* (GPIT/RE/3185) (v. Huene 1923, Robinson 1975, this work). Lingham-Soliar (2000) also calculated the AR of different plesiosaurian taxa, and estimated that the fleshy trailing edge represented a third of the overall limb surface area. His results of the AR of four taxa are distinctly lower than those of O'Keefe (2001b) for the same taxa. Furthermore the direct comparison of plesiosaur wings to those of birds, bats and aeroplanes as made by O'Keefe (2001b) is arguable. AR is certainly a good indicator for effectiveness versus manoeuvrability, but the wings of underwater-fliers and aerial fliers differ in their proportions relative to the body mass, making comparison between such different animal orders highly difficult. Birds need always to provide lift against

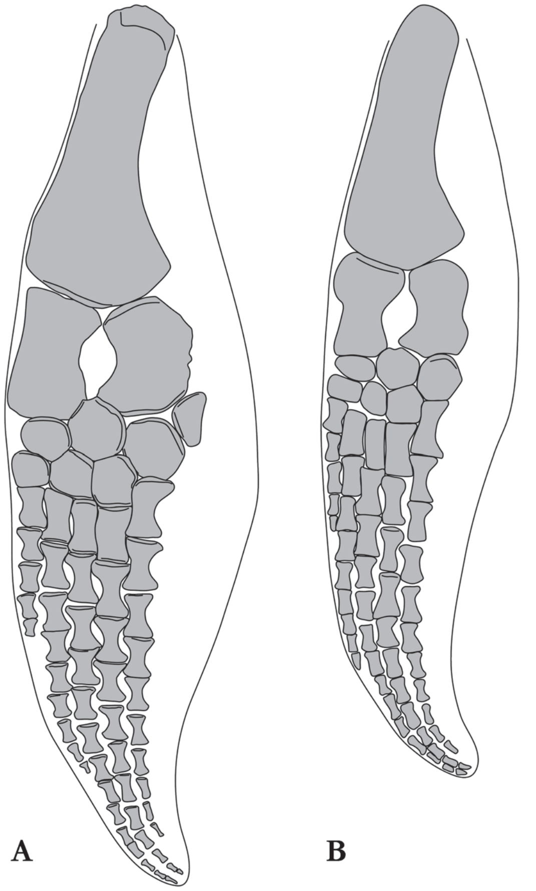
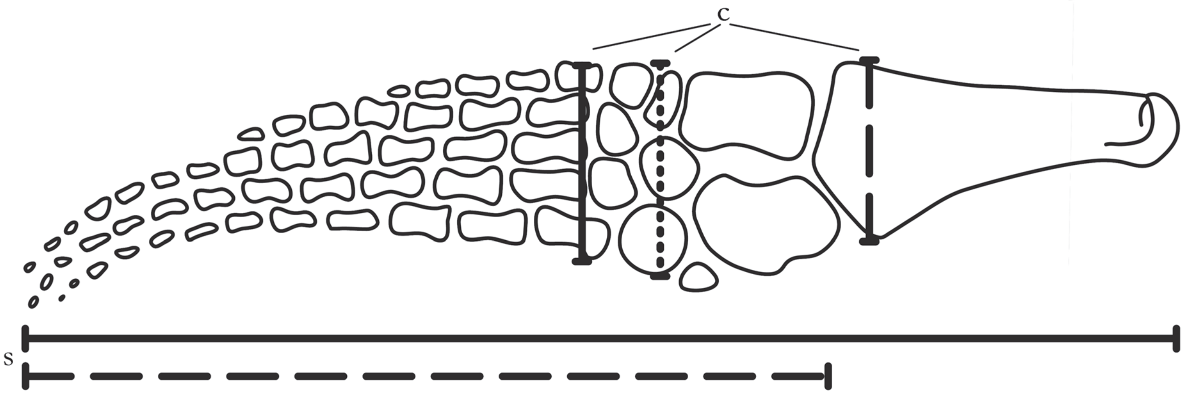


Fig. 5.6: Comparison of the fore limbs of *Seeleyosaurus guilelmiimperatoris* (A) and *Hydrorion brachypterygius* (B), drawn to the same scale. The outline indicates the size of the fleshy trailing edge, deduced from the soft-tissue preservation in GPIT/RE/3185.



$$AR = s/\bar{c} \text{ or } s^2/a \text{ or } a/\bar{c}^2$$

Fig. 5.7: Determinants for the aspect ratio (AR) (modified after STORRS 1993). Solid lines as given by STORRS (1993), loosely dashed lines as used by O'KEEFE (2001b) and densely dashed line as used in this study. a = surface area; c = chord, $\bar{c}$ = mean chord, s = span.

the force of gravity, whereas underwater swimmers are more or less neutrally buoyant. Any lift generated by the flippers is used for propulsion and manoeuvrability. When diving, underwater fliers have to overcome buoyancy and generate a downward force. Lift is only needed below compensation depth.

However, the AR of the two German taxa was calculated following O'KEEFE (2001b), because he included more taxa in his study than LINGHAM-SOLIAR (2000) and covered a broader spectrum of plesiosauroid and pliosauroid taxa, thus providing a better basis for comparison. Accordingly only the limb length distal of the propodial was used for the calculations. Contrary to O'KEEFE's (2001b) method the width of the limb over radius and ulna was taken instead of the maximal width of the distal propodial. The calculated AR of the German specimens are slightly smaller as if the propodial width was used, but since the two measurements differ only slightly, the results are still comparable to each other.

Since the limb size of the two German genera studied shows a distinct difference in length (Fig. 5.5), it is not surprising that the calculated AR also differ. The ARs for the adult specimens of *Hydrorion* have an average of about 6.5 in the fore-limb and 7.0 in the hind-limb (see appendix B). In adult specimens of *Seeleyosaurus* the fore-limbs have an average AR of 9.5 and the hind-limbs of 10.5 (see appendix B). In most specimens the AR of the hind-limb was higher than that of the fore-limb, although in two specimens (MB.R.1992 and SMNS 51143) the fore-limb AR is higher than the hind-limb AR. The two juvenile specimens SMNS 16812 and SMNS 51141 have distinctly lower ARs than adult specimens, as their limbs are not yet fully developed. Additionally the paddles of SMNS 16812, which is three-dimensionally prepared and mounted for display, have probably been reconstructed with insufficient spacing of the bones (see chapter 2).

If these results are compared to the list of ARs O'Keefe (2001b) calculated for 13 plesiosaur taxa, *Hydrorion* is best comparable with the pliosauroid *Dolichorhynchops* from the Upper Cretaceous of North America. The AR of *Hydrorion* lies well within the range of six to eight that O'Keefe (2001b) assigned to "traditional pliosauromorphs such as *Peloneustes*, *Liopleurodon* and *Dolichorhynchops*" (p. 989). Only one genus commonly regarded as a plesiosauroid has a lower AR, *Cryptoclidus* from the English Upper Jurassic. In contrast to this, the ARs of *Seeleyosaurus* are similar to the basal plesiosauroid *Thalassiodracon* from the Lower Jurassic of England. *Muraenosaurus*, the taxon that has the greatest osteological similarity to *Seeleyosaurus* and is closely related (see phylogenetic analysis in this work) has distinctly lower ARs of about 7.8 and 9.1 in fore- and hind-limb respectively.

Regarding the locomotory abilities of the two German genera it can clearly be stated that *Hydrorion* was a highly manoeuvrable swimmer, capable of swimming tight turns and changing direction quickly. In contrast, *Seeleyosaurus* had a more efficient but less manoeuvrable locomotion, maybe coupled with higher swimming speeds. This taxon was better suited for extended cruising than *Hydrorion*. According to Motani (2002) the swimming speed of *Hydrorion brachypterygius* was about 1 m/s (3.6 km/h). Following her method, a similar speed has to be assumed for *Seeleyosaurus guilelmiimperatoris*, since the two taxa do not differ significantly in size and body proportions. However, since neither Massare (1988) nor Motani (2002) included the actual form and qualities of the plesiosaur hydrofoils into their calculations, the effect of the flipper form on swimming speed remains unstudied, and it is possible that taxa with similar body proportions but different flipper forms do not have the same swimming speed. The implications the different swimming abilities had for the hunting strategies of the two studied taxa will be discussed in the next chapter.

O'Keefe (2001b) deduced from his results that pliosauroids usually have lower ARs than plesiosauroids, with the exception of *Cryptoclidus*, and that a high AR is probably primitive for the whole Plesiosauria. In this work *Hydrorion* and *Seeleyosaurus* are shown to be basal elasmosauroids (chapter 4). Since *Hydrorion* has ARs that correspond to those of pliosauroids it is probable that Liassic plesiosaurs already showed a wide range of wing morphologies and that the two major plesiosaur groups did not differ that significantly in this character. To assign either pliosaurs or plesiosaurs a "ambush" or "cruising" way of hunting and locomotion seems to over-simplify the subject. However, further studies on wing morphology and the ecological implications resulting from these are needed

PALAEOECOLOGY

Introduction

Palaeoecology aims to reconstruct prehistoric ecosystems and build a detailed model of the environment in which the fossil organisms lived, including diet, predator-prey relations, habitat and the interrelations between these. Information about the fossils themselves and the concomitant fauna and flora is needed for this, as well as data for other ecological factors such as climate or water depth in marine organisms. As fossils are incomplete records of the extinct organism they represent, the amount of available information is dependent on the preservation of a fossil ecosystem. The exceptionally good preservation within the Posidonia shale makes it especially well-suited for palaeoecological reconstructions.

To accomplish this, the fossil content of the Posidonia shale will be compared with existing information concerning adaptations for feeding and swimming, and the possible prey will be deduced for both taxa under investigation, *Seeleyosaurus guilelmiimperatoris* and *Hydrorion brachypterygius*. The environment during these times will be interpreted after a closer look at the general habitat of plesiosaurs, and after a review of the special conditions within the Posidonia shale. Focusing on the revised taxonomy and phylogeny the genera under study will then be compared to other Liassic plesiosaurs providing further information about the early distribution and evolution of plesiosaurs.

Diet and feeding

Little is known about the food of plesiosaurs, and much has been speculated. The large pliosaurs with their huge heads and large teeth are usually considered to feed on all kinds of prey, including animals larger than themselves, whereas the small-headed plesiosauroids were limited to small prey (Massare 1987). Several methods of predation (ambush and pursuit strategy) have been suggested for both groups (Taylor 1981, Massare 1988, O'Keefe 2001b).

Direct proof of what was eaten by an extinct animal can only be obtained from fossilized stomach contents, which are generally rare. Twenty stomach contents have been reported for plesiosaurs worldwide throughout the Jurassic and Cretaceous (Table 6.1). They contain predominantly fish and cephalopods, but also some proof of possible scavenging on non-marine reptiles like pterosaurs (Brown, B. 1904) and dinosaurs (Taylor *et al.* 1993). Contrary to what one would think, scavenging on large corpses was apparently not restricted to the large predatory pliosauroids. For example, a pterosaur bone was found in a plesiosauroid (Brown, B. 1904), and an elasmosaur contained the

Species	Age	Location	Stomach contents	Reference
Styxosaurus snowi	Middle Campanian	Kansas, USA	teleost fish, gastroliths	Cicimurri & Everhart 2001
Elasmosaurus platyurus	Middle Campanian	Kansas, USA	six species of teleost fish	Cope 1868
Elasmosauridae indet.	Middle Campanian	Kansas, USA	mosasaur	Cope 1877, Storrs 1999
Plesiosauridae indet.	Middle Campanian	South Dakota, USA	teleost fish, gastroliths	Martin & Kennedy 1988
Plesiosauridae indet	Middle Campanian	South Dakota, USA	teleost fish, pterosaur, scaphites, gastroliths	Brown, B. 1904
Dolichorhynchops osborni	Middle Campanian	Manitoba, Canada	teleost fish	Nicholls 1988
Elasmosauridae indet.	Middle Campanian	Manitoba, Canada	teleost fish, gastroliths	Nicholls 1988
Plesiosauridae indet.	Santonian	Hokkaido, Japan	cephalopods, gastroliths	Matsumoto *et al.* 1982
Polycotylidae indet.	Late Cenomanian	Hokkaido, Japan	cephalopods, gastroliths	Sato & Tanabe 1998
Thalassomedon hanningtoni	Early Cenomanian	Nebraska, USA	cephalopods, gastroliths	Cicimurri & Everhart 2001
Elasmosauridae indet.	Late Albian	Australia	decapod carapace, crustacean fragment, one fish scale, gastroliths	McHenry *et al.* 2005
Elasmosauridae indet.	Late Aptian	Australia	bivalves, gastropods, crinoids, belemnite endoskeleton, one teleost plate, bromalite, gastroliths	McHenry *et al.* 2005
Brancasaurus brancai	Wealden, Lower Cretaceous	Westphalia, Germany	small broken bones and rounded bone fragments, one gastrolith & sand grains	Wegner 1914
Pliosaurus brachyspondylus	Kimmeridge	England, UK	cephalopods	Tarlo 1959
Pliosaurus brachyspondylus	Kimmeridge	England, UK	ornithischian dinosaur scutes	Taylor *et al.* 1993
Tricleidus laraminsis	Late Oxfordian	Wyoming, USA	cephalopods, hybodont shark, gastroliths	Wahl 1998
Simolestes vorax	Middle Callovian	England, UK	cephalopods, gastroliths	Martill 1992
Peloneustes sp.	Middle Callovian	England, UK	cephalopods, gastroliths	Andrews 1910
Pliosauridae indet.	Middle Liassic	Saxony-Anhalt, Germany	two belemnite rostra, one reptile tooth, gastroliths & sand grains	Janensch 1928
Pliosauridae indet.	Lower Liassic	England, UK	teleost fish	Patterson 1975

Table 6.1: Plesiosauroid and pliosauroid specimens with preserved stomach contents in chronological order of specimen age.

remains of a mosasaur in its stomach (Cope 1877, Storrs 1999). Recently the stomach contents of two Australian elasmosaurs were described, which consisted of benthic organisms including bivalves, gastropods, crinoids, decapods and crustaceans (McHenry *et al.* 2005).

The existing data shows a predominance of cephalopods in the diet of Jurassic plesiosaurs, and of fish in the Cretaceous plesiosaurs (Cicimurri & Everhart 2001), which led McHenry *et al.* (2005) to postulate a shift in dietary preferences. However, data is still too scarce to establish alimentary trends for time periods or taxonomic groups. The stomachs of pliosauroids, which occur more often in the Jurassic than plesiosauroids, seem to contain mostly cephalopods and very few fish, but it is known from bite-marks on plesiosauroids (Clarke & Etches 1991, Thulborn & Turner 1993) that pliosauroids also attacked or at least scavenged on larger prey. Although stomach contents are direct proof of the last meal of an organism, only hard material is likely to resist the stomach acids. It has been argued that these insoluble parts accumulated in the stomach, and were occasionally regurgitated (Martill 1992). It is unclear if the cephalopod dominated stomach contents of Jurassic pliosaurs are due to (1) a predominant feeding on cephalopods of pliosaurs, (2) a preference for cephalopods for all Jurassic plesiosaurs, or (3) just the only prey of theses animals hard enough to be preserved in the intestines.

Gastroliths are commonly found associated with plesiosaurs (for example Williston 1892, 1894 & 1903, Brown, B. 1904, Wegner 1914, Janensch 1928, Darby & Ojakangas 1980, Kanie *et al.* 1998, Martill 1992, Everhart 2000, Cicimurri & Everhart 2001, McHenry 2005), and may have been used in the processing of food (Williston 1894, Brown, B. 1904, Everhart 2000, McHenry 2005). However, it has been argued that plesiosaurs probably used them for buoyancy control, in analogy to crocodiles (Darby & Ojakangas 1980, Taylor 1981, 1993 & 2000). Recently, some authors argued that the weight of the gastroliths is often too low to have had any impact on the buoyancy in these large animals (Everhart 2000, Cicimurri & Everhart 2001). However, one must bear in mind that not the whole weight of the animal was to be altered significantly, but that the stones were probably only used to compensate for the buoyancy of the lungs and provide a horizontal position in the water (Taylor 1981). The gastroliths of adult crocodiles weigh approximately 1 per cent of the body mass (Darby & Ojakangas 1980). If Everhart's (2000) estimation of the weight of the studied elasmosaur (2.800 kg) is correct, the preserved gastroliths (13 kg) would represent 0.5 per cent of the body weight, and may well have been able to cause an effect. It is not easily understandable why gastroliths were needed for digestion, especially because the prey was relatively soft (fish, cephalopods and large reptiles), and several stomach contents were uncrushed despite the presence of gastroliths (Kanie *et al.* 1998, Martill 1992). Since gastroliths in plesiosaurs are not unusual, an accidental swallowing can be excluded, at least if nectic prey was preferred.

Massare (1987) used an indirect method to gain insights about the prey preference of extinct marine reptiles. She compared the tooth morphology of recent predators with the teeth of fossil marine reptiles and deduced possible prey from observed similarities. Concerning plesiosaurs, she concluded that since most plesiosauroids have very slender and recurved teeth which do not show any wear, they could only have preyed upon soft animals like teleost fish and cephalopods. The teeth of pliosauroids are more robust and conical, and according to Massare (1987) they belong to a group of less specialised predators, which fed on a larger variety of prey. Geister (1998) interpreted gutter-like furrows in Callovian sediments of Liesberg, Switzerland as feeding traces of marine reptiles, most likely plesiosaurs and ichthyosaurs. The possible prey would have been benthic organisms like crustaceans, bivalves and worms. He concluded that plesiosauroids and pliosauroids did not feed exclusively on nectic prey, but also took up mouthfuls of sediment, either to feed on the organisms within it or as an aid to digestion. However, the hypothetical mode of formation of the gutter-like traces formed by plesiosauroids and pliosauroids as proposed by Geister (1998) is impossible due to the structure of the cervical vertebra (Noè 2001). Plesiosaurs usually have high neural arches, which severely limit dorsal flexion. Noè (2001) suggested that these traces rather belong to the giant filter feeding fish *Leedsichthys*.

To summarize: plesiosaurs are known to eat fish and squid, at least some elasmosaurs fed on benthic organisms, pliosaurs also attacked other large marine reptiles and plesiosauroids, and both groups scavenged if suitable carcasses were found. This indicates that the alimentation and feeding strategies of plesiosaurs were far more diverse than previously thought. It is most probable that specialisation on certain prey groups existed among coexisting plesiosauroid and pliosauroid taxa, in order to minimize competition. Noè (1999 & 2001) attributed to three pliosauroid genera from the Oxford Clay different feeding strategies, based on skull morphology, tooth form and preserved stomach contents. He concluded that *Peloneustes* was a piscivor, *Liopleurodon* mainly preyed upon large, hard-boned prey and that *Simolestes* almost exclusively fed on softer bodied invertebrates. It has also been suggested that feeding strategies changed during ontogeny (Wiffen *et al.* 1995, Cruickshank *et al.* 1996, Cicimurri & Everhart 2001, McHenry *et al.* 2005). Wiffen *et al.* (1995) described the ontogenetic evolution of bone structure in Late Cretaceous plesiosaurs from New Zealand. They found that the bones of juvenile specimens are often thickened (pachyosteosclerotic) while adults have lighter (osteoporotic-like) bones. Pachyostosis can be seen as an adaptation for shallow water habitat (Taylor 2000). Wiffen *et al.* (1995) concluded that the juveniles had a more plesiomorphic ecology and were poorly mobile, lagoon or shore dwellers, where they fed on sessile organism or non-elusive prey, whereas the adults had a more active behaviour in the open sea as pelagic predators. Cruickshank *et al.* (1996) described a juvenile pliosauroid with pachyostosis and also concluded that it probably was a benthic feeder.

Despite the extraordinary preservational environment, no stomach contents or gastroliths are preserved in any plesiosauroids from the Posidonia shale, and therefore no direct conclusion can be drawn about their food. As anoxic conditions prevailed during the deposition of the Posidonia shale at the bottom of the sea (Kaufmann 1978 & 1981, Schmid-Röhl *et al.* 1997, Röhl *et al.* 2001), very few benthic organisms existed. Certain horizons indicate higher amounts of oxygen, and in these, benthic life was possible, as indicated by the occurrence of one species of echinoderm in the εII_4, or the highly bioturbated "Seegrasschiefer" (εI_3) and several beds of bivalves. However, it seems very unlikely that the plesiosauroids fed on benthic organisms, as they were scarce compared to the abundance of nekton, especially in the levels where most plesiosaurs were found. Due to the morphology of the teeth hard prey can also be excluded. The teeth of both *Hydrorion* and *Seeleyosaurus* are fine, elongated, recurved and show no signs of wear or breakage. Massare (1987) studied specimens of *Hydrorion* and classified them as belonging to her guild Pierce I, which can only pierce soft prey items such as small fish and cephalopods. The teeth of *Seeleyosaurus* are very similar to those of *Hydrorion*, in general they appear to be even more slender and more distinctly curved than those of *Seeleyosaurus*, but due to the deformation of all specimens this is difficult to see clearly. Furthermore, the skulls of *Hydrorion* and *Seeleyosaurus* are very small, about 200 mm length. Prey size is limited to the size of the gullet (Massare 1987), whose maximum approximates the width of the skull. Therefore the prey of both German taxa probably did not exceed 100 mm length. These two specifications (1) only soft prey; (2) prey smaller than 100 mm in length, severely restrict the possible prey. Hard-shelled organisms like ammonites, bivalves or gastropods have to be excluded, as well as fishes with hard ganoid scales, which comprise about 90 per cent of all fishes in the Posidonia shale (Jäger 1985). Most of the remaining teleost fish have body lengths exceeding 100 mm. A genus of small, sprat-like fish, *Leptolepis*, and coleoids, soft-bodied cephalopods remains as possible prey for *Hydrorion* and *Seeleyosaurus*. *Leptolepis* probably swam in schools and is very common in some layers of the Posidonia shale. The coleoids are present with three major groups, belemnites, phragmotheutids and decapodiforms (squids and cuttlefish).

As described in the previous chapter, *Seeleyosaurus* and *Hydrorion* differ in their cranial musculature and flipper form, thus providing them with different biting and swimming abilities. To recapitulate, *Seeleyosaurus* had a faster but weaker bite and was capable of more efficient swimming, whereas *Hydrorion* could exert higher biting forces and was highly manoeuvrable. These differences probably resulted in divergent feeding strategies.

Seeleyosaurus was a very efficient swimmer, suited for pursuit of fast nektonic organisms, such as coleoids. The skull, cranial musculature and the teeth of *Seeleyosaurus* are slightly more delicate than those of *Hydrorion*, but strength is not needed for the consumption of soft coleoids. For this hunting strategy speed is advantageous, both in terms of swimming and closing of the jaws, and in these respects *Seeleyosaurus* is more efficient than *Hydrorion*.

In contrast, *Hydrorion* was a highly manoeuvrable swimmer with biting forces exceeding those of *Seeleyosaurus*, and could have specialised on schools of fish like *Leptolepis*. One possible hunting strategy may have involved swimming into a school catching a fish, and turning around immediately after exiting the school to repeat the action. Alternatively, *Hydrorion* may have dispersed a swarm to catch as many individual fish as possible. *Hydrorion* relied predominantly on its manoeuvrability rather than speed, to catch as much prey as possible in a rather small area.

Leptolepis is very common in certain horizons within the Posidonia shale, as for example the εII_4. This is also the level in which most plesiosaurs are found. Personal counts of the material (complete and incomplete) from the Lias ε in the collections of the SMNS, GPIT and MH (see appendix D) showed that 11 out of 16 specimens originate from the εII_4. Among the complete specimens, only two (SMNS 51747 and SMNS 51945) are from alternative horizons. Additionally, *Hydrorion* is the most common genus among the plesiosaurs from the Posidonia shale - five out of the 12 complete specimens belong to this genus. All *Hydrorion* specimens were found in the εII_4. The number of specimens are too low to draw sound conclusions but a correlation between the occurrence of preferred prey and its predator seems to be present.

However, since no direct evidence in form of fossilised stomach contents exists, prey preference and hunting strategies in the two plesiosauroid genera from the Posidonia shale remain assumptions. It is most probable that the actual spectrum of prey was larger than described here, and that *Leptolepis* and coleoids were predominant prey groups upon which the plesiosaurs specialised.

Habitat

Plesiosaurs are found worldwide in the Jurassic and Cretaceous. Some famous plesiosaur localities are the Lower Jurassic Posidonia shale of Holzmaden, Germany and Yorkshire, England, the Upper Jurassic Oxford Clay of Peterborough, England, the Lower Cretaceous Great Artesian Basin of Australia, and the Upper Cretaceous Western Interior Sea of Kansas, U.S.A. All these sediments were deposited in shallow epicontinental seas, and represent the usual environment in which plesiosaurs are thought to have lived (Kanie *et al.* 1998). However, several finds of plesiosaurs remains in fresh water deposits of England (Andrews 1922), Canada (Russel, L. S. 1931) and Australia (Bartholomai 1966) indicate that at least some plesiosaurs also lived in rivers or brackish river deltas. So far, no plesiosaurs have been found in off-shore sediments, but this may simply reflect the lack of deep oceanic sediments. Most oceanic sediments of Jurassic age are already subducted, and those of Cretaceous age lie at the bottom of the oceans, covered with younger deposits (Press & Sievers 1995).

Plesiosaurs are members of the group Sauropterygia and the Triassic members of this group, placodonts, nothosaurs and pachypleurosaurs, are clearly inhabitants of shallow coastal waters, lagoons and fresh-water habitats. *Pistosaurus*, usually considered to be the sister-taxon to all plesiosaurs (Sues 1987, Rieppel 1999, O'Keefe 2001a), was well adapted to a marine environment relative to other basal sauropterygians (Sues 1987) and therefore an evolutionary transition from near coastal to off-shore inhabitants is apparent in the sauropterygians (Sues 1987, Wiffen *et al.* 1995). Several juvenile plesiosaurs exhibiting pachyostosis (Wiffen *et al.* 1995, Cruickshank *et al.* 1996) suggest that such a transition is recapitulated during the ontogeny of plesiosaurs, with juveniles showing a plesiomorphic life style occupying coastal waters and lagoons, and later migrating as adults into more open marine environments (Martill 1992, Wiffen *et al.* 1995 , Noè 2001).

The Posidonia shale was a shallow epicontinental sea and Holzmaden was situated about 150 km from the shore during the Toarcian. Most plesiosaurs were found in the $\varepsilon\mathrm{II}_4$ (see above and appendix D). During these times the redox boundary lay within the water column (Röhl *et al.* 2001) and benthic life was absent. The only macrofossils on the sea bottom were belemnite rostra, ammonite shells and similar debris, along with the sporadic fish or reptile carcass. Benthic organisms are only reported from the lower εII_4, in the form of echinoid spines belonging to the genus *Diadomopsis*, and just below the εII_5 is a horizon rich in shells of the bivalve *Pseudomytoloides* and oysters (Hauff 1921). Life was rich in the water column, the εII_4 is one of the layers of the Posidonia shale where nectic forms are most abundant. Here the largest specimens of *Dactylioceras* are found with 14 cm diameter, together with specimens of *Harpoceras*, *Lytoceras* and *Phylloceras*, although the latter genera are less common (Hauff 1921). Coleoids are comparatively rare and most belemnites only appear higher in the Posidonia shale, although some phragmotheutids (*Belotheutis* and *Geotheutis)* are present (Hauff 1921).

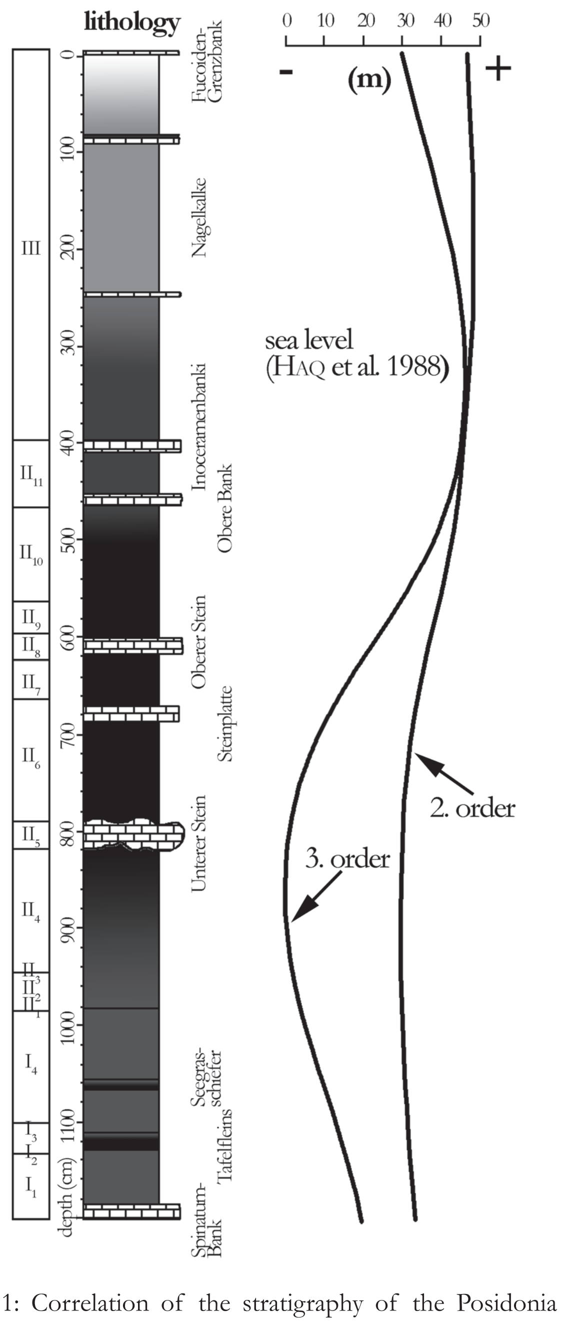


Fig. 6.1: Correlation of the stratigraphy of the Posidonia shale and the world wide sea level stand (altered after Röhl *et al.* 2001).

Fishes are abundant in the εII_4, the ganoid-scaled fishes are represented by the genera *Lepidotus*, *Dapedius*, *Tetragonolepis*, *Pholidophorus* and *Pachycormus* (Hauff 1921). As mentioned previously, the teleost fish *Leptolepis* is common in this layer, and near to the εII_5 the large predatory teleostei *Euthynotus* is numerous (Hauff 1921).

The plesiosaurs shared their environment with two other groups of marine reptiles, the ichthyosaurs and the crocodiles, and both are distinctly more abundant than plesiosaurs. Approximately 3000 ichthyosaurs have been found in Holzmaden of which about 80 per cent belong to the genus *Stenopterygius* (Wild, *pers. comm.* in Godefroit 1994), and 10 per cent each to the genera *Temnodontosaurus* and *Eurhinosaurus* (McGowan 1979). The three crocodile taxa *Steneosaurus bollensis*, *Pelagosuchus typus* and *Platysuchus multiscrobiculatus* comprise approximately 15 per cent of the marine reptile fauna from Holzmaden (Godefroit 1994). Two additional genera of plesiosaurs are described from the Posidonia shale of Holzmaden: the pliosauroids *Rhomaleosaurus victor* (Fraas 1910) and *Hauffiosaurus zanoni* (O'Keefe 2001a).

Correlation of the different stratigraphic levels of the Posidonia shale with worldwide sea level shows that during the deposition of the εII_4 the sea level was at a short-term low stand (Haq *et al.* 1988, Schmid-Röhl *et al.* 2001) (Fig. 6.1). The fact that most plesiosaurs were found in this level might indicate a preference for relatively shallow waters, as might be expected from descendants of shallow water inhabitants. However, as in the εII_4 not only plesiosaurs are comparatively abundant, but also ichthyosaurs, crocodiles, fishes and invertebrates (Hauff 1921), it appears more probable that this abundance is indicative of better preservational properties at this time, due to the nature of the sediment (Martill 1993), to high rates of sedimentation (Hauff 1921) and/or to the position of the redox boundary (Schmid-Röhl *et al.* 1997, Röhl *et al.* 2001).

Interestingly, plesiosaurs are generally rare in the Liassic. From the Posidonia shale, 12 complete plesiosaur specimens are known, but this contrasts sharply with approximately three thousand ichthyosaurs (Wild, *pers. comm.* in Godefroit 1994). The situation is similar in the Posidonia shale of Luxembourg and Yorkshire, England (Benton & Taylor 1983, Godefroit 1994, O'Keefe 2004, Maisch & Ansorge 2004). Although in England the absolute and relative numbers of plesiosaur findings are higher, there is still a huge disparity compared to the number of ichthyosaurs. This might be caused by the recent radiation of the Plesiosauria. The ichthyosaurs already appeared in the upper Lower Triassic, completely adapted for an fully aquatic lifestyle (Sander 2000). In the Lower Jurassic they were widespread, but their diversity is low in the Upper Jurassic and the ichthyosaurs finally became extinct in the Cenomanian. In contrast the first plesiosaurs are known from the Rhaetian (uppermost Triassic) of England and Scotland (Storrs 1994a, Storrs & Taylor 1996, Taylor & Cruickshank 1993a). The first major radiation of plesiosaurs occurred in the Lower Jurassic, they become abundant during the Middle Jurassic and are subsequently worldwide in distribution until the end of the Cretaceous.

The distribution of plesiosaurs within the German Posidonia shale may also indicate palaeobiogeographic preference. Personal counts conducted in the collections of the SMNS, GPIT and Museum Hauff show plesiosaur discoveries were almost exclusive to localities around Holzmaden and Stuttgart with two fragments from Franconia (see appendix D). No complete plesiosaurs have been found in Dotternhausen near Balingen, another locality situated approximately 60 km south west of Stuttgart. In this large quarry many fossils have been found, including crocodiles and ichthyosaurs, but only one serpulid encrusted bone of possible plesiosaur identity (JAEGER*, pers. comm.*). Again, this disparity might represent different palaeoenvironmental factors like preference for a certain water depth or the abundance of prey during the Toarcian, or might be the result of preservational factors. Unfortunately there is a study bias for particular Posidonia shale localities. Although HAUFF (1921) was the first to give a very detailed description of the fossil content of the Posidonia shale from Holzmaden and surrounding areas, modern studies combining sedimentology, palaeoecology and geochemistry (SCHMID-RÖHL *et al.* 1997, RÖHL *et al.* 2001, SCHMID-RÖHL *et al.* 2002) focus mainly on the Dotternhausen area. Without a detailed analysis of the Posidonia shale at Holzmaden, combining several scientific approaches, and a comparison to Dotternhausen, the answer to the question why no plesiosaurs were found in Dotternhausen will remain open.

Palaeobiogeography

GODEFROIT (1994) studied the palaeobiogeographic distribution of the marine reptiles of the Toarcian. He distinguished four zones: (1) a Swabian–franconian zone; (2) a Yorkshire zone; (3) a Luxembourgian zone and (4) a Norman zone. Slightly extended and altered, this zonality can describe the distribution of plesiosaurs during the whole Liassic (Table 6.2): The Swabian–franconian zone is expanded to a German zone which includes also northern Germany (see also MAISCH & ANSORGE (2004) for ichthyosaurs); the English zone includes not only the numerous findings from Yorkshire, but also those from Somerset and Dorset; and the Luxembourgian and Norman zones are merged into a Norman–Benelux zone, analogous to MAISCH & ANSORGE (2004).

The oldest findings from the English zone are from the lower Hettangian of Street (Somerset), its basal portion (the 'Pre–*planorbis*–Beds') may even be Rhaetian (see STORRS & TAYLOR 1996 for a short summary of stratigraphy and plesiosaur findings). From Scotland plesiosaur remains are known from the Linksfeld erratic, which is of Rhaetian or Lower Liassic age (TAYLOR & CRUICKSHANK 1993a).

From the Hettangian of the German zone fragmentary plesiosaur remains were described as cf. *Thaumatosaurus megacephalus* (V. HUENE 1921). Unfortunately both specimens are not diagnostic above family level, and can only be identified as Pliosauridae indet.

CHARIG (1971) reported *Plesiosaurus pentagonus* and *P. trigonus* from the lower Liassic of Calvados, France, but both taxa are represented by a few vertebrae only.

	English zone	German zone	Norman–Benelux zone	others
Hettangian	Plesiosauridae: *Eurycleidus arcuatus* *Thalassiodracon hawkinsi* Pliosauridae: *Rhomaleosaurus megacephalus* Elasmosauridae: *Eretmosaurus rugosus*	Pliosauridae indet.	Plesiosauridae: *Plesiosaurus trigonus* *Plesiosaurus pentagonus*	Plesiosauridae indet. (Scotland)
Sinemurian	Plesiosauridae: *Plesiosaurus dolichodeirus* *Attenborosaurus conybeari* Pliosauridae: *Pliosaurus macromerus* *Eurycleidus arcuatus* Elasmosauridae: *Eretmosaurus sp.*	Plesiosauridae indet Pliosauridae: *Thaumatosaurus* aff. *megacephalo* Pliosauridae indet.	Elasmosauridae indet. Pliosauridae indet.	Plesiosauridae indet. (Canada)
Pliensbachian	*Plesiosaurus* sp.			
Toarcian	Pliosauridae: *Macroplata longirostris* *Pliosaurus macromerus* *Rhomaleosaurus zetlandicus* *Sthenarosaurus dawkinsi* Elasmosauridae: *Microcleidus homalospondylus* *Microcleidus macropterus*	Plesiosauridae indet. Pliosauridae: *Hauffiosaurus zanoni* *Rhomaleosaurus victor* Elasmosauridae: *Hydrorion brachypterygius* *Seeleyosaurus guilelmiimperatoris* Elasmosauridae indet.	Elasmosauridae indet.	Plesiosauridae indet. (Australia) Elasmosauridae: *Occitanosaurus tournemirensis* (south France)

Table 6.2: Plesiosaur distribution in the Liassic.

The lower Sinemurian plesiosaurs found in Lyme Regis (Dorset) are distinctly different from those found in Street. *Plesiosaurus dolichodeirus*, a common species in Lyme Regis is not found in Street, and *Thalassiodracon hawkinsi* is absent in Lyme Regis (see Storrs & Taylor 1996). Other taxa known from Lyme Regis are *Attenborosaurus conybeari*, *Eretmosaurus* sp., *Pliosaurus macromerus* and *Eurycleidus arcuatus* (see Delair 1959 and Powell & Edmonds 1978).

Most of the described findings from the German zone are not diagnostic above family level. Both *Plesiosaurus nothosauroides* Dames, 1895 and *P. robustus* Dames, 1895 are surely pliosaurs, but no more can be said about them. Both species are therefore declared *nomen dubia*. The vertebrae and girdle–elements Reiff (1935) described as *P. dolichodeirus* are only identifiable as Plesiosauridae indet. The only plesiosaur find from northern Germany (Halberstadt, Saxony–Anhalt) is *Thaumatosaurus* aff. *megacephalo* (Brandes 1914). The specimen, a fragmentary snout and lower jaw and some postcranial remains, resembles *Rhomaleosaurus victor* more than *R. megacephalus* and is probably synonymous with the German taxon. However, final identification requires a revision of *R. victor* as well a study of the specimen of *T.* aff. *megacephalo*. GODEFROIT (1995) described plesiosaurid and elasmosaurid remains from Belgium. The fact that plesiosaur remains were also found in Canada (NICHOLLS 1976) indicates that plesiosaurs were already dispersed over the northern hemisphere.

Only one plesiosaur is known from the Pliensbachian, *Plesiosaurus* sp. from Charmouth, Dorset (STORRS 1994b).

The black shale deposits of the Toarcian yield the best preserved plesiosaurs. In England, numerous plesiosaurs have been found in Yorkshire, mostly near Whitby (see BENTON & TAYLOR 1984). From the Posidonia shale of Württemberg, (south west Germany) four genera are known: *Seeleyosaurus guilelmiimperatoris* (DAMES 1895, FRAAS 1910), *Hydrorion brachypterygius* (V. HUENE 1923), *Rhomaleosaurus victor* (FRAAS 1910) and *Hauffiosaurus zanoni* (O'KEEFE 2001a). Additionally DAMES (1895) described *Plesiosaurus* (?*Eretmosaurus*) *bavaricus* from Franconia and redescribed *P. posidoniae* QUENSTEDT, 1885 and *P. suevicus* QUENSTEDT, 1858 from the Lias ε of Württemberg (south west Germany). In fact the specimens of these three species cannot be identified above family level and are here regarded as *nomen dubia*. The Norman–Benelux zone is represented by elasmosaurid remains from the Posidonia shale of Luxemburg (GODEFROIT 1994).

Occitanosaurus tournemirensis (SCIAU *et. al* 1990, BARDET *et al.* 1999) is remarkable, because this complete specimen from south France is the best preserved plesiosaur from France, but unlike all other finds of Jurassic (Lower to Upper) and Cretaceous age it comes from the region directly south of the Massif Central (Tournemire, Aveyron Department, south France) and not from the north of France. Other Toarcian plesiosaur findings are from Queensland, Australia (THULBORN & WARREN 1980).

Since the Toarcian yields the most abundant record of plesiosaur findings distributed over Europe, it is best suited for palaeobiogeographic comparison (see also GODEFROIT 1994, MAISCH & ANSORGE 2004, O'KEEFE 2004). It is remarkable that each Toarcian species is restricted to a small geographic region (Fig. 6.2). Specification is high at species level, no plesiosaur species is known from more than one zone. As the present work restricts the genus *Plesiosaurus* to the single species *P. dolichodeirus*, specification is also high at genus level. There is only one genus which is present in more than one zone: *Rhomaleosaurus zetlandicus* is known to occur in Yorkshire, whereas *R. victor* is found in the Posidonia shale.

In contrast to this, the faunal composition of the different zones shows similarities at family level.

In all zones elasmosaurs prevail, with two species in both the English and the German zones, and the finds in the Norman–Benelux zone and south France. Plesiosauroids are distinctly less abundant in

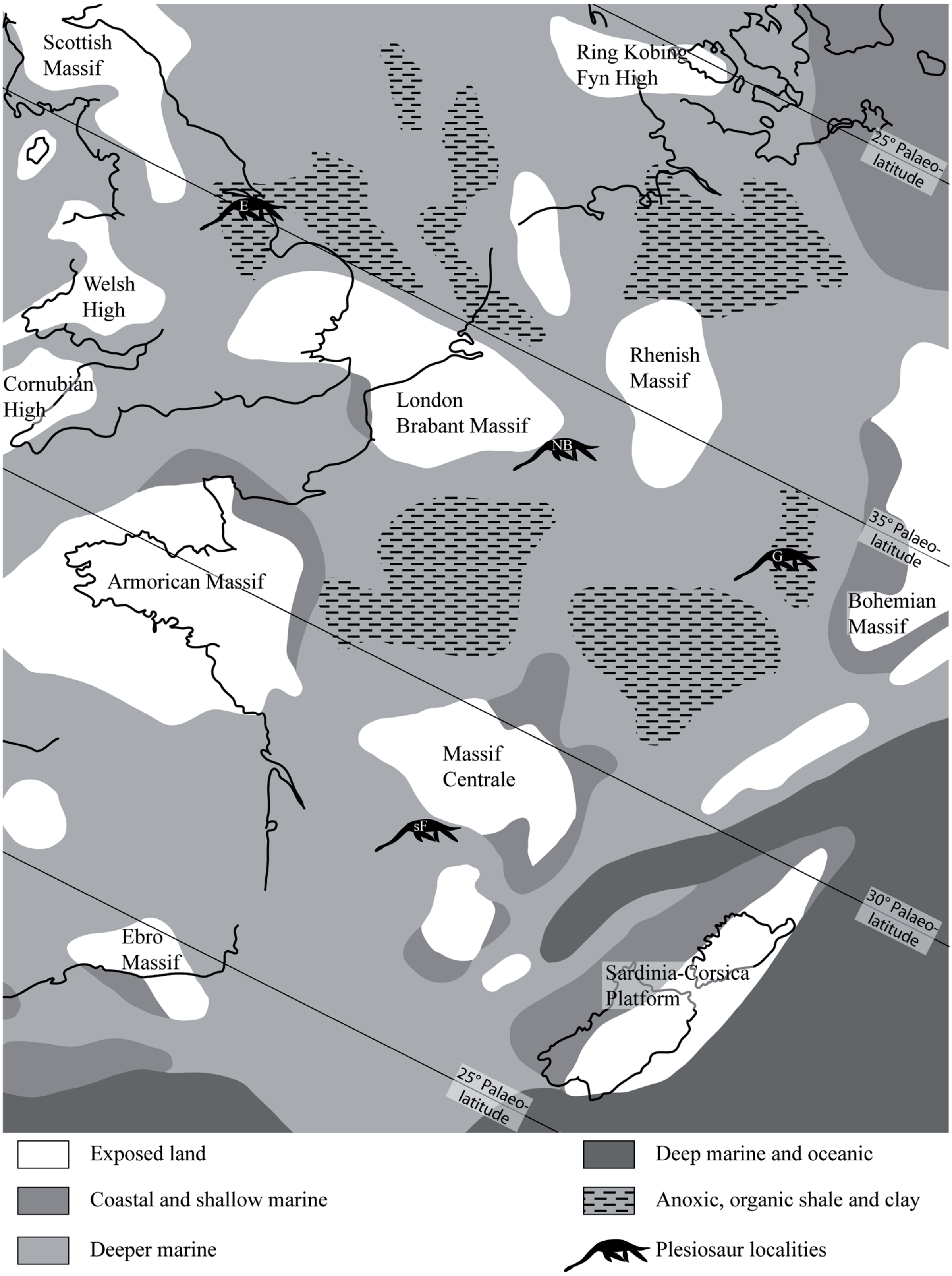


Fig. 6.2: Palaeobiogeographic map of the Middle Toarcian (180 Ma) (modified after Thierry *et al.* 2000). Letters in plesiosaurs indicate the palaeobiogeographic zones (E, English zone; G, German zone; NB, Norman–Benelux zone; sF, south France).

the Toarcian than in the Hettangian and Sinemurian, and cryptoclidids have not yet appeared. Similar morphotypes of pliosauroids are known from both the English and the German zones. As mentioned before, the robustly build genus *Rhomaleosaurus* is found in both zones. The more gracile *Hauffiosaurus zanoni* from the Posidonia shale is morphologically similar to the English *Macroplata longirostris* and, according to O'KEEFE (2001a), these two taxa are closely related.

It is concluded that palaeobiogeographic zonation was present among Toarcian plesiosaurs. Zonation was high at species and genus level, but similarities exist at family level. As similar morphotypes existed in different zones, it can be assumed that the ecological role of each morphotype was similar. Elasmosaurs are the most widespread family in the Toarcian, which indicates an early radiation and successful adaptation of this taxon in the upper Liassic.

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A: Abbreviations used in text and figures

a,	angular
art,	articular
bo,	basioccipital
bo.ap,	bodenaponeurosis
bs,	basisphenoid
ch,	choana
csa,	*canalis semicircularis anterior*
csp,	*canalis semicircularis posterior*
cv,	cervical vertebra
d,	dentary
ec,	ectopterygoid
exop,	exoccipital-opisthotic
f,	frontal
fci,	*foramen carotis interna*
fcsh,	*foramen canalis semicircularis*
fhyp,	*fenestra hypoglossis*
fv,	*fenestra vomeronasalis*
j,	jugal
l,	denotes left
M,	*Musculus*
M.am	*Musculus adductor mandibulae*
M.ame,	*Musculus adductor mandibulae externus*
M.amem,	*Musculus adductor mandibulae externus medialis*
M.amep,	*Musculus adductor mandibulae externus profundus*
M.ames,	*Musculus adductor mandibulae externus superficialis*
M.amp,	*Musculus adductor mandibulae posterior*
M.dm,	*Musculus depressor mandibulae*
M.ps,	*Musculus pseudotemporalis*
M.pt,	*Musculus pterygoideus*
mx,	maxilla
nc,	nuchal crest
p,	parietal
pal,	palatine
pmx,	premaxilla
po,	postorbital
pof,	postfrontal
prf,	prefrontal
proo,	prootic
ps,	parasphenoid
pt,	pterygoid
q,	quadrate
r,	denotes right
ru,	*recessus utricularis*
sa,	surangular
so,	supraoccipital
sq,	squamosal
st,	stapes
t,	tooth
v,	vomer
?,	denotes uncertainty

specimen number	SMNS 12039	SMNS 16812	SMNS 51141	SMNS 51143	SMNS 51747	SMNS 51945	MB.R.1991	MB.R.1992	GPIT/ RE/3185	MH Nr. 8
species	*Seeleyosaurus guilelmiimperatoris*	*Seeleyosaurus guilelmiimperatoris*	*Hydrorion brachypterygius*	*Hydrorion brachypterygius*	*cf. Hydrorion brachypterygius*	*spec. nov.*	*Hydrorion brachypterygius*	*Seeleyosaurus guilelmiimperatoris*	*Hydrorion brachypterygius*	*Hydrorion brachypterygius*
horizon	Lias $\varepsilon\mathrm{II}_4$	Lias $\varepsilon\mathrm{II}_4$	Lias $\varepsilon\mathrm{II}_4$	Lias $\varepsilon\mathrm{II}_4$	Lias $\varepsilon\mathrm{II}_9$	Lias $\varepsilon\mathrm{II}_1$	Lias $\varepsilon\mathrm{II}_4$	Lias $\varepsilon\mathrm{II}_4$	Lias $\varepsilon\mathrm{II}_4$	Lias $\varepsilon\mathrm{II}_4$.
measurements										
overall body length [m]	3.40	2.44	1.73	2.88	4.04	3.55	3.09	2.88	3.00	2.85
skull [mm]	170	130	174	180	235	220	200	160	180	230
neck [mm]	1300	840	729.3	1262.5	1660	1132.7	1177	1230	805	1100
body [mm]	900	766	535.7	770.3	940	1059.7	893	759	735	809
tail [mm]	1030	705	446.7	663	1207	869.7	825	720	275	720.5
fore limb. length [mm]	810	489	/	678	933	458.7	602	778	625	610
hind limb. length [mm]	890	495	330	691.3	884	565.3	636	740	640	630
fore limb. width [mm]	172	100	99.1	224.3	173	69	108	112	205	200
hind limb. width [mm]	135	95	120.3	224.2	172	102	101	122	200	175
humerus [mm]	265	154	/	120	298	148.7	190	228	/	100
femur [mm]	260	155.5	70	140	288	171.8	183	220	130	110
number of vertebrae										
cervical	35	38	29	33	37	36	29	37	36	35
dorsal	20	24	23	21	19	29	20	20	19	19
sacral	2	3	3	2	2	3	3	2	2	3
caudal	43	41	36	28	31	39	37	37	42	28
presacral	53	62	52	54	59	65	52	57	55	57
all vertebrae	100	106	91	84	90	106	89	94	99	85
AR										
fore limb	7.63	8.07	/	5.99	8.84	10.82	9.19	10.37	6.05	6.14
hind limb	10.4	8.35	5.2	5.92	8.34	9.29	10.81	10.66	6.14	7.16

Appendix B: Table of measurements for the studied plesiosauroid specimens, number of vertebrae and AR calculated after O‘Keefe (2001b).

specimen number	SMNS 12039	SMNS 16812	SMNS 51141	SMNS 51143	SMNS 51747	SMNS 51945	MB.R.1991	MB.R.1992	GPIT/ RE/3185	MH Nr. 8
ratios										
skull / overall body length	0.05	0.05	0.10	0.06	0.06	0.06	0.06	0.06	0.06	0.08
skull / neck	0.13	0.15	0.24	0.13	0.14	0.19	0.17	0.13	0.22	0.20
neck / body	1.44	1.09	1.36	1.74	1.77	1.07	1.32	1.64	1.09	1.37
skull / body	0.19	0.17	0.23	0.23	0.25	0.21	0.22	0.21	0.24	0.29
neck / overall body length	0.38	0.34	0.42	0.45	0.41	0.32	0.38	0.43	0.27	0.39
body / overall body length	0.26	0.31	0.301	0.26	0.23	0.30	0.29	0.26	0.24	0.28
fore / hind limb	0.91	0.99	/	0.98	1.06	0.80	0.95	1.14	0.98	0.97
humerus / fore limb length	0.32	0.31	/	0.18	0.32	0.32	0.32	0.32	0.18	0.16
femur / hind limb length	0.29	0.31	0.21	0.20	0.33	0.31	0.29	0.29	0.20	0.17
length / width fore limb	4.71	4.89	/	5.65	5.39	6.56	5.57	6.34	5.68	6.10
length / width hind limb	6.59	5.21	4.71	4.94	5.72	5.54	6.30	6.44	4.92	5.73
fore limb / overall body length	0.24	0.20	/	0.23	0.23	0.13	0.19	0.25	0.21	0.21
hind limb / overall body length	0.26	0.20	0.19	0.23	0.22	0.16	0.21	0.26	0.21	0.22
humerus / femur	1.02	0.99	/	1.00	1.03	0.87	1.04	1.04	0.84	1.14

Appendix B (continued): Table of ratios calculated from the measurements of the studied plesiosauroid specimens, used for the SPSS analysis.

Hydrorion brachypterygius				
jaw gape	0°	20°	40°	60°
M.ame profundus	45°	37°	28°	18°
M.ame medialis	112°	86°	68°	45,5°
M.ame superficialis	62°	52°	39,5°	31°
M. pterygoideus	166°	151°	138°	123°
M.am posterior	10°	9,5°	6°	~1°
M. pseudotemporalis	117,5°	89°	71°	55°
Seeleyosaurus guilelmiimperatoris				
jaw gape	0°	20°	40°	60°
M.ame profundus	64°	50°	37°	25,5°
M.ame medialis	85°	75°	59°	45°
M.ame superficialis	73°	57°	43,5°	30°
M. pterygoideus	24°	40°	55°	72°
M.am posterior	19°	16°	12°	7°
M. pseudotemporalis	86,5°	69°	54°	41°

Tab. C.1: Changes in the angle of insertion of the muscles with increasing jaw gape for *Hydrorion brachypterygius* and *Seeleyosaurus guilelmiimperatoris*; for abbreviations, see appendix A.

Hydrorion brachypterygius				
jaw opening	0°	20°	40°	60°
M.ame profundus	0.28	0.25	0.25	0.25
M.ame medialis	0.33	0.37	0.27	0.31
M.ame superficialis	0.35	0.31	0.27	0.22
M. pterygoideus	0.03	0.01	0.06	0.10
M.am posterior	0.10	0.09	0.07	0.04
M. pseudotemporalis	0.31	0.37	0.36	0.32
Seeleyosaurus guilelmiimperatoris				
jaw opening	0°	20°	40°	60°
M.ame profundus	0.23	0.20	0.18	0.12
M.ame medialis	0.26	0.26	0.23	0.20
M.ame superficialis	0.25	0.23	0.19	0.15
M. pterygoideus	0.02	0.01	0.03	0.05
M.am posterior	0.11	0.10	0.07	0.05
M. pseudotemporalis	0.30	0.28	0.25	0.22

Tab. C.2: Changes in the relation of force to load arm with increasing gape for *Hydrorion brachypterygius* and *Seeleyosaurus guilelmiimperatoris*; for abbreviations, see appendix A.

Hydrorion brachypterygius				
jaw opening	0°	20°	40°	60°
M.ame profundus	100%	131%	160%	180%
M.ame medialis	100%	138%	177%	213%
M.ame superficialis	100%	139%	171%	195%
M. pterygoideus	100%	100%	100%	100%
M.am posterior	100%	112%	120%	127%
M. pseudotemporalis	100%	140%	188%	229%
Seeleyosaurus guilelmiimperatoris				
jaw opening	0°	20°	40°	60°
M.ame profundus	100%	123%	134%	157%
M.ame medialis	100%	123%	145%	167%
M.ame superficialis	100%	125%	142%	160%
M. pterygoideus	100%	100%	98%	95%
M.am posterior	100%	116%	121%	128%
M. pseudotemporalis	100%	141%	174%	202%

Tab. C.3: Changes in the length of the muscles (in per cent of the resting length) with increasing jaw gape for *Hydrorion brachypterygius* and *Seeleyosaurus guilelmiimperatoris*; for abbreviations, see appendix A.

Appendix C: Tables of the empirically gained values for the functional analysis of the cranial musculature of *Hydrorion* and *Seeleyosaurus*.

specimen	species	description	horizon	location
SMNS 51747	Plesiosauridea indet.	nearly complete skeleton with incomplete head	Lias εII9	Holzmaden, Swabia
SMNS 53044	?*R. victor*	both coracoids of a ?juvenile specimen	Lias εII6	Holzmaden, Swabia
SMNS uncat.	?*R. victor*	right femur head	Lias εII5?	Holzmaden, Swabia
Hauff Nr. 8	*H. brachypterygius*	complete skeleton	uppermost Lias εII4, directly below II5	Holzmaden, Swabia
Hauff Nr. 7	*H. zanoni*	complete skeleton	uppermost Lias εII4, directly below II5	Holzmaden, Swabia
SMNS 81854	?*Plesiosaurus* sp	two fragmentary cervical vertebrae	Lias εII4/5	Holzmaden, Swabia
MB.R.1992	*S. guilelmiimperatoris*	complete skeleton	Lias εII4	Holzmaden, Swabia
MB.R.1991	*H. brachypterygius*	complete skeleton	Lias εII4	Holzmaden, Swabia
GPIT/RE/3185	*H. brachypterygius*	complete skeleton	Lias εII4	Holzmaden, Swabia
SMNS 12039	*S. guilelmiimperatoris*	complete skeleton	Lias εII4	Holzmaden, Swabia
SMNS 51141	*H. brachypterygius*	nearly complete skeleton with incomplete head	Lias εII4	Holzmaden, Swabia
SMNS 51143	*H. brachypterygius*	nearly complete skeleton with incomplete head	Lias εII4	Holzmaden, Swabia
SMNS 16812	*S. guilelmiimperatoris*	complete mounted skeleton	Lias εII4	Holzmaden, Swabia
SMNS 51942	*Plesiosaurus* sp	thoracic and ?sacral vertebra	Lias εII4	Holzmaden, Swabia
SMNS uncat.	„*Plesiosaurus*“ sp.	two remains of a ?femur	Lias εII4	Holzmaden, Swabia
SMNS 54052	?*Plesiosaurus*	fragmentary ?humerus	Lias εII3	Holzmaden, Swabia
SMNS uncat.	*R. victor*	complete skeleton	Lias εII3	Holzmaden, Swabia
SMNS 51945	Plesiosauridae indet.	complete skeleton without head	Lias εII1	Holzmaden, Swabia
Fossilienmuseum Dotternhausen	?Plesiosauria	serpulid encrusted bone	Lias ε	Dotternhausen, Swabia
SMNS 50845	*Plesiosaurus* sp.	16 vertebra, one proximal humerus and several fragments	Lias ε	Forchheim, Franconia
SMNS uncat.	„*P.*“ *guilelmi imperatoris*	two posterior cervical vertebrae	Lias ε	Holzmaden, Swabia
SMNS 50847	?*Rhomaleosaurus*	cervical vertebra	Lias ε	Forchheim, Franconia

Appendix D: Table of plesiosaur specimens from the Liassic in the collections of the SMNS, the Museum Hauff, the GPIT and the Fossilienmuseum Dotternhausen.

Name, Vorname: Großmann, Franziska

Geburtsdatum: 21.10.1974

Geburtsort: Bochum

Schulgang:

Schule:

1981 – 1983: Grundschule Bühlbusch in Verl, Kreis Gütersloh

1983 – 1987: Deutsche Schule in Barcelona, Spanien

1987 – 1990: Gymnasium Verl, Kreis Gütersloh

1990 – 1994: Anne-Frank-Schule, Städtische Gesamtschule Gütersloh, Abschluß mit dem Abitur

Universität:

1994 – 1998: Studium der Geologie/Paläontologie an der Christian-Albrechts-Universität zu Kiel; Abschluß mit dem Vordiplom

1998 – 2001: Studium der Geologie/Paläontologie an der Eberhardt-Karls-Universität Tübingen, Studienschwerpunkte Wirbeltierpaläontologie und Zoologie

2000 Diplomkartierung in La Vecilla, Kantabrisches Gebirge, Nord-West-Spanien

Juni 2001: Abschluß des Studiums mit dem Diplom in Geologie/Paläontologie mit der Diplomarbeit „Neues Nothosaurus-Material aus dem Lettenkeuper von Südwest-Deutschland“, Betreuer: Prof. H.-U. Pfretzschner, Prof. F. Westphal

Promotion:

2003 – 2006 Promotionsarbeit am Geowissenschaftlichen Institut der Universität Tübingen: „Taxonomy, phylogeny and palaeoecology of the plesiosauroids (Sauropterygia, Reptilia) from the Posidonia shale (Toarcian, Lower Jurassic) of Holzmaden, south west Germany“ unter der Betreuung von Prof. H.-U. Pfretzschner und Prof. W. E. Reif