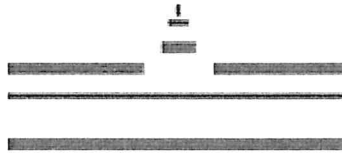


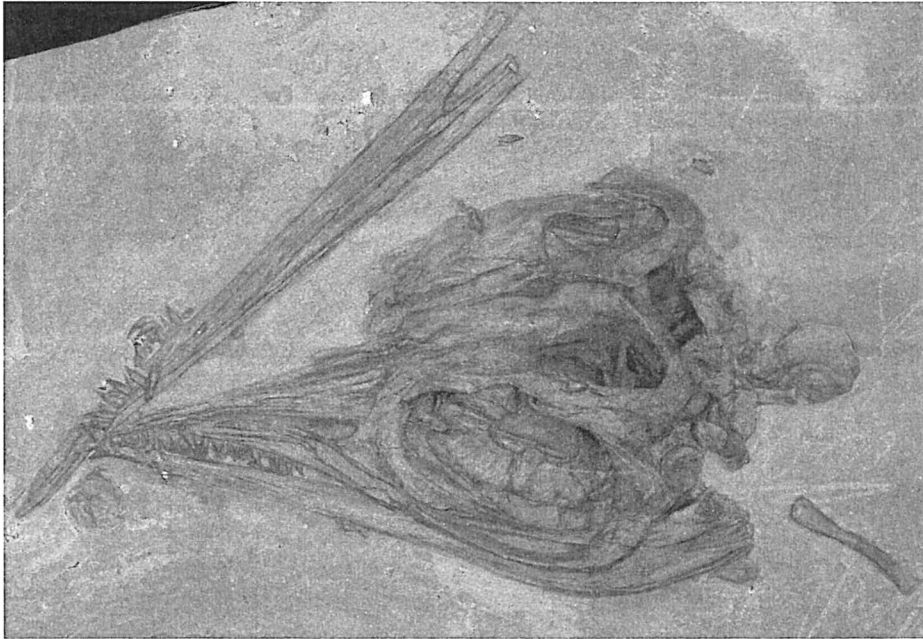
Westfälische Wilhelms-Universität Münster

Institut für Geologie und Paläontologie



WESTFÄLISCHE
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Bachelorarbeit



An ichthyosaur skull from the lower Toarcian (Early Jurassic) of Schandelah (Lower Saxony)

handed in by

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Abstract

An exceptionally well-preserved ichthyosaur skull of Toarcian age, SNHM 2753-R, from the locality of Geopunkt Jurameer Schandelah, Lower Saxony, Germany, is placed within the family Leptonectidae by virtue of its small teeth that are conical, slender and lack enamel ornamentation, its slender snout, its quadratojugal in posterior position as well as its small supratemporal fenestra and its very orbit. The skull is short, and its teeth also possess marginally recurved crowns and large, bulbous, infolded roots. Its snout is long and delicate with a short mandible, resulting in an overbite and its basioccipital features a large extracondylar area. For these reasons it is placed within the genus *Wahlisaurus*. However, SNHM 2753-R features a far more distinct overbite than *Wahlisaurus massarae* at 97 mm, is smaller in skull size at 301 mm and anteriorly, its surangular only extends to the anterior half of its naris unlike in the holotype of *Wahlisaurus massarae*, which has a surangular reaching its maxilla's anterior margin. It is also considerably younger at Toarcian instead of Hettangian age. Thus, it is placed within *Wahlisaurus* sp. nov., which is left in open nomenclature. The diagnosis formerly in effect for both the genus of *Wahlisaurus* as well as the species of *Wahlisaurus massarae* is used solely for generic distinction and new diagnoses are introduced to differentiate *Wahlisaurus massarae* and *Wahlisaurus* sp. nov. based on the characters mentioned.

Introduction

The first ichthyosaur remains that were identified as such were discovered by Joseph Anning in 1811 (Joger 2014) and described in 1814, being considered a link between fishes and crocodiles (Home 1814; Appleby 1961). In 1819, the phylogenetic relationships were revisited, *Ichthyosaurus* instead being placed between salamanders and lizards (Home 1819). The first good accounts of an ichthyosaur skull were given in 1821 and 1822 and included the first use of binomial nomenclature in ichthyosaurs (De la Beche & Conybeare 1821; Appleby 1961) with *Leptonectes tenuirostris* (Conybeare 1822) but relied largely on composite illustrations (Appleby 1961). In 1846 a fossil of *Ichthyosaurus communis* that showed a smaller individual protruding from its pelvis was discovered, suggesting that it died giving birth, giving the first evidence for ichthyosaurs being viviparous (Pearce 1846). In the following decades, numerous new species of ichthyosaurs were established, including such examples as *Eurhinosaurus longirostris* and *Suevoleviathan integer* (Bronn 1844; Mantell 1851). However, most of these species had been referred to the genus *Ichthyosaurus* before Lydekker considered sub-dividing the genus in 1889 (Appleby 1961). Two years prior, it had been concluded that the ichthyosaurs originated from relatives of the Sphenodontidae and the new genus *Mixosaurus* and its family, Mixosauridae were established (Baur 1887). Subsequently, new genera for newly found and old species were introduced in the following years, including *Stenopterygius* (Jaekel 1904) and *Eurhinosaurus* (Abel 1909). In 1948, it was concluded that the high degree of aquatic specialisation in ichthyosaurs does not allow for any speculation on their origin from any known terrestrial reptile group (Romer 1948). Already, Holzmaden in Germany was established as one of the most important sites of ichthyosaur discovery as over 200 specimens were being unearthed there annually (Ley 1951). In 1956, the first evidence of brown pigmentation was found (Whitear 1956), in 1965 it was hypothesised that ichthyosaurian descended from cotylosaurs (Colbert 1965) and in 1968 it was concluded that *Temnodontosaurus* fed on a diet of cephalopods (Pollard 1968). By examining the cranial morphology of *Ichthyosaurus* in 1973, it was found to possess a very large brain with a large cerebellum and corpus striatum compared to other reptiles, leading to the interpretation that the animals displayed a high degree of movement coordination, instinctive behaviour and possibly social and parental behaviour while the lagena was found to be small, suggesting an underdeveloped sense of hearing (McGowan 1973). It was

also speculated on their overwhelming abundance in the deposits of southern Germany being caused by taphonomy, not biogeographical distribution, and doubts on the phylogenetic value of differentiating between latipinnate and longipinnate ichthyosaurs were expressed (McGowan 1979). In 1991, the remains of an ichthyosaur of ca. 21 m in length were discovered in Canada, which were later described as *Shonisaurus sikanniensis*, the largest known specimen at the time (Nicholls & Manabe 2004). In the same year, it was suggested that some ichthyosaurs may have been homeothermic or may at least have been helped in maintaining stable body temperatures by their large mass (McGowan 1991). In 1992, the theory that ichthyosaurs were replaced by mosasaurs was challenged because they were not in direct competition and instead suggested that they were affected by the disappearance of many cephalopod species, which were their main source of nutrition, caused by an extinction event at the Cenomanian-Turonian boundary (Bardet 1992). In 1996, the large number of vertebrae in the primitive *Chensaurus* were interpreted as signs of an eel-like movement, suggesting that ichthyosaurs may have evolved from an eel-like body to a jack-like body before reaching a tuna-like body plan, suggesting an anguilliform, carangiform and thunniform movement pattern, respectively (Motani, You & McGowan 1996). In 1997, of several species of *Mixosaurus*, only two were regarded as valid and several species of *Phalarodon* were also described as synonymous with these two *Mixosaurus* taxa (Callaway 1997). In 1998, the leptonectid family was established for *Eurhinosaurus*, *Excalibosaurus* and *Leptonectes* based on their large eyes, long overbite and long and three- to four-fingered flippers (Maisch 1998). *Suevoleviathan* and other genera were also described (Maisch & Matzke 2000).

A phylogeny of ichthyosaurs was published in 1999, also naming two new genera (Motani 1999). In the same year, *Temnodontosaurus's* eyes were found to have measured up to 26 cm in diameter, which is larger than any other known animal (Motani et al. 1999; Joger 2014). Also in that year, it was suggested that ichthyosaurs might have faced extinction due to competing with ambush predators such as plesiosaurs and mosasaurs after all as faster swimming fishes had evolved during the Cretaceous (Lingham-Soliar 1999). Via CT-scan it was found that *Platypterygius's* ear morphology would not have allowed it to hear, making it deaf but sensory structures allowing it to smell as well as a system of channels and grooves were also discovered (Ellis 2003), which were later speculated to be an electrosensory system like those in modern sharks (Ellis 2002).

Following his 1998 review on ichthyosaur taxonomy, a revision of the genus *Stenopterygius* was published in 2008, regarding only *Stenopterygius quadricissus* and *S. triscissus* of the previously eight species of *Stenopterygius* as valid, establishing a new species using the already existent but formerly invalid name *S. uniter*, also referring *Ichthyosaurus longipes* and *I. longifrons* to these taxa as well as establishing a new genus and elevating the former subspecies *S. hauffianus forma typica* to species level in *Hauffiopteryx typicus* based on severe morphological differences between it and *Stenopterygius*, thus continuing the trend of simplification in ichthyosaur taxonomy (Godefroit 1994; Maisch 1998; Maisch 2008). A fourth species of *Stenopterygius* was described in 2012 in *S. aaleniensis* (Maxwell et al. 2012). The same year saw the description of *Temnodontosaurus azerguensis* (Martin et al. 2012). In 2015 and 2016, three new species of *Ichthyosaurus* were described in *Ichthyosaurus anningae* (Lomax and Massare 2015), *I. larkini* and *I. somersetensis* (Lomax and Massare 2016). Finally, a new leptonectid genus and species were established in 2016 under the name of *Wahlisaurus massarae* (Lomax 2016). The purpose of this thesis is to describe the recently unearthed fossil skull of an ichthyosaur from Schandelah, Lower Saxony, Germany for the first time and classify it taxonomically.

Material and Methods

Geological Background and Material

During the early Jurassic, an extensive intracontinental shelf sea was formed in central Europe, the water temperature of which was estimated to be 20-27 °C (Zellmer 2014). The Posidonia Shale formation, a series of black shales rich in organics with intercalated limestone horizons that was deposited in the Southwest German Basin during the early Toarcian (early Jurassic) is one of the Central European Epicontinental Basins, which is a group of such Toarcian formations throughout central Europe (Röhl & Schmid-Röhl 2005; Dick 2015).

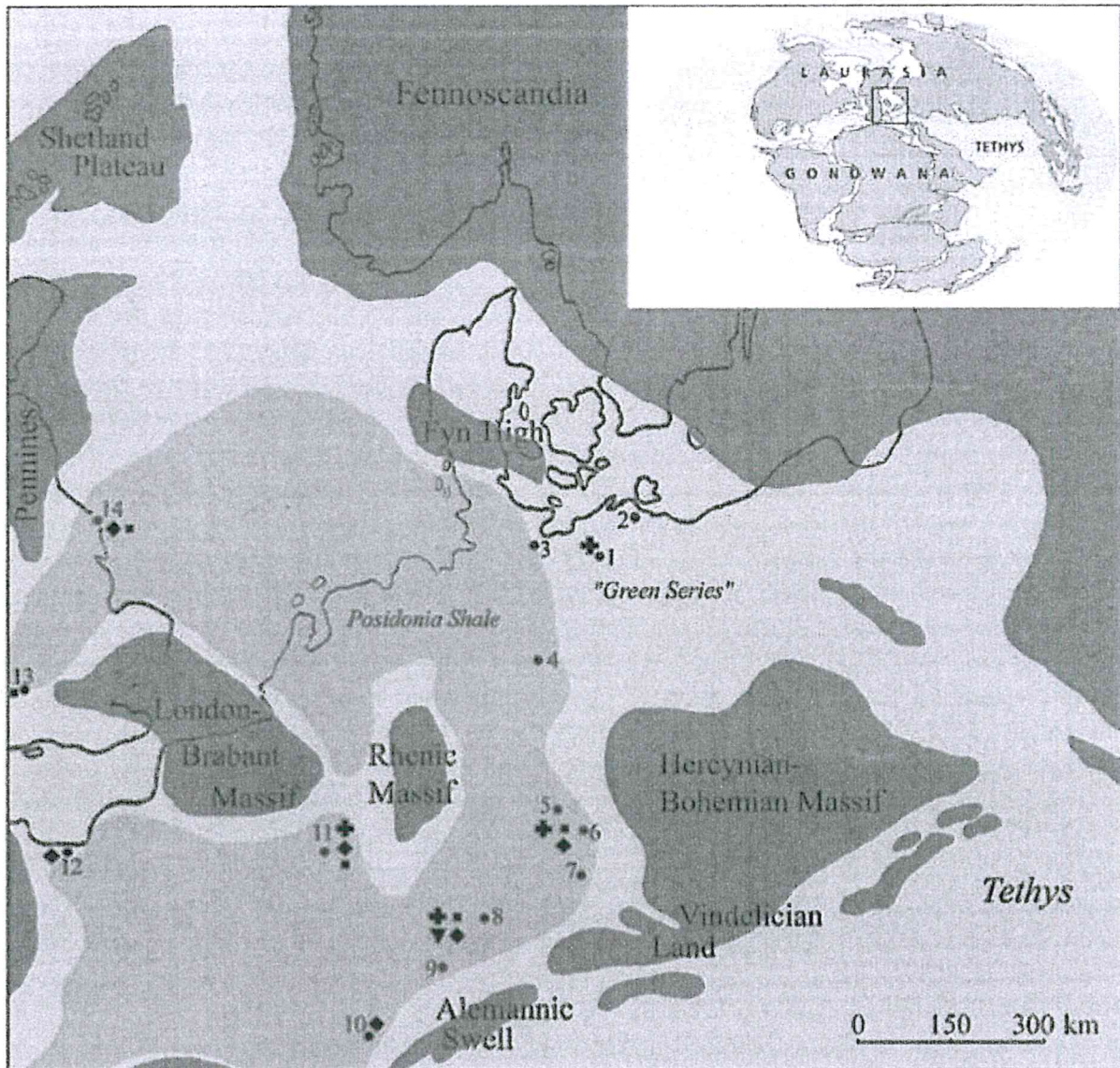


Figure 1. Central and Western Europe during the lower Toarcian. Dark grey areas indicate land, light grey areas marine deposits and medium grey areas bituminous shale deposits. Digits indicate digsite localities, of which number 4 is Schandelah, Lower Saxony, Germany. The map has been modified by Maisch and Ansoerge after Riegraf (1985) and the insert map has been taken from Hauff (1997). (Maisch & Ansoerge 2004)

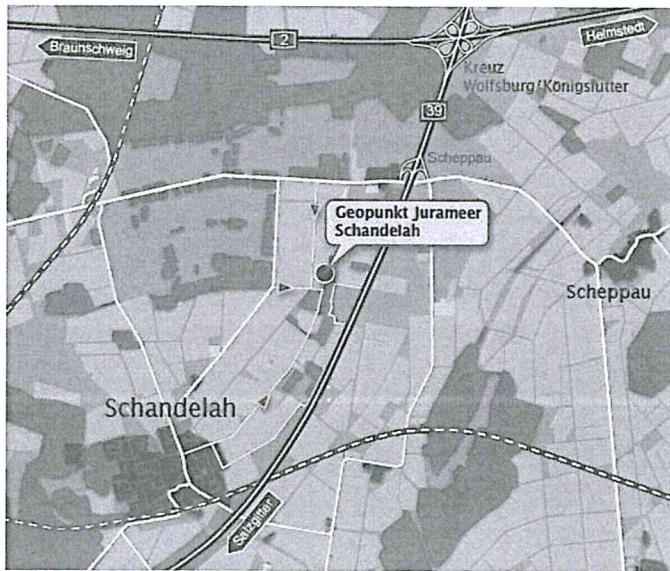


Figure 2. The geographic position of Geopunkt Jurameer Schandelah relative to the village of Schandelah (map: <http://www.geopunkt-schandelah.de/Kontakt-Besuch/>).

However, this formation can also be found in the Lower Saxonian Basin (fig 1), at the edge of which Brunswick and Cremlingen are located (Zellmer 2014). The Posidonia Shale is known for its exceptional fossil preservation, especially of ichthyosaurs, which are mostly found near Holzmaden (Maxwell 2012). These fossil-rich deposits were named after the ubiquitous genus *Posidonia* and formed under anoxic conditions, thus enabling this level of preservation, even sometimes yielding skin impressions in ichthyosaurs (Zellmer 2014). Also named Lias Epsilon (Lias ϵ), it is divided into three sections of unequal thickness, which are ϵI , corresponding to the *Dactyloceras tenuicostatum* ammonite zone, ϵII , corresponding to the *Dactyloceras*

tenuicostatum and *Harpoceras falciferum* ammonite zones, and ϵIII , corresponding to the *Hildoceras bifrons* ammonite zone (Riegraf et al. 1984; Maxwell 2012). The area near Brunswick has yielded a great number of well-preserved fossils of different taxa. These include but are not limited to ichthyosaurs, crocodylians, insects and fishes (Hauff et al. 2014). For this reason, in cooperation with the Dr. Scheller Stiftung, the State Museum of Natural History Brunswick and the Harz – Brunswick Land – Eastphalia National Geopark, permanent sites of excavation were established in Hondelage, a district within the city of Brunswick, and in Schandelah, a village within the municipality of Cremlingen. Excavations at Geopunkt Jurameer Schandelah (fig. 2) began in 2014 and more than 700 fossils of different species such as the fishes *Acidorrhynchus* and *Tetragonolepis* have been found in the first three years, the number increasing each year (<http://www.geopunkt-schandelah.de/Hintergrund/>). The specimen examined in this thesis was recovered on 12 May 2015, given the inventory number SNHM 2753-R and subsequently prepared by Sebastian Radecke, State Museum of Natural History Brunswick (Kosma, pers. comm. 2017). On 23 September 2015, 16 zoned sediment samples were taken, of which 13 were used for micropalaeontological examination (Heunisch, pers. comm. 2015; <http://www.geopunkt-schandelah.de/Hintergrund/>). The palynological work showed only small numbers of palynomorphs because the samples were taken close to the sediment surface, which is why quantitative analyses did not take place (Heunisch, pers. comm. 2015). The samples contained mainly amorphous clasts, which partially consisted of small algae like *Halosphaeropsis liassica* (fig 3; Heunisch, pers. comm. 2015). Further components of the Posidonia Shale that were found include Prasinophyceae, namely *Tythyodiscus*, *Pleurozonaria*, *Pterosphaeridia*, *Cymatiosphaera*, *Tasmanites* and *Campenia* (fig 3; Heunisch, pers. comm. 2015). Neither spores nor pollen found allowed any exact dating of the samples as they can also be found in a greater range of strata (Heunisch, pers. comm. 2015). Dinocysts found were related to the *Dodekovia/Reutlingia/Susadinium* ssp. group (fig 3) and to *Evansia* cf. *granochagrinata* and thus indicate a late-Toarcian age (Heunisch, pers. comm. 2015). However, no further fossil evidence for this assessment was found, which is why it remains dubitable (Heunisch, pers. comm. 2015).

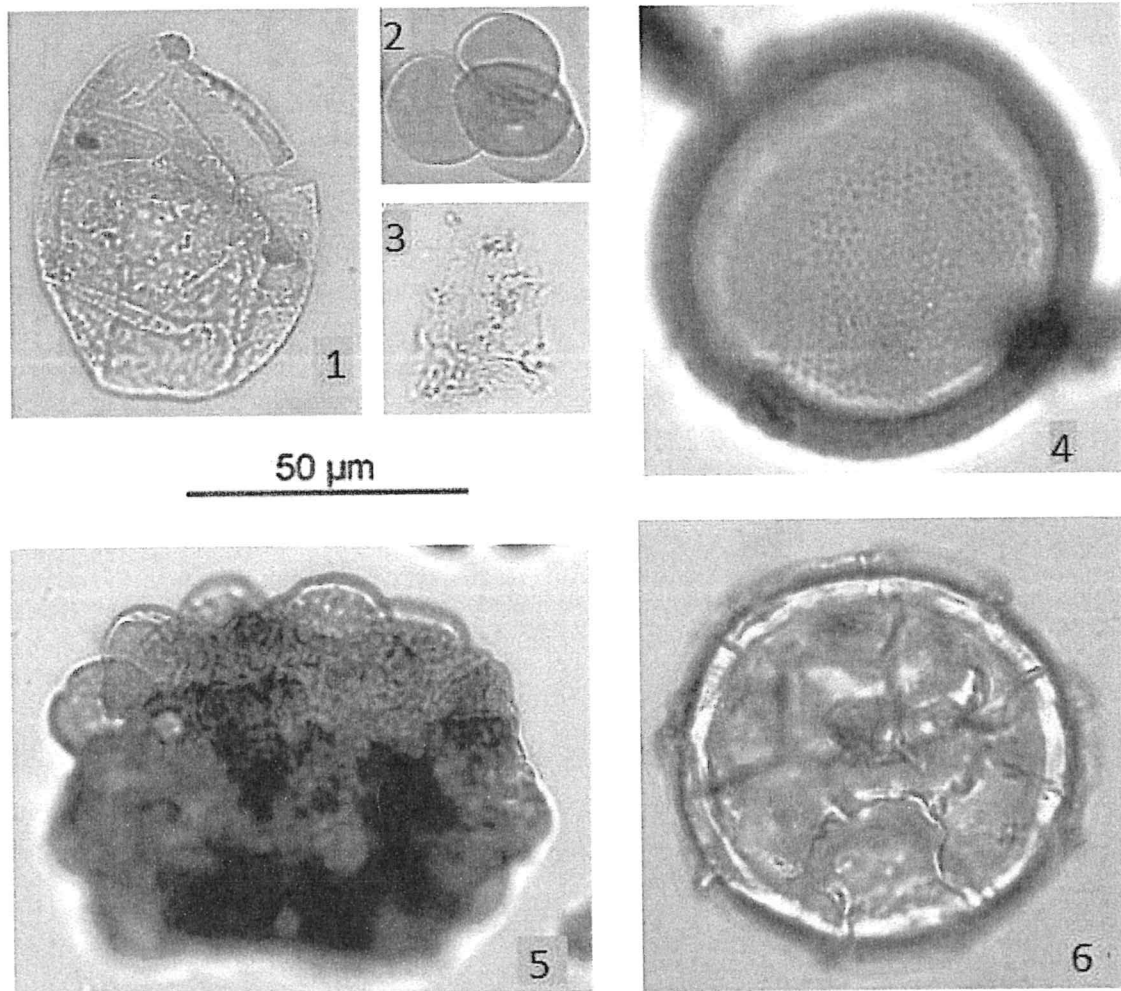


Figure 3. Some of the species found in the palynological analysis of sediments at Geopunkt Jurameer Schandelah. 1 = ?*Mikrocysta* sp; 2, 5 = *Halosphaeropsis liassica*; 3 = *Dodekovia/Reutlingia/Susadinium* spp.; 4 = *Tytthodiscus* sp.; 6 = *Pterosphaeridia undulata* (Heunisch, pers. comm. 2015).

Methods

The specimen was visually examined to determine all relevant anatomical features, such as points of contact between the individual elements, the shape and condition of bones and sutures, surface structure and ornamentation and taphonomic features. Then, measurements were taken and ratios to be used in determining the specimen's species were calculated. The findings were analysed by comparison to data found in the scientific literature pertinent to the subject of Early Jurassic ichthyosaurs.

Description

Taphonomy

SNHM 2753-R is a complete skull, which has been deformed during diagenesis (fig 4). The ventral to anteroventral half of its sinistral side has been fully flattened, its dorsal to dorsoposterior half of the sinistral side as well as the sinistral half of its skull roof and its neurocranium appear to be intact and the dextral half of its skull roof has been partially crushed. It is embedded in sediment ventrodextrally, leaving its sinistral side, most of its skull roof and parts of its neurocranium well exposed, with its posterior skull partially visible but mostly obscured from view by sediment and neurocranial elements. The premaxilla has been dislocated posterodorsally and rotated along its anteroposterior axis by 180° as well as counterclockwise by 45°. It is embedded next to the rest of the skull anterodorsally. The mandibular tip is either overlapped by the dislocated premaxilla or missing entirely. Several premaxillary, maxillary and dentary teeth can still be identified but many have been dislocated, covering parts of the maxilla, lower jaw and skull roof. A few teeth can also be found in isolation in dorsal position to the specimen.

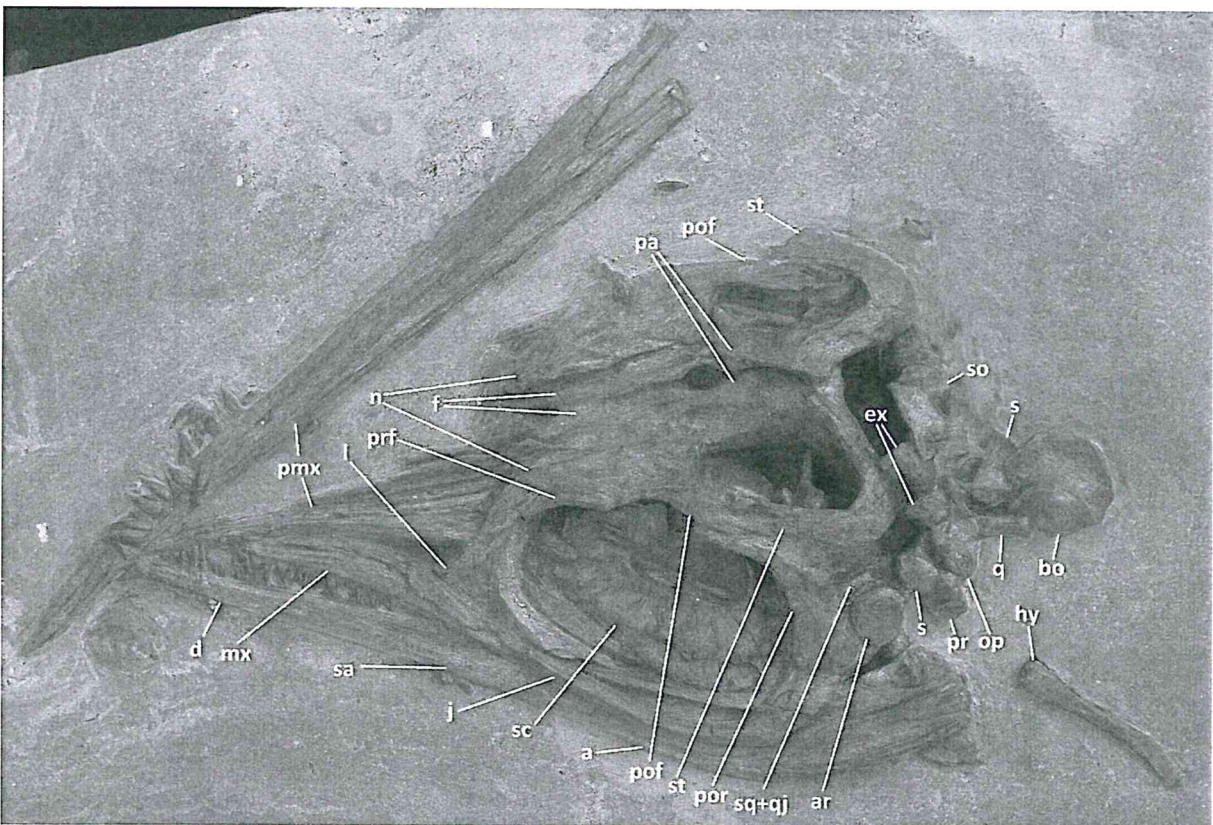


Figure 4. SNHM 2753-R in dorsolateral view. Abbreviations: pmx = premaxilla; mx = maxilla; l = lacrimal; n = nasal; j = jugal; prf = prefrontal; pof = postfrontal; f = frontal; pa = parietal; st = supratemporal; por = postorbital; sq = squamosal; qj = quadratojugal; sc = sclerotic ring; so = supraoccipital; ex = exoccipital; bo = basioccipital; s = stapes; pr = prootic; q = quadrate; ar = articular; hy = hyoid rod; d = dentary; sa = surangular; a = angular.

A small portion of the exposed orbital margin is missing dorsally. Due to the aforementioned crushing of the skull roof, the dextral parietal is now overhanging its sinistral counterpart and the skull has been fissured along its lateral axis and partially displaced anteriorly at its dextral supratemporal fenestra's margin. The neurocranial elements are located near their original positions. However, they have been slightly displaced, partially rotated and eventually fused during diagenesis. A single hyoid rod has been rotated by 180° and displaced from the hyoid apparatus posteriorly, thus exposing it to be visible in this specimen.

Preorbital skull

Premaxilla

The 181 mm long (Table 1) sinistral premaxilla is dislocated by a few centimetres from its initial position, having been turned over along its anteroposterior axis by 180° (fig 4). Thus, its original connections to other elements of the skull and measurements including the premaxilla can only be estimated. However, an upper jaw bone adjacent to the maxilla, apparently the other premaxilla, is still connected to the skull but it appears to be much shorter than the dislocated one. So, it is likely that its tip has either been broken off or is embedded deeper in the claystone, still.

Preorbital skull and mandible	
Measured feature	Length in mm
Premaxilla (tip to naris)	181
Mandible	204
Overbite	122
Maxilla	68
Naris	19
Distance posterior naris – anterior orbit	13
Lacrima (anterior face)	28
Lacrima (ventral face)	53
Lacrima (posterior face)	42
Preorbital skull/snout length	213
Snout height at naris	47

Table 1. Measurements taken from the preorbital skull and mandible of SNHM 2753-R.

Which of these is the case cannot be determined as the upper jaw's tip is overlain by the dislocated premaxilla. Both the processus supranarialis and the processus subnarialis of this dislocated bone are relatively long and straight, almost parallel to one another and seem to have enveloped almost the entire naris in their original position. The supranarial process is about a centimetre shorter than its counterpart and ends posteriorly in a slight eminence. A ridge extends from the tip of the naris to about the centre of the premaxilla, where it gradually recedes into the bone. Ventrally, it is adjacent to the fossa praemaxillaris, which also originates at the naris but extends up to the very tip of the premaxilla. About 8 cm away from the bone's tip a small fovea can be found within the fossa praemaxillaris. Another ridge can be found along the premaxilla's entire dorsal margin. Only 6 teeth can unequivocally be attributed to the dislocated premaxilla and are still preserved in articulation. 10 more teeth are dislocated and situated on top of the premaxilla, partially obstructing the view on it. Another 12 teeth are still connected to the articulated upper jaw, most of them to the maxilla. All teeth still in articulation appear to be tightly packed with little space in between. The posteriormost of them are located 25 mm anterior to the orbit, the anteriormost about 60 mm posterior to the tip of the premaxilla. All teeth are conical in shape and appear to have featured smooth crowns in life, not showing any form of serration or other enamel ornamentation. They measure up to 11 mm in length and are either straight or slightly bent toward the tip. Their roots are nearly cylindrical in shape and possess large, bulbous roots, some of which show infolding.

Maxilla

The maxilla is 68 mm in length (Table 1) and appears to have been enveloped by both the dextral and sinistral premaxilla in life when the latter was still in articulation. Anterodorsally, it is bordered by a still articulated bone of the upper jaw that is supposedly the dextral premaxilla. Posterodorsally, it is partially overlain by a small plateau, which is dorsally convex, about 25 mm in length and offset to its surrounding bones by a few millimetres, possibly part of the premaxilla. It appears that the maxilla does or did not contact the external naris. The elongate, approximately triangle shaped bone possesses a smooth surface and no further noticeable features other than a slight ridge along its anterodorsal margin. At least 11 maxillary teeth can be seen. Their shape does not differ from the premaxillary teeth.

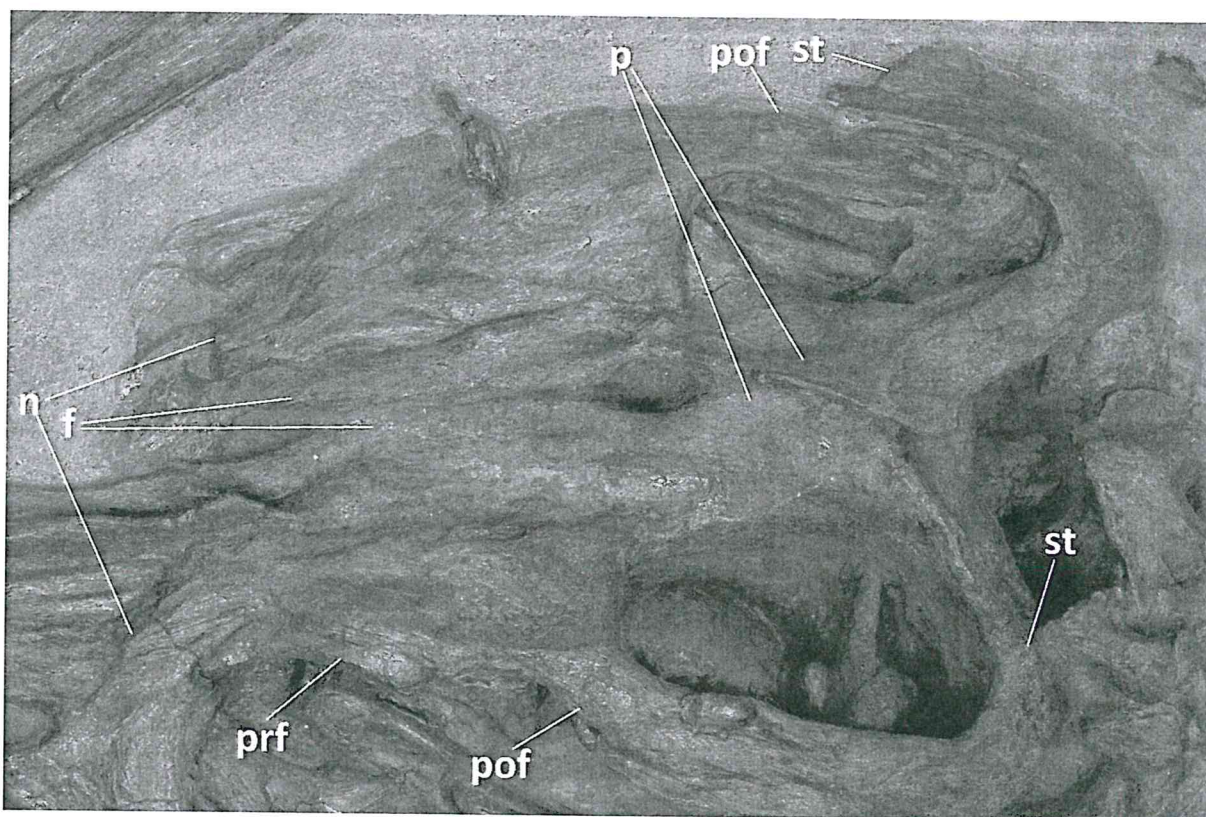


Figure 5. The skull roof of SNHM 2753-R in dorsolateral view. Abbreviations: n = nasal; prf = prefrontal; pof = postfrontal; f = frontal; p = parietal; st = supratemporal.

Lacrimal

The lacrimal makes up the posterior and half of the ventral margin of the naris, so it prevents the nasal from touching the naris. It is concave where in contact with the laterally oriented 19 mm long naris, thus giving the latter the shape of a flattened, overturned dome. The bone's anterior margin measures 28 mm in length, its ventral margin 53 mm and its posterior margin 42 mm (Table 1). The lacrimal borders the nasal dorsally, is overlapped by the prefrontal posterodorsally, borders the orbit posteriorly and touches or is partially overlapped by the jugal ventrally. It is anteroventrally overlapped by the same small plateau that overlaps the maxilla posterodorsally. Its processus ventralis anterior possibly overlaps the dextral

premaxilla. Lastly, ventroposteriorly, it borders the surangular in an unserrated suture, both bones having a sharp edge at their respective margins followed by a steep drop-off, their surfaces receding into the skull until they meet at the suture. The lacrimal resembles a triangle in shape, the dorsoposterior side of which flexes inward drastically to follow the orbital margin in a concave shape. This processus ventralis posterior extends to about mid orbit, where it thins out to a point. The crista lacrymalis is situated laterally, reaching from the lacrimal's ventral edge to near its anterodorsal margin where it gradually recedes into the bone, approximately following the shape and orientation of the orbital margin. Anterior to the crista lacrymalis, the lacrimal is nearly level but posterior to it, the lacrimal's surface is inclined toward the orbit and convexly curved outward.

Skull roof, orbit and cheek elements

Nasal

Nasal sutures in this specimen are rather faint and difficult to distinguish (fig 5), which is why their full extent and their connections to other bones in the skull are in part estimated. However, the sinistral nasal appears to be ca. 34 mm in length (Table 2). Its suture to the premaxilla cannot be seen because it is dislocated, as described before. The anteroventral suture to the lacrimal is faint but probably slightly undulating and approximately straight in orientation. The nasal may partially overlay the lacrimal. The ventroposterior suture to the prefrontal is anterodorsally convex and simple, without any serrations. Posteriorly, toward the frontal, the nasal diverges into two processes, both of which recede gradually into the skull, so their sutures are barely distinguishable. The lateroventral process extends about as far back as the prefrontal. Towards its posterior margin, it seems to be bifurcated, itself, if only for about 2 mm. Its surface is mostly smooth and slightly convex. The dorsal processus also extends about as far posteriorly as the prefrontal. It possesses two small anteroposteriorly oriented ridges, which are both smooth, convex and about half as long as the entire nasal. They converge posteriorly where the nasal recedes into the skull roof. Anterodorsally,

Skull roof, orbit and cheek	
Measured feature	Length in mm
Nasal	34
Jugal	85
Jugal (height)	16
Prefrontal	29
Orbit	69
Orbit (height)	38
Orbit (diameter, mean)	53.50
Scleral ring	56
Scleral ring (height, estimated)	44
Scleral ring (diameter, mean)	50
Aperture	28
Aperture (height)	12
Aperture (diameter, mean)	20
Internasal fenestra	11
Frontal + Parietal (indiscernible)	61
Sinistral frontal (width)	13
Dextral frontal (width)	7
Dextral postfrontal	52
Sinistral supratemporal fenestra	39
Dextral supratemporal fenestra	36
Sinistral postorbital	15
Postorbital skull length	32

Table 2. Measurements taken from the skull roof, orbit and cheek of SNHM 2753-R.

the nasal is convex in shape toward what is presumably the dextral premaxilla. Towards its pointed anterior margin, it bends ventrally toward the lacrimal and maxilla. The dextral nasal's sutures are partially obscured by being embedded in sediment laterally and anteriorly. Its dorsal margin terminates in a steep edge, offsetting it to the dextral frontal by ca. 5 mm, likely due to deformation. The dextral nasal is bifurcated posteriorly similarly to its sinistral counterpart and similarly shaped and smooth of surface but

possibly twice as far across, laterally, likely also due to deformation. Furthermore, the dorsal process appears to converge into a single point posteriorly. The dextral nasal also features two posteriorly converging ridges, but these converge just 5 mm posterior to the nasal bifurcation into two separate processes and border three shallower, anteriorly convergent ridges to their own anterior margin. The anterior margin of the dextral nasal itself ends in two small planes, offset to one another by less than a millimetre, somewhat resembling human incisors. The dorsal plane is the one lower in position. It is jagged at its dorsal margin and straight at its anterior margin. Both these margins are offset to the adjacent surfaces on the skull. The lateral plane possesses nearly straight margins, which are again offset to the adjacent bone but only by less than a millimetre.

Jugal

The jugal measures 85 mm in length and 16 mm in height (Table 2). Its dorsoposterior margins are hardly distinguishable at all as the jugal-postorbital suture is presumably situated at or near a point of stark deformation that creates an anteroposteriorly oriented fold at about a 130° angle in the postorbital skull (fig 4). The crescent-shaped jugal overlaps the surangular laterally, reaching from well above the SA at its origin to about half-way down the bone dorsoventrally at mid-orbital length and back up to the aforementioned fold that is well above the SA. Anteriorly, the jugal is in contact with the unidentified bony plateau that is wedged between the lacrimal and the maxilla. Anterodorsally and dorsally, it borders the lacrimal. Posterodorsally, it must contact the postorbital, even though the suture cannot be clearly determined. Posteriorly, ventrally and dorsally, it is connected to the surangular, as described above. All sutures are simple and without serrations. The bone is dorsally concave, thin and elongate, essentially comprising of just a laterally convex ridge anteriorly and flattening out posteriorly towards the postorbital.

Prefrontal

In this specimen, the prefrontal is a rather short bone of only 29 mm in length (Table 2). It either overlaps or borders the lacrimal anteriorly with a very faint suture (fig 5). Dorsally, it connects to the nasal in a relatively simple suture that only features a single notch. Posteriorly, it overlaps either the postfrontal or the frontal, which cannot be visually discerned and ventrally it follows the orbital margin. Anteriorly, it is dorsally convex and posteriorly, it appears to be approximately hexagonal in shape.

Postfrontal, Frontal and Parietal

Visually, in this specimen, these elements' sutures cannot be distinguished (fig 5). The frontal and parietal combined extend over a total length of 61 mm (Table 2). The dextral postfrontal measures ca. 52 mm in length. While the sinistral frontal measures 13 mm in width, the dextral frontal is only 7 mm wide. They enclose the internasal fenestra anteriorly, which measures 11 mm in length. The postfrontal seems to participate in the supratemporal fenestra's margin, the sinistral of which measures 39 mm in length, the dextral 36 mm, as well as the orbit and the parietal certainly borders the supratemporal, the supratemporal fenestra and the frontal but no detailed description can be made. One possible anterior suture of the parietal can be seen on the dextral side of the skull. This, however, could also be a simple crack, having been formed during the collapse of the dextral temporal fenestra. In general, the skull roof

appears closer to its original shape sinistrally than it does dextrally. A central fossa can be seen from the point that presumably connected to the disarticulated premaxilla to a point between the nasals. The separation between the sinistral and dextral side of the skull can be clearly seen as the dextral side has been raised relative to the sinistral side by deformation. This appears as a small offset of just a few millimetres anteriorly, supposedly between the frontals and as a larger offset of more than a centimetre posteriorly, behind the foramen parietalis and between the parietals. Overall, the skull roof is undulating in shape and this, too, more so on its dextral side.

Postorbital

Anterodorsally, the postorbital is overlain by the indiscernible elements of the skull roof but presumably the postfrontal (fig 4). Anteriorly, it terminates at about mid orbit, reaching into a small, dome-shaped indentation of the orbital margin, which is possibly the result of a piece of bone having been broken off. Ventrally, it follows the orbital margin until it contacts the jugal ventroposteriorly, the suture being too faint to determine clearly. Posteriorly, the postorbital borders the squamosal and the articular. Posterodorsally, it is in contact with the supratemporal in a faint suture. The postorbital is crescent shaped, reaching from near mid orbit at the dorsal orbital margin to the orbits posterior or ventroposterior margin where it contacts the jugal. While it appears wider externally at its posterior end at about 15 mm (Table 2), it thins out anteriorly, probably because it is being overlapped by the postfrontal. Furthermore, it forms a slight ridge or edge at three points. Anteriorly, its external appearance is comprised of only a single ridge. Posterodorsally, near its contact with the supratemporal, there is a slight ridge following the shape of the bone at near a 45° angle to the dorsoventral plane. Ventroposteriorly, there is a small edge parallel to its near margins, essentially splitting the bone in half in that area. Laterally, the postorbital appears convex in shape.

Supratemporal

The view on the sinistral supratemporal is partially obstructed in a minor way by neurocranial bones contacting it posteriorly (fig 5). Anteriorly, it contacts the postfrontal and the parietal in sutures that cannot be clearly determined. Anteroventrally, it borders the postorbital and dorsally, it contacts the other supratemporal in a clear offset of more than a centimetre. Lastly, it is posteriorly connected to the squamosal in a simple suture that folds inward slightly. Overall, it forms a U-shape, the opening of which is oriented anteriorly, making up the posterior half of the temporal fenestra's margin. Its surface is concave, ventrally, and nearly planar, dorsally. Towards the temporal fenestra's margin, it forms an edge at about a 130° angle to the adjacent supratemporal plane, giving it a wedge-like appearance, if seen from the inside the temporal fenestra.

The dextral supratemporal shares most of these features. However, deformation has separated it from the dextral postfrontal in a distinct break, highly deforming the temporal fenestra but also suggesting that it reached about half-way along the fenestra's margin, anteriorly. Its anterodorsal suture to the parietal can be seen clearly, as well. Here, the supratemporal reaches forward along about a quarter of the temporal fenestra's margin. Lastly, the dextral supratemporal is not in contact with any elements of the neurocranium. It is, however, still partially embedded in sediment, posteriorly and ventrally.

Squamosal and Quadratojugal

These two elements of the posterior skull are indiscernible in this specimen (fig 4). While the squamosal-supratemporal suture and the squamosal-postorbital suture can be identified, any distinction between these two elements is made difficult by their partial embedding in sediment and by the articular overlying this area of the skull, ventrally. While it cannot be determined, which element it is, one of these two posteriorly contacts the stapes, apparently having been fused together during diagenesis and one ventrally borders the surangular, just below the position of the articular.

Orbit and Scleral Ring

SNHM 2753-R features a large oval sinistral orbit of 69 mm in length and 38 mm in height (Table 2). It is mostly regular in shape but an area of ca. 30 mm in length slightly anterior to the centre of the orbit's dorsal margin features a convex recess of irregular shape into the adjacent skull roof where a piece of bone has broken off (fig 4). Inside the orbit, the scleral ring can be found. It is 56 mm long and an estimated 44 mm high. It consists of narrow, concentrically arranged plates, 13 of which are visible in the specimen. The view on further elements of the scleral ring is obstructed by the skull roof dorsally to posterodorsally. The individual plates feature concentric striations. Inside the aperture, which measures 28 mm in length and 12 mm in height, the pronounced ridge of an elongate, anterodorsally oriented bone can be seen. Ventrally, two more unidentified skull elements border the scleral ring. A plane bone, which is overlapped by the scleral ring, borders the lacrimal and is angled so it recedes into the skull dorsally can be found from the centre of the orbits lower margin to its anterior margin. A dorsoventrally convex bone that overlaps this bone anteriorly, borders the scleral ring dorsally and the surangular ventrally. A section of this bone ca. 10 mm in length has broken off near the posterior orbital margin. The surface visible underneath cannot with certainty be identified as either another underlying bone or a deeper layer of the same element. It extends from its suture with the adjacent anterior unidentified element to the posterior orbital margin.

Neurocranium

Despite having been embedded mostly laterally, a few of the neurocranial bones from both sides of the skull can be seen in this specimen as they have been dislocated postmortally (fig 6). These bones are in part tightly pressed together, having been fused during diagenesis. These discernible elements are the supraoccipital, both exoccipitals, the basioccipital, the opisthotic, the prootic, both stapes and the quadrate.

Supraoccipital

The supraoccipital can be seen in disarticulation in posterior view, its lateral faces being concealed by neurocranial elements, sinistrally and by the quadratojugal, dextrally (fig 6). It measures 30 mm at its widest point (Table 3). The concave dorsal surface is still filled with sediment and thus exempt from view apart from the outermost edge. Its posterior surface is medially convex from side to side before levelling out again, giving it the appearance of a cylinder with minute wings on the sides. It is also slightly convex

dorsoventrally. The anteroposteriorly oriented foramen cannot be seen in this specimen. The dorsal edge of the bone's posterior side is a simple, very slightly dorsally convex line that also slopes outward sinistrally to a very small extent, likely due to deformation. What little of the ventral side of the supraoccipital can be seen reveals a very narrow foramen magnum and part of both marginally concave exoccipital facets.

Exoccipital

The sinistral exoccipital can be found in disarticulation atop the tightly packed group of neurocranial bones at the rear of the skull. It contacts the supratemporal anteriorly, about 8 mm posterior to the sinistral supratemporal fenestra. Dorsally, it is situated near the supraoccipital but not in contact with it. ventrally, it is fused to the dextral exoccipital and posteriorly to an unidentified element that reaches out of the tightly packed neurocranial group as an elongate, dorsoventrally oriented ridge. In its elevated position, a large portion of the exoccipital's surface can be seen. However, the finer details of the bone, such as the nervous foramina, cannot be discerned, at all and the neurocranial elements below are fused

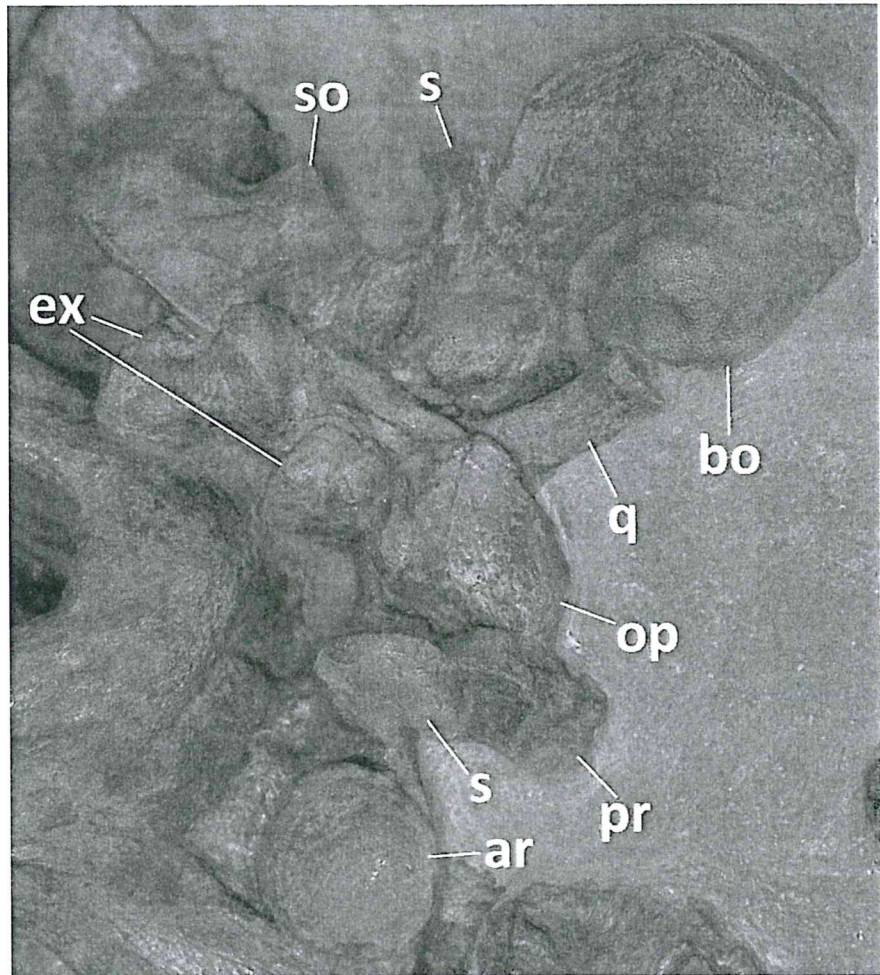


Figure 6. The neurocranium of SNHM 2753-R. Abbreviations: so = supraoccipital; ex = exoccipital; bo = basioccipital; s = stapes; op = opisthotic; pr = prootic; q = quadrate; ar = articular.

to it as well, further complicating the identification of clear margins. Despite these complications, its shape identifies it as the sinistral exoccipital with its anterior side facing outward laterally, its inner side facing ventrally and its ventral basioccipital facet, including the triangular process, facing posteriorly. This facet's surface is faintly pitted but less so than most other neurocranial elements in this specimen. In its current articulation, the basioccipital facet's surface is irregular and bulbous in shape, possibly indicating fracture or alteration during diagenesis. Given its extensive overall loss of features, the identification as the sinistral exoccipital with its anterior face pointing outward is still likely but not certain.

The dextral exoccipital is overlapped by its counterpart dorsally and borders the opisthotic posteroventrally and the mentioned unidentified von posteriorly. However, the dextral exoccipital has been damaged and altered more than the sinistral element, thus preventing detection of any additional features besides its general shape and identity.

Basioccipital

The basioccipital can be found in disarticulation as the posteriormost bone of the neurocranium, its posterior half mostly reaching out of the sediment, its dorsal side facing ventrally and vice versa (fig 6). It measures 25 mm, both in width and height (Table 3). The Condylus basioccipitalis measures 21 mm in width and 14 mm in height. It could be partially embedded in sediment on its dorsal side, though it looks, as if its edge, around where the floor of the foramen magnum would be, just happens to align with the sediment surface. As such, the exoccipital facet cannot be seen.

Neurocranium, hyoid and complete skull	
Measured feature	Length in mm
Sinistral articular (concave face)	14
Dextral Stapes (length)	19
Dextral Stapes (width)	11
Supraoccipital (width)	30
Exoccipital (estimated)	26
Basioccipital (height)	25
Basioccipital (width)	25
Condylus basioccipitalis (height)	14
Condylus basioccipitalis (width)	21
Sinistral opisthotic (anterior face)	14
Sinistral opisthotic (dorsal face)	14
Sinistral opisthotic (ventroposterior face)	18
Sinistral hyoid rod (length)	46
Sinistral hyoid rod (width)	4-9
Distance anterior naris – posterior quadratojugal	120
Total skull length (estimated)	301

Table 3. Measurements of the neurocranial and hyoid elements of SNHM 2753-R as well as the entire skull.

It is also partially overlapped by the dextral stapes, dextrally and by an unidentified elongate bone dextrodorsally. It appears as a dome-like ellipsoid that terminates in a point, rather than being rounded, on either side, laterally. Just off the centre, slightly dextral to the condyle's pitted surface, a small fovea, the notochordal pit, can be found. Ventral of that feature is a small, dorsally concave ridge that terminates just off the centre of the condyle, sinistrally and near the edge of the condyle, dextrally. A bit further ventrally, the condylar surface inclines toward the bone before levelling out again, giving the appearance of a dorsal dome within the Condylus occipitalis. This dome is most pronounced at its ventralmost point and recedes into the general condylar surface, laterally. Yet ventral of that feature, the condyle terminates in a narrow, level plane, ending in a sudden, pronounced edge. The extracondylar surface is well as wide ventrally as the condyle, building a well pronounced posterior shield in a slope outward from the condylar edge. Ventrolaterally, it is about half as wide and thins out dorsally. It either terminates or enters the sediment laterally where the condyle's near-elliptical surface is pointed, laterally. Dorsally, the extracondylar surface cannot be seen. Medially, it is posteriorly convex whereas towards its edges it is level to posteriorly concave. In posterior view, the basioccipital appears to be approximately hexagonal in shape with its two ventrolateral sides having a slight indentation or bifurcation. Ventrally and ventrolaterally, the bone's edges are distinct at a 90° angle whereas the posteriorly convex surface recedes into the sediment without forming an edge, laterally.

Opisthotic

The sinistral opisthotic has been dislocated enabling the view on its medial face. Its shape is approximately triangular, with its anterior and dorsal margin measuring 14 mm and its ventroposterior margin measuring 18 mm (fig 6; Table 3). Being exposed posteriorly, the basioccipital facet can be seen, which was ventrally oriented originally and has a surface that appears scaly or faintly pitted. Anteriorly, or dorsally in life, the paroccipital process can be found, which is less easily discernible and appears as a slight eminence. Its surface, too, is faintly pitted. It is partially obstructed in view by contact to the sinistral stapes' shaft anteriorly, by the dextral exoccipital anterodorsally and by another bone that could not be identified dorsally. This bone is roughly of the shape of a quartered cylinder, but further features cannot be discerned as it is situated amidst several other basicranial elements and only partially visible. The impression of the sacculus on the opisthotic cannot be clearly made out.

However, a slight rise from the nearly level plane of the bone's originally internal surface towards the tips of its near triangular shape, which terminates in a clear edge, can be seen in all directions, giving the bone a distinct and well pronounced shape. On the other hand, its posterior margin does not form any kind of edge and is ventroposteriorly convex. A fissure can be found reaching from near the saccular impression to the opisthotic's posterior edge, reaching it about a third of its length away from the paroccipital process. The internal surface of the opisthotic possesses slightly larger but more isolated pits, which are certainly distinct but not nearly sufficient to give the bone a rugose structure. These pits are more concentrated near the basioccipital facet. Posterodorsally, another element that could not be identified contacts the bone, this one appearing as a dorsoventrally oriented ridge of ca. 17 mm in length rising out of this group of tightly packed bones. Posteriorly, the opisthotic overlaps the sinistral quadrate, which itself overlaps the basioccipital's condylar surface. Lastly, the opisthotic is in contact with the prootic, anteroventrally.

Quadrate

The sinistral quadrate bone can be seen in external view (fig 6), if only for the 19 mm of its shaft, which are not covered by the opisthotic. Neither the quadratojugal facet nor the bone's condylus are visible. The shaft is slightly cambered in shape in that its surface rises slightly toward its posterior edge, forming an eminence posteriorly to posterodorsally. Furthermore, there is a shallow groove originating at its now ventral margin, about 3 mm off its posterior edge, which extends to the opisthotic-quadrate overlap where it reaches the centre of the shaft, dorsoventrally. 1-3 mm posterior of the opisthotic-quadrate overlap there is a fissure, which is oriented perpendicular to the aforementioned groove.

Prootic

The sinistral prootic is fused to the opisthotic dorsally to posterodorsally and to the head of the sinistral stapes anteriorly to anterodorsally (fig 6). In lateral view, three sides of the bone are partially visible. Posterodorsally, there is an irregular surface, which is faintly convex. Posteriorly, this surface grows more irregular, forming two distinct tuberosities at its end. This surface is faintly pitted with the highest concentration of these sculptural elements to be found anteriorly. Ventrally, the prootic bone is separated into an anterior and a posterior plane. The anterior plane is concave and features a distinct, approximately straight edge dorsally, which turns into an anterodorsally convex edge ventroposteriorly at the point where all three planes intersect. The ventroposterior plane is also concave but smoother than the other

surfaces. Dorsally, it does not feature a distinct edge but is rather bordered by the dorsal plane's posterior tuberosities. The anteroventral plane surface could possibly be an impression of one of the ear canals. However, the lack of distinct features and loss of details during diagenesis prevents an unequivocal identification.

Stapes

Both stapes' are visible in this specimen (fig 6). The sinistral stapes' head is easily discernible, pointing out lateroventrally and possessing a clear edge offset from the shaft around its outer margins, thus giving the stapes a mushroom-like appearance. Ventroposteriorly, the sinistral stapes overlaps the sinistral prootic with its head and proximal shaft. Ventrally, it is fused to the narrow ridge of an unidentified bone, which connects it to the sinistral articular. Dorsally, its distal shaft is overlapped by the sinistral opisthotic. The head is dome-like in shape and its surface features several small pits dorsally but lacks this ornamentation ventrally near the adjacent unidentified bone. Other small features cannot be identified. Neither the groove for the stapedia artery nor the posterodorsal facet for reception of the opisthotic can clearly be seen. The shaft is very faintly pitted, straight and lacks any additional prominent features.

The dextral stapes is oriented dorsoventrally, its head pointing ventrally and exposed with its originally anterior side. It measures 19 mm in length and 11 mm in width at its widest point (Table 3). Posteriorly, it contacts the basioccipital, which marginally overlaps the shaft. Anteriorly, it is fused to the unidentified ridge-like bone that is also fused to the sinistral exoccipital and the sinistral opisthotic. The stapes' surface is covered in small pits and more so than its sinistral counterpart. The head, again, is offset to the nearly straight shaft by a distinct edge and dome-like in appearance, so the dextral stapes resembles the shape of a mushroom, too. However, the head's edge is not oriented perpendicular to the shaft, so the latter is slightly angled posteriorly. Near the bone's distal margin, a slightly depressed and rugose area can be seen. Furthermore, the distal facet of the shaft which was in cartilaginous contact with the quadrate can be seen, dorsally. This facet is flat, oriented anterodorsally and possesses a straight edge laterally, bordering the formerly anterior plane of the shaft. Its now medial edge is embedded in sediment. Like in the sinistral stapes, no further detailed surface ornamentation can be seen.

Hyoid Apparatus

Of the hyoid apparatus, only the dislocated sinistral hyoid rod is visible in this specimen, which can be seen with its ventral side reaching out of the sediment (fig 4). It is situated posterior to the lower jaw and approximately anteroposteriorly oriented with its anterior margin pointing posteriorly. This elongate bone of 46 mm in length and 4-9 mm in width (Table 3) is slightly curved. While the bone is nearly cylindrical around a central area of ca. 10 mm in length, it features depressed, slightly concave planes towards its posterior and anterior margins. However, at nearest to its now anterior margin it is again convex in shape. This margin represents the area that the branchial arches of the hyoid apparatus were connected to in life.

Lower Jaw

While the tip of the lower jaw is shielded from view by the overlapping dislocated premaxilla and it is also overlapped by the jugal, most of the lower jaw in this specimen is visible and well preserved (fig 4). However, the sutures in the anterior half of the jaw are very faint and barely visible. The mandible is approximately 204 mm in length (Table 1). The splenial cannot be seen.

Dentary

Anteriorly, the tip of the dentary is overlapped by the dislocated premaxilla (fig 4). Posteriorly, it is bifurcated and fused to the surangular in a faint but simple suture. Posterodorsally, its dorsal posterior process is overlapped by the maxilla. Only three teeth near the tip of the jawbone are still in articulation. These share the same qualities as the maxillary and premaxillary teeth. Its surface features distinct anterodorsally oriented striations.

Surangular

Anteriorly, the surangular is fused to the dentary in a very faint suture, forming a pointed tip wedged in between the dentary's two posterior processes (fig 4). Dorsally, it borders the lacrimal and the posterior unidentified bone inside the orbit in a simple suture. Ventrally, it is fused to the angular in a curved suture that is distinctly pronounced posteriorly but fades out anteriorly. This suture is slightly dorsally concave posteriorly, then angled at a 40° angle ventrally 3 mm posterior to the postorbital before it is once again concave dorsally, approximately following the jawline and the jugal before it recedes into the sediment anteriorly near the tip of the jugal. Laterally, the surangular is overlapped by the postorbital and the jugal, both of which appear to be slightly dislocated ventrally. Posteriorly, the surangular is very narrow in shape, accounting for less than half of the mandible's height. 1-5 mm, dorsally to ventrally, off its posterior margin, the coronoid surangular process can be found where the *Musculus adductor mandibulae internus pseudotemporalis* inserted. Dorsally, encased by the overlapping jugal, its margin ends in a well pronounced ridge that is clearly offset to the rest of the bone's surface. This surface features anterodorsally oriented striations not unlike the dentary but these are individually shorter and far less prominent.

Angular

Anteriorly, dorsally and posteriorly along its entire length, the angular is fused to only the surangular (fig 4). This suture is slightly dorsally convex, both anteriorly and posteriorly with it being very prominent posteriorly and faint anteriorly as well as its two crescent shaped lines meeting at a 40° angle 3 mm posterior to the postorbital. Ventroposteriorly, the angular overlaps an unidentified bone, which appears as a wedge-like shape of ca. 15 mm in length. Ventrally, the angular borders the sediment, which it recedes back into anteroventrally near the tip of the jugal, appearing pointed in shape. Posteriorly, it accounts for more than half the mandible's height, while anterior to the angle in its dorsal suture it rapidly thins out to just a few millimetres in height before then gradually, less extremely continuing to thin out towards its anterior margin.

Like the other mandibular elements, the articular features anterodorsally oriented striations, which are longer, more numerous and more pronounced anteriorly than posteriorly. Its posterior section can be divided into a slightly larger dorsal plane, which features a single faint anterodorsally oriented groove and the smaller but elevated crest, which features a central, more slightly more pronounced anterodorsally oriented groove and a prominent ventral edge.

Articular

The sinistral articular in this specimen can be found posterior to the fused elements of the skull's orbital margin and dorsal to the lower jaw's posterior margin with these two areas framing its own anterior and ventral margins (fig 4; fig 6). Its slightly concave

Anatomical ratio	Determined value
Mandible to skull ratio	0.664
Orbit (diameter, mean) to skull ratio	0.18
Aperture (diameter, mean) to scleral ring (diameter, mean)	0.4
Snout ratio (snout length to jaw length)	1.065
Snout ratio (snout length to skull length)	0.708
Snout height at naris to snout length ratio	0.221
Premaxillary ratio	0.887
Overbite to skull length ratio	0.322
Orbital ratio (mean orbital diameter to jaw length)	0.262
Orbital ratio (mean orbital diameter to skull length)	0.178
Orbital ratio (orbital length to skull length)	0.229
Naris to orbit ratio (by mean orbital diameter)	0.355

articular surface, 14 Table 4. Anatomical ratios calculated for SNHM 2753-R.

mm in diameter (Table 3) and now visible in dorsolateral view but anteriorly oriented in life, features only a few small pits and has a nearly smooth surface. The articular surface's margins terminate in a well pronounced edge that encompasses it in its entirety and is between circular and hexagonal in shape. Beyond that edge, the sides of the bone are mostly shielded from view by adjacent bones and the sediment surface. Where it can be seen its surface features distinctly more numerous small pits than where it articulated.

Calculated Anatomical Ratios

Several diagnostic anatomical ratios were determined for this specimen (Table 4). These are the mandible to skull ratio at 0.644, the mean orbit diameter to skull length ratio at 0.18, the mean aperture diameter to mean scleral ring diameter ratio at 0.4, the snout ratio by snout length to jaw length and skull length at 1.065 and 0.708, the snout height at naris to snout length ratio at 0.221, the premaxillary ratio at 0.887, the overbite to skull length ratio at 0.322, the orbital ratio by mean orbital diameter to jaw length at 0.262, by mean orbital diameter to skull length at 0.178 and by orbital length to skull length at 0.229 as well as the naris to orbit ratio by mean orbital diameter at 0.355.

Discussion

Systematic palaeontology

Order **Ichthyosauria** de BLAINVILLE, 1835

Minorder **Parvipelvia** MOTANI, 1999

Suborder **Neoichthyosauria** SANDER, 2000

Family **Leptonectidae** MAISCH, 1998

Genus ***Wahlisaurus*** LOMAX, 2016

Type species. *Wahlisaurus massarae* Lomax, 2016

Definition. The last common ancestor of *Wahlisaurus massarae* and *Wahlisaurus* sp. nov. and its descendants.

Diagnosis. Small-bodied leptonectid ichthyosaur with the following autapomorphies: coracoid with a large, ovoid foramen, a coracoid foramen is present in *Cymbospondylus* but it is much smaller in this genus; presence of both a coracoid foramen and scapular-coracoid foramen (fenestra coracoscapularis), the latter formed by articulation of the coracoid and scapula; a coracoid with a posterior notch that is much more developed than the anterior notch. Three other features may be autapomorphies: humerus deltopectoral crest prominent and 2.5 times greater than the dorsal process; dorsoventral width of the humerus is greater than the anteroposterior width, which results in a D-shape in proximal view; and slender, long, needle-like teeth with marginally recurved crowns and large, bulbous infolded roots.

Wahlisaurus massarae is also characterized by the following combination of features shared with other taxa: very slender, delicate and relatively long snout with mandible shorter than snout, which produces an overbite; basioccipital with extensive extracondylar area; coracoid anteroposteriorly longer than mediolaterally; extensive contact between the anterolateral border of coracoid (lateral scapular facet and medial scapular facet) and scapula forms a small, semi-circular scapular coracoid; a small, emarginated anterior notch in coracoid; a well-developed posterior notch in the coracoid; long scapula with greatly expanded proximal region but without prominent acromion process; long femur with thin, slender shaft and distal end wider than proximal; notched tibia; pelvis tripartite with pubis widely expanded distally and approximately equal in size to ischium.

Wahlisaurus massarae LOMAX, 2016 emend. OMMER, 2017

Holotype. LEICT G454.1951.5, a partial skull and an associated incomplete skeleton comprising the pectoral girdle, humeri, pelvic elements, partial hind fins, vertebrae and ribs.

Occurrence. Normanton Hills, near Normanton on Soar, Nottinghamshire, England, UK.

Material. The holotype, LEICT G454.1951.5, recovered at Normanton Hills is the only known specimen.

Stratigraphic range. Lower Jurassic, either the top of the Preplanorbis beds or the base of the planorbis Zone (lowermost Hettangian: perhaps the Scunthorpe Mudstone Formation, Barnstone Member).

Diagnosis. Small-bodied ichthyosaur corresponding to the genus of *Wahlisaurus* showing the following synapomorphies: overbite to skull length ratio of ca. 0.106; surangular extends anteriorly to the tip of the maxilla, well before the maxilla's widest point; adult skull size of ca. 42.5 cm.

Wahlisaurus sp. nov.

Holotype. SNHM 2753-R, a complete skull.

Occurrence. Posidonia Shale formation of Schandelah (Cremlingen), Lower Saxony, Germany.

Material. The holotype, SNHM 2753-R, recovered at Geopunkt Jurameer Schandelah is the only known specimen.

Stratigraphic range. The only specimen is Toarcian in age.

Diagnosis. Especially small-bodied ichthyosaur corresponding to the genus of *Wahlisaurus* showing the following synapomorphies: overbite to skull length ratio of ca. 0.322; surangular extends anteriorly to the anterior half of the naris, well behind the maxilla's widest point; adult skull size of ca. 30 cm.

Maturity

In ichthyosaurs, maturity is determined by characteristics of the humerus such as a smooth surface texture (Johnson 1977; McGowan 1995), a method which cannot be used in this specimen. Likewise, the stage of fusion of the basisphenoid and the parasphenoid, indicative of osteological maturity (Kear 2005; Fischer et al. 2011), cannot be determined. Furthermore, the fusion of cranial sutures in the skull roof is an indicator of maturity (Maxwell et al. 2012). With the sutures between frontal, parietal and postfrontal being indistinguishable, this criterion is certainly met. In some species, small relative tooth size has been cited as a characteristic of adults (Dick & Maxwell 2015). This is present but could also be normal in juveniles, depending on species. Lastly, surface texture of osteological elements in general can indicate maturity (Hone et al. 2016). As such, in ichthyosaurs, development of the distinct shape of the neurocranial elements and a lack of rugose surface texture in these indicates osteological maturity (Kear & Zammit 2014). This specimen's neurocranium partially lacks finer characteristics such as impressions of canals but this is likely due to diagenetic alteration. In shape, most elements are still very well-developed, and they possess only very faintly pitted sculpturation. Thus, SNHM 2753-R was osteologically mature at its time of death.

Comparison

Because of the discovery of SNHM 2753-R in the Posidonia Shale formation and its Toarcian age, only taxa of the suborder Neoichthyosauria of appropriate age were included in the anatomical comparison. Namely, the following families were considered: Temnodontosauridae, Leptonectidae, Suevoleviathanidae, Ichthyosauridae and Stenoperygiidae. In case of correspondence between the specimen's anatomy and a family's diagnostic features, the individual genera of this family were considered. In case of correspondence to one of these genera, the genus's species were considered.

Comparisons at the family level

Temnodontosauridae MCGOWAN, 1994

Temnodontosaurids are defined by relatively small orbits and a long maxilla (McGowan 1974). In SNHM 2753-R, the orbit is extremely large and the maxilla large to medium sized. Temnodontosaurids feature very large jaws of at least 600 mm in length (McGowan 1974) in accordance with their great overall size. The new skull from Schandelah, however, only possesses an estimated overall skull length of 301 mm and a jaw length of 204 mm. Temnodontosauridae feature orbital ratios of at most 0.21, aperture to scleral ring ratios of less than 0.35, premaxillary ratios of at most 0.40 and naris to orbit ratios that are often over 0.45 (McGowan 1974). On the other hand, the new specimen yields ratios of 0.262, 0.4, 0.887 and 0.355, respectively. Thus, almost all relevant features rule out the temnodontosaurid family for the specimen at hand.

Leptonectidae MAISCH, 1998

The leptonectid family was established as the last common ancestor of *Eurhinosaurus longirostris* and *Leptonectes tenuirostris* without a clear definition of the clade (McGowan & Motani 2003). However, several diagnostic features have since been indicated. Leptonectidae possess slender, conical, smooth teeth without any enamel ornamentation and a quadratojugal in posterior position (Maisch & Matzke 2000; Maisch & Matzke 2003). SNHM 2753-R shares both features. The squamosal and quadratojugal cannot be discerned from one another and are partially shielded from view by the articular but their positioning at the back of the skull is unequivocal. Furthermore, leptonectids share an extremely slender snout (Maisch & Matzke 2003; McGowan & Motani 2003) and relatively small teeth in comparison to their skull width with a ratio of less than 0.05 (McGowan & Motani 2003). SNHM 2753-R does possess a very long and slender snout. The skull roof in the new Schandelah specimen has been largely deformed, preventing any exact measurements pertaining to this ratio. Yet, the maximum length of 11 mm in the larger teeth found and the combined width of both frontals at 200 mm suggest that this requirement would be met in an entirely undeformed specimen. Lastly, a very large orbit and small supratemporal fenestrae are cited for the leptonectid family (Maisch & Matzke 2003), features which are extremely well pronounced in this specimen's skull. In conclusion, since all determinable requirements for affiliation to Leptonectidae have been met, SNHM 2753-R is unequivocally identified as a member of this family.

Suevoleviathanidae MAISCH, 2001

The suevoleviathanid family is defined as all descendants of the last common ancestor of *Suevoleviathan integer* and *Suevoleviathan disinteger* (Maisch 2001). Since *Suevoleviathan* is the family's only genus, the diagnoses at generic and family level are identical (Maisch 2001). Suevoleviathanids are defined by their large adult size of more than 4 m (Maisch & Matzke 2000; McGowan & Motani 2003; Joger 2014) and are thus much larger than the specimen from Schandelah. They have medium sized orbits and a slightly concave dorsal skull profile as well as prominent alternating secondary fossae at their Fossa praemaxillaris and Fossa dentalis (Maisch & Matzke 2000; Maisch 2001). These are features that SNHM 2753-R does not share. A concave skull roof is possible but cannot be clearly identified or dismissed given the skull's state of deformation. Their jugal and anterior maxilla are described as short and stout, with the former being very straight in shape and featuring only a short Ramus postorbitalis (Maisch & Matzke 2000; Maisch 2001) while the examined specimen has both a long, crescent shaped jugal and a long, slender maxilla. Also, Suevoleviathanidae have large squamosals with a long ventral process along the posterior quadratojugal margin that reaches down to the ventral margin of the skull, thus separating the Processus quadratus from the quadratojugal's main body (Maisch & Matzke 2000; Maisch 2001), a feature which could not be proven or disproven in SNHM 2753-R because the squamosal could not be discerned from the adjacent quadratojugal. Lastly, *Suevoleviathan*'s teeth have robust and short crowns with finely crenulated enamel, widened roots and without carninae (Maisch & Matzke 2000; Maisch 2001) unlike the Ichthyosaur from Schandelah, which features slender, elongate, conical teeth without any kind of ornamentation that are slightly recurved toward their tips. So SNHM 2753-R differs from *Suevoleviathan* in every anatomical feature that can be unequivocally identified and is thus not a member of the family Suevoleviathanidae.

Ichthyosauridae BONAPARTE, 1841

Ichthyosauridae are medium sized ichthyosaurs of less than 4 meters in length and less than 70 cm in skull length (Godefroit 1994; Storrs et al. 2000) defined as all descendants of the last common ancestor of *Macgowania*, *Hudsonelpidia* and *Ichthyosaurus* (Motani 1997). While the skull of SNHM 2753-R certainly does not exceed 70 cm in length, it measures far less than that at 301 mm, being small rather than medium sized. However, a minimum size is not mentioned in any diagnosis of ichthyosaurids. They possess extremely large oval orbits (Storrs et al. 2000) with an orbital length to skull length ratio of more than 0.2 in adults (Godefroit 1994). At a ratio of 0.229 for its oval orbit, the Schandelah specimen is well within that range. They also yield snout length to skull length ratios of less than 0.7 and snout height at the naris to snout length ratios of over 0.12 (Godefroit 1994). The former value is only just surpassed at 0.708, so SNHM 2753-R could just be at the extreme end of the spectrum, the latter is almost doubled at 0.221. Ichthyosauridae carry only sparse dentition in the anterior part of their jaws or none at all (Storrs et al. 2000) whereas the skull from Schandelah carries a number of premaxillary, maxillary and dentary teeth. Finally, ichthyosaurid basioccipitals possess a large extracondylar area and a well-developed basioccipital peg (McGowan & Motani 2003). The former is certainly present in this specimen while the latter is embedded in sediment, if present. Most features and ratios would allow a classification of SNHM 2753-R inside Ichthyosauridae, if as an extreme case in some regards. However, the largely reduced dentition should rule out this group unless no better match can be found, in which case it could either be a highly derived form or a member of a sister-taxon.

Stenopterygiidae WOODWARD IN ZITTEL, 1932

Stenopterygiidae are of medium size of less than 1 m in skull length, less than 6 m in total length and commonly less than 4 m in total length (Maisch 1998; McGowan & Motani 2003) except for *Hauffiopteryx*, which is ca. 2 m in length (Maisch 2008; Joger 2014). While *Stenopterygius* is estimated at 3-4 m in length (Joger 2014), the newly described specimen from Schandelah measures less than a third of the requirements in skull length at 301 mm, making it the smallest member of this family by far, if it is a stenopterygiid. Like the new skull, the stenopterygiid postorbital skull is greatly reduced in length (Maisch 1998). However, unlike SNHM 2753-R, they feature a large Fenestra temporalis, a short maxilla and are missing the Foramen internasale entirely (Maisch 1998). Their teeth are small to medium sized, lacking carinae but carrying slightly to very distinctly crenulated crown enamel and furrowed roots (Maisch 1998) whereas the Schandelah specimen's teeth also lack carinae but are free of any kind of enamel ornamentation and possess wide, infolded roots. The quadratojugal in stenopterygiids is short and ventrally terminates well before reaching the lower jaw joint with a small, short Processus quadratus that is posteromedially oriented (Maisch 1998), which cannot be confirmed or denied for SNHM 2753-R. Another feature of stenopterygiids that can neither be confirmed nor denied for this specimen is an extensive triangular squamosal which mostly overlaps the quadratojugal laterally (Maisch 1998). Similarly, the parasphenoid is shielded from view, thus its diagnostic features cannot be considered. The stenopterygiid basioccipital features an extensive Area extracondylaris without clearly visible stapedial facets (Maisch 1998), which is also true for SNHM 2753-R but it also features a well-developed Processus cuneiformis (Maisch 1998), which cannot be seen in this specimen. In conclusion, SNHM 2753-R and Stenopterygiidae are set apart by enough differences to unequivocally rule out any close affiliation.

Comparisons to leptonectids on the generic level

Eurhinosaurus ABEL, 1909

This genus is defined by the membership of its only valid species, *Eurhinosaurus longirostris* (Godefroit 1994). It is a species of great size at more than 6 m and up to or just above 7 m in body length as well as more than 70 cm and up to 150 cm in skull length (McGowan 1979; Godefroit 1994; Maisch & Matzke 2000; Sander 2000; Joger 2014) that is characterised by extreme development of the slender, elongate snout extending far beyond the tip of the lower jaw resulting in a distinct overbite (fig 7), which accounts for about half the length of the skull (McGowan 1997; Godefroit 1994; Maisch & Matzke 2000; Sander 2000; Buchholtz 2001; Lawrence 2008; Dick & Maxwell 2015). On the other hand, the skull of SNHM 2753-R measures in at only a fraction of this size at 301 mm. It does also carry an overbite but at 204 mm of jaw length this only accounts for about a third of the total skull length, the overbite to skull length ratio being 0.322. The posterior end of *Eurhinosaurus's* premaxilla is described as concave with its ventral process being longer than the dorsal (Lawrence 2008), the latter of which is true in this specimen but both premaxillary processes are straight and posteriorly oriented. Both the nasal and the maxilla are not in contact with the external naris in this genus (Lawrence 2008), a feature that is shared by SNHM 2753-R. Furthermore, it shares *Eurhinosaurus's* lack of contact between the nasal and parietal, postfrontal participation in the upper temporal fenestrate, absence of an anterior terrace of the upper temporal fenestra, jugal J-shape and conical teeth that are small at a length to skull width ratio of below 0.05 (Buchholtz 2001; Lawrence 2008). However, SNHM 2753-R differs from *Eurhinosaurus* by not showing postorbital participation in the upper temporal fenestra (Lawrence 2008). The genus also possesses large orbits (Sander 2000) at a ratio of over 0.18 and probably over 0.22 (McGowan 1979), which is shared by the skull from Schandelah at 0.262 or 0.229, depending on the definition used. However, in contrast to the genus (Maisch & Matzke 2000; Maisch & Ansorge 2004), these orbits are not anteriorly oriented. The maxillary tooth count is given at usually less than 16 (McGowan 1979), all of which are homodont and correspond to the pierce feeding guild (Dick & Maxwell 2015), which does not fit the 11 maxillary teeth found here, which are short and resemble the smash guild more closely. The ascribed mostly ventral large extracondylar area (McGowan 1979) is likewise found in SNHM 2753-R. The typical absence of stapedial facets (McGowan 1979) is another feature shared by the specimen. Thus, several characters concerning the genus's typical overbite, its skull roof configuration, jugal shape, the orbits, teeth and the basioccipital shape can be found in SNHM 2753-R. However, its comparatively minute size, great difference in the extent of the overbite and shape of the posterior premaxilla as well as orbital orientation and differences in skull roof configuration exclude the specimen from membership in *Eurhinosaurus*. In conclusion, SNHM 2753-R is likely a close relative but not a representative of *Eurhinosaurus*.

This genus, defined by membership of its only species, *Excalibosaurus costini*, has been described as nearly identical to *Eurhinosaurus longirostris* in cranial morphology (Maisch & Matzke 2000; Lawrence 2008; Dick & Maxwell 2015). Therefore, unless otherwise specified, the same conclusions are drawn for membership of SNHM 2753-R in this genus. However, a difference in overbite and mandible length was identified (Maisch & Matzke 2000; McGowan & Motani 2003). The holotype of *Excalibosaurus costini* (fig 7) carries a mandible to skull length ratio of 0.76 (McGowan & Motani 2003), corresponding to an overbite to skull length ratio of 0.24 in contrast to an average mandible to skull length ratio of 0.52 or an overbite ratio of 0.48 in *Eurhinosaurus longirostris* (McGowan & Motani 2003) and an overbite to skull length ratio of 0.322 in SNHM 2753-R, placing the specimen in between the two species in this regard, if closer to *Excalibosaurus costini*. Yet, in a newer specimen's skull of *Excalibosaurus* of approximately 1540 mm in length, a jaw length to skull length ratio of 0.68 (McGowan 2003) and thus an overbite to skull length ratio of 0.32 were identified, which is approximately identical to the value determined for the skull from Schandelah. In conclusion, SNHM 2753-R differs from *Excalibosaurus* in the shape of its posterior premaxilla, its orbital orientation, its lack of postorbital participation in the upper temporal fenestra's margin and greatly in its size, so it is not placed within this taxon but due to their identical overbite ratio in adult animals, the Schandelah specimen is likely more closely related to *Excalibosaurus* than *Eurhinosaurus*.

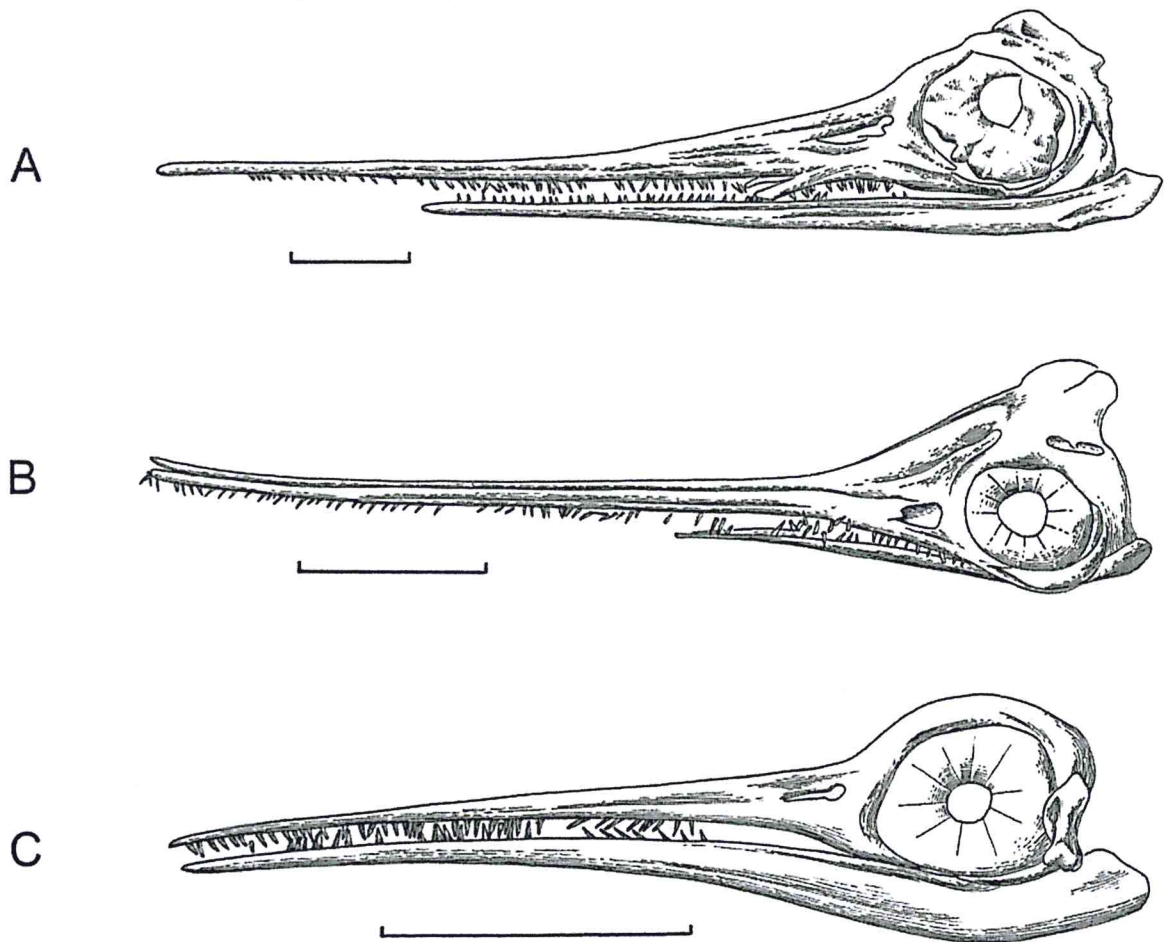


Figure 7. Cranial osteology of three leptonectid type species: A *Excalibosaurus costini* (holotype, BRSMG Cc881, scale equals 100 mm); B *Eurhinosaurus longirostris* (MNHN 1946-20, scale equals 200 mm); C *Leptonectes tenuirostris* (OUMNH J10305, scale equals 200 mm; McGowan 2003).

Leptonectes MCGOWAN, 1996

Only a few characters pertaining to the cranial morphology are included in this taxon's diagnosis. It is described as a moderate-sized (Dick & Maxwell 2015) to large ichthyosaur, having a slender snout and mandible (fig 7) as well as a long snout of up to 1000 mm in length (McGowan 1996; Maisch & Matzke 2000; McGowan & Motani 2003; Lawrence 2008; Dick & Maxwell 2015), which is present in SNHM 2753-R but in contrast, it does not feature an overbite (Maisch & Matzke 2000). The orbit is large, comprising most of the skull posterior to the rostrum (McGowan 1996; Maisch & Matzke 2000; McGowan 2003) and mostly directed laterally instead of clearly facing anterolaterally (Maisch & Matzke 2000), which is also true for the examined specimen from Schandelah. Especially in large individuals, this genus carries relatively small and slender teeth (McGowan 1996; McGowan 2003), which are homodont and ascribed to the smash feeding guild (Dick & Maxwell 2015). Likewise, the newly described skull features relatively small, homodont teeth fitting into this guild. Given the small number of identifying characters provided, less features excluding SNHM 2753-R from this genus can be found but similarly, less confirming its membership in this clade can be found either. While the large, laterally oriented orbit, its teeth and its slender snout would fit into this genus, its most striking features, namely its very small size and distinct overbite unequivocally exclude it from *Leptonectes*.

Wahlisaurus LOMAX, 2016

This newest genus inside the leptonektid family is represented by the only specimen of its type species, *Wahlisaurus massarae* (fig 8), which is of Hettangian age (Lomax 2016). It is described as a small-bodied leptonektid ichthyosaur, carrying slender, long, needle-like teeth with marginally recurved crowns and large, bulbous infolded roots (Lomax 2016). The species possesses a long, slender and delicate snout with a shorter mandible, producing an overbite and a basioccipital with an extensive extracondylar area (Lomax 2016). SNHM 2753-R shares these features. However, other than the given diagnosis, *Wahlisaurus massarae*'s skull's description shows some differences in these two specimens. The holotype, namely LEICT G454.1951.5, features a premaxilla of approximately 20 cm in length, which is calculated as 0.52 of the jaw length, which itself is identified as approximately 38 cm (Lomax 2016). In this, SNHM 2753-R differs drastically at a similar premaxillary length of 181 mm but a jaw length of only 204 mm. Furthermore, the holotype's overbite is estimated at about 45 mm (Lomax 2016) whereas the skull from Schandelah features an overbite of 97 mm. This yields overall skull lengths of 425 mm and 301 mm and overbite to skull length ratios of 0.106 and 0.322, respectively (Table 5). Both specimens might be missing a part of their jaw's tips but in neither case, should this exceed 10 mm (Lomax 2016). Also, the surangular in LEICT G454.1951.5 extends farther anteriorly than the maxilla in lateral view (Lomax 2016) whereas in SNHM 2753-R it only extends toward the maxilla's posterior margin anteriorly where the maxilla is overlapped by the jugal's anterior tip. In conclusion, these two specimens are certainly more closely related to each other than to any other ichthyosaur yet found. Still, the extreme differences in relative overbite as well as in external surangular position positively identify them as corresponding to different species. The smaller adult size of the skull of SNHM 2753-R at about 71% the size of *Wahlisaurus massarae* and its much younger Toarcian age support this assessment, even if both qualities are not outside the realm of possibility for a single species. Thus, a new species is established for SNHM 2753-R while the current diagnosis for *Wahlisaurus massarae* is kept only for distinction at generic level and new diagnoses pertaining to their differentiating cranial morphological features are introduced.

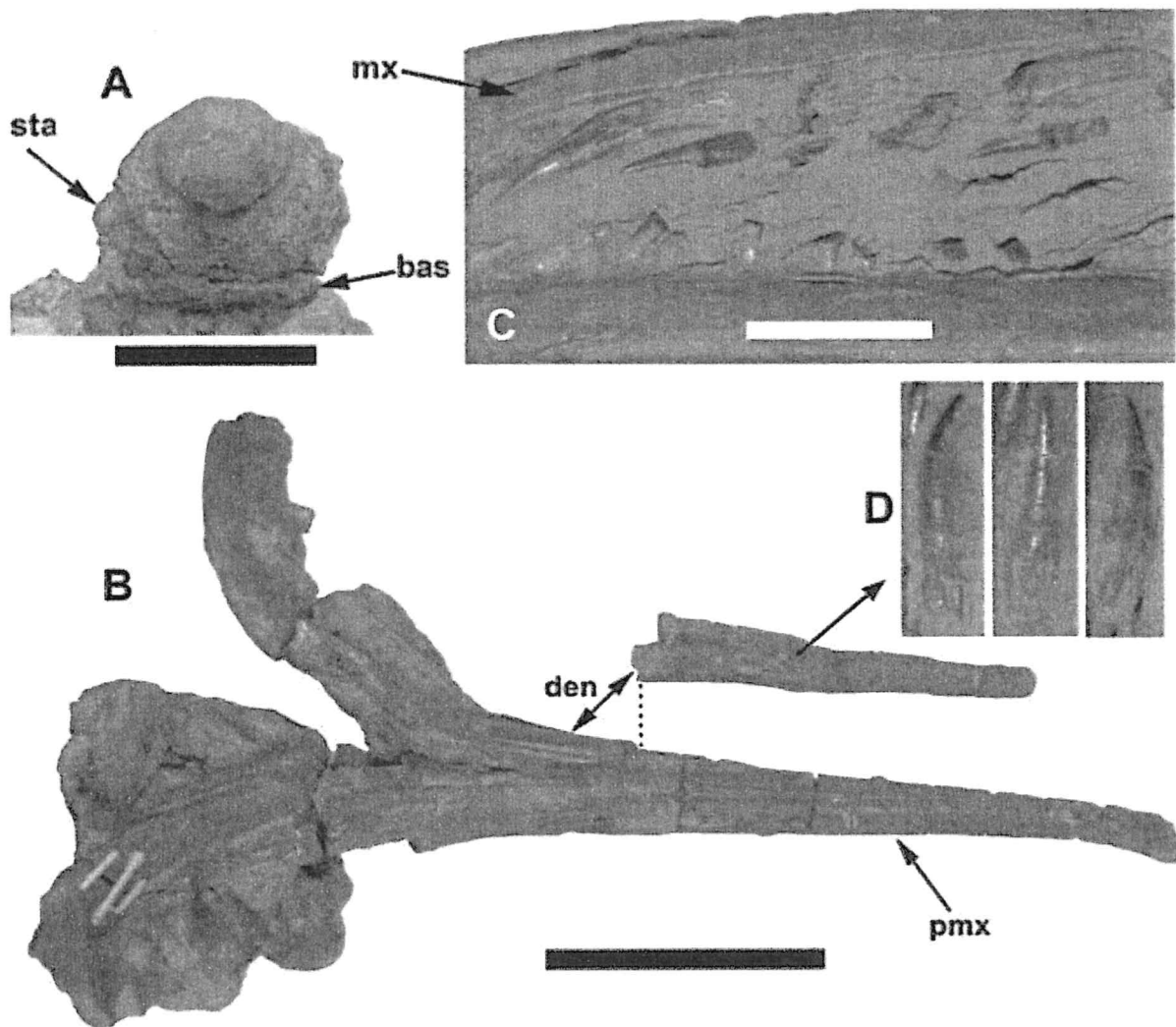


Figure 8. Basioccipital, rostrum and dentition of LEICT G454.1951.5, holotype of *Wahlisaurus massarae*; A basioccipital in posterior view B ventral view of mandible and snout with anterior portion of dentary rotated (in dorsal view) and positioned adjacent (dashed line indicates point of fit); C close-up of teeth at and near the maxilla; D close-up of three dentary teeth. Abbreviations: bas, basisphenoid; den, dentary; mx, maxilla (right maxilla); pmx, premaxilla; sta, stapes. Scale bars: A D 5 cm; B D 10 cm; CD3 cm (Lomax 2016).

Measured feature or anatomical ratio	Length in mm or determined value
Premaxilla (<i>Wahlisaurus massarae</i>)	200
Mandible (<i>Wahlisaurus massarae</i>)	380
Overbite (<i>Wahlisaurus massarae</i>)	45
Total skull length (<i>Wahlisaurus massarae</i>)	425
Overbite to skull length ratio (<i>Wahlisaurus massarae</i>)	0.106

Table 5. Measured and calculated lengths and ratios of anatomical features in *Wahlisaurus massarae*. Premaxillary length, mandibular length and overbite taken from the holotype's description (Lomax 2016). Total skull length and overbite to skull length ratio calculated.

Conclusions

Wahlisaurus sp. nov. has been described from the Lower Jurassic (Toarcian) of Schandelah, Germany. It shares all defining characters of the previously established species *Wahlisaurus massarae* but differs from the holotype in a larger overbite, both relative and absolute, an anteriorly shorter surangular and a shorter overall skull length. Because of the extent of these differences, a new species of *Wahlisaurus* is erected that is left in open nomenclature before further examination can take place. Furthermore, the former diagnosis of both *Wahlisaurus* and *Wahlisaurus massarae* is now used only for the generic level, the definition of the latter being amended to account for the interspecific differences found in both specimens.

The establishment of *Wahlisaurus* sp. nov. as a member of this genus more closely related to *Wahlisaurus massarae* than to other leptonectids supports the validity of the taxon in distinction from *Eurhinosaurus*, *Excalibosaurus* and *Leptonectes*. It adds another member to the number of valid species within Leptonectidae for a total of seven species, which also includes *Leptonectes tenuirostris*, *Leptonectes solei*, *Leptonectes moorei*, *Excalibosaurus costrini*, *Eurhinosaurus longirostris* and *Wahlisaurus massarae* (Lomax 2016). Including *Wahlisaurus* sp. nov., Moreover, it adds to the number of taxa currently known from the localities of Geopunkt Jurameer Schandelah, Hondelage and the Brunswick Land in general, also encompassing *Stenopterygius* sp. (Heunisch 2014; Joger 2014; <http://www.geopunkt-schandelah.de/Hintergrund/>) and *Eurhinosaurus longirostris* (Heunisch 2014; Joger 2014). Along with the discovery of plesiosaurs (Kosma 2014a; <http://www.geopunkt-schandelah.de/Hintergrund/>), crocodylians (Kosma 2014b) and pterosaurs (Kosma 2014c; <http://www.geopunkt-schandelah.de/Hintergrund/>), the documentation of these ichthyosaurs emphasises the value of the Brunswick Land in general and the excavation sites Hondelage and Geopunkt Jurameer Schandelah in particular for the research of Lower Jurassic ecosystems.

Overall, adding *Wahlisaurus* sp. nov., 28 species of the order Ichthyosauria are now recognized from the Lower Jurassic, pertaining to the following families:

Temnodontosauridae in *Temnodontosaurus platydon*, *Temnodontosaurus eurycephalus*, *Temnodontosaurus nuertingensis*, *Temnodontosaurus trigonodon*, *Temnodontosaurus acutirostris* (Maisch 1998) and *Temnodontosaurus azerguensis* (Martin et al., 2012); Leptonectidae in *Eurhinosaurus longirostris* (McGowan 1994), *Excalibosaurus costini* (McGowan 1986), *Leptonectes moorei*, *Leptonectes solei*, *Leptonectes tenuirostris*, *Wahlisaurus massarae* (Lomax 2016) and *Wahlisaurus* sp. nov.; Suevoleviathanidae in *Suevoleviathan disinteger* and *Suevoleviathan integer* (Maisch 2001); Ichthyosauridae in *Ichthyosaurus breviceps* (Owen 1881), *Ichthyosaurus conybeari* (Lydekker 1888), *Ichthyosaurus anningae* (Lomax & Massare 2015), *Ichthyosaurus larkini*, *Ichthyosaurus somersetensis*, *Ichthyosaurus communis* (Lomax & Massare 2016), *Protoichthyosaurus prostaialis* (Appleby 1979) and *Protoichthyosaurus applebyi* (Lomax et al. 2017); Stenopterygiidae in *Stenopterygius quadricissus*, *Stenopterygius triscissus*, *Stenopterygius uniter* (Maisch 2008), *Stenopterygius aaleniensis* (Maxwell et al. 2012) and *Hauffiopteryx typicus* (Maisch 2008).

Finally, before a name is chosen for *Wahlisaurus* sp. nov., further examination of SNHM 2753-R should take place in hopes that additional differentiating characters can be found. These characters, if distinct enough, could provide inspiration for the name that is eventually chosen. For this further examination, imaging techniques such as X-ray and CT-scans are recommended. Given the possibility of using 3D-scanning equipment at the State Museum of Natural History Brunswick to accurately determine the specimen's outer morphology, use of this technique is also advised.

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References

- Abel, O. (1909): Cetaceenstudien. 1. Mitteilung: Das Skelett von *Eurhinodelphis cocheteuxi* aus dem Obermiozän von Antwerpen. – Sitzungsberichte der Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse 118: 241-253; Wien.
- Appleby, R.M. (1961): On the cranial morphology of Ichthyosaurs. – Proceedings of the Zoological Society of London 137: 333–370; London.
- Baur, G. (1887): Geology and Palaeontology. – The American Naturalist 21: 837-848; Chicago.
- Bardet, N. (1992): Stratigraphic evidence for the extinction of the ichthyosaurs. – Terra Nova 4: 649–656; Hoboken.
- Bronn, H.G. (1844): Nachträgliche Beobachtungen an Ichthyosauren. – Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde: 676–679; Stuttgart (E. Schweizerbart's Verlagshandlung).
- Buchholtz, E.A. (2001): Swimming styles in Jurassic ichthyosaurs. – Journal of Vertebrate Paleontology 21: 61-73; Abingdon.
- Callaway, J.M. (1997): A new look at *Mixosaurus*. – Ancient marine reptiles: 45-59; Cambridge.
- Colbert, E. (1965): The World Naturalist. – 1. Aufl., 228 pages; New York (Norton).
- Conybeare, W.D. (1822): Additional notes on the fossil genera *Ichthyosaurus* and *Plesiosaurus*. – Transactions of the Geological Society London 2, 1: 103–123; London.
- De la Beche, H.T. & Conybeare, W. D. (1821): notice of the discovery of a new Fossil Animal, forming a link between the *Ichthyosaurus* and Crocodile, together with general remarks on the Osteology of the *Ichthyosaurus*. – Transactions of the Geological Society London, 1: 559–594; London.
- Dick, D.G. (2015): An ichthyosaur carcass – fall community from the Posidonia Shale (Toarcian) of Germany. - Palaios 30: 353-361; Tulsa.
- Dick, D.G. & Maxwell, E. E. (2015): Ontogenetic Tooth Reduction in *Stenopterygius quadriscissus* (Reptilia: Ichthyosauria): Negative Allometry, Changes in Growth Rate, and Early Senescence of the Dental Lamina. – PLoS ONE 10: e0141904 doi: 10.1371/journal.pone.0141904; international.
- Ellis, R. (2003): Sea Dragons: Predators of the Prehistoric Oceans. – 1. Aufl. 326 pages; Lawrence.
- Fischer, V.; Guiomar, M. & Godefroit, P. (2011): New data on the palaeobiogeography of Early Jurassic marine reptiles: the Toarcian ichthyosaur fauna of the Vocontian Basin (SE France). – Neues Jahrbuch für Geologie und Paläontologie 261: 111-127; Stuttgart.
- Godefroit, P. (1994): Les reptiles marins du Toarcien (Jurassique Inferieur) Belgo-Luxembourgeois. – Mémoires pour servir à l'Explication des Cartes Géologique et Minières de la Belgique 39: 1-98; Brussels.
- Hauff, R.B. (1997): Urwelt-Museum Hauff. Leben im Jura Meer. – 1. Aufl., 37 pages; Holzmaden (Urwelt-Museum Hauff).
- Hauff, R.B.; Heunisch, C.; Hochsprung, U.; Ilger, J.-M.; Joger, U.; Klopschar, M.; Kosma, R.; Krüger, F.J.; Thies, D. & Zellmer, H. (2014): Jurameer. Niedersachsens versunkene Urwelt. – 1. Aufl., 96 pages; München (Dr. Friedrich Pfeil).

- Heunisch, C. (2014) Welche Informationen liefert der Aufschluss Hondelage? – In: Kosma, R. (ed.): Jurameer. Niedersachsens versunkene Welt: 8-10; München (Dr. Friedrich Pfeil).
- Home, E. (1814): Some Account of the Fossil Remains of an Animal More Nearly Allied to Fishes Than Any of the Other Classes of Animals. – Philosophical Transactions of the Royal Society of London 104: 571-577; London.
- Home, E. (1819): Reasons for Giving the Name *Proteo-Saurus* to the Fossil Skeleton Which Has Been Described. – Philosophical Transactions of the Royal Society of London 109: 212-216; London.
- Hone, D.W.E.; Farke, A.A. & Wedel, M.J. (2016): Ontogeny and the fossil record: what, if anything, is an adult dinosaur? – Biology Letters: DOI: 10.1098/rsbl.2015.0947; London.
- <http://www.geopunkt-schandelah.de/Hintergrund/>: Geopunkt Jurameer Schandelah. Ein naturhistorischer Forschungs- und Erlebnisort. Last visited 22. November 2017
- <http://www.geopunkt-schandelah.de/Kontakt-Besuch/>: Geopunkt Jurameer Schandelah. Ein naturhistorischer Forschungs- und Erlebnisort. Last visited: 22. November 2017.
- Jaekel, O. (1904): Eine neue Darstellung von *Ichthyosaurus*. – Zeitschrift der deutschen geologischen Gesellschaft 56: 26-34; Berlin.
- Joger, U. (2014) Ichthyosaurier. – In: Kosma, R. (ed.): Jurameer. Niedersachsens versunkene Welt: 69-73; München (Dr. Friedrich Pfeil).
- Johnson, R. (1977): Size independent criteria for estimating relative age and the relationships among growth parameters in a group of fossil reptiles (Reptilia: Ichthyosauria). – Canadian Journal of Earth Sciences 14: 1916-1924; Ottawa.
- Kear, B.P. (2005): Cranial morphology of *Platypterygius longmani* Wade, 1990 (Reptilia: Ichthyosauria) from the Lower Cretaceous of Australia. – Zoological Journal of the Linnean Society 145: 583-622; London.
- Kear, B.P. & Zammit M. (2014): In utero foetal remains of the Cretaceous ichthyosaurian *Platypterygius*: ontogenetic implications for character state efficacy. – Geological Magazine 151: 5-6; Cambridge.
- Kosma, R. (2014a) Die Plesiosaurier und Pliosaurier des Jurameeres. – In: Kosma, R. (ed.): Jurameer. Niedersachsens versunkene Welt: 78-82; München (Dr. Friedrich Pfeil).
- Kosma, R. (2014b) Die Krokodile des Jurameeres. – In: Kosma, R. (ed.): Jurameer. Niedersachsens versunkene Welt: 83-85; München (Dr. Friedrich Pfeil).
- Kosma, R. (2014c) Flugsaurier. – In: Kosma, R. (ed.): Jurameer. Niedersachsens versunkene Welt: 86-87; München (Dr. Friedrich Pfeil).
- Lawrence, J.D. (2008): A total evidence analysis of the evolutionary history of the thunnosaur ichthyosaurs. – Electronic Master Thesis, 77 pages; retrieved from <https://etd.ohiolink.edu/>.
- Ley, W. (1951): Dragons in Amber. – 1. Aufl., 328 pages; New York City (Viking Press).

- Lingham-Soliar, T. (1999): Rare soft tissue preservation showing fibrous structures in an ichthyosaur from the Lower Lias (Jurassic) of England. – Proceedings of the Royal Society of London 266: 2367–2373; London.
- Lomax, D.R. (2016): A new leptonectid ichthyosaur from the Lower Jurassic (Hettangian) of Nottinghamshire, England, UK, and the taxonomic usefulness of the ichthyosaurian coracoid. – Journal of Systematic Palaeontology 14: 387-401; London.
- Lomax, D.R. & Massaræ, J.A. (2015): A new species of *Ichthyosaurus* from the Lower Jurassic of West Dorset, England, U.K. – Journal of Vertebrate Paleontology: e903260 1-14; Abingdon on Thames.
- Lomax, D.R. & Massaræ, J.A. (2016): Two new species of *Ichthyosaurus* from the lowermost Jurassic (Hettangian) of Somerset, England. – Papers in Palaeontology Online Edition: [doi:10.1002/spp2.1065](https://doi.org/10.1002/spp2.1065) 1-20; Hoboken.
- Mantell, G.A. (1851): Petrifactions and their teachings; or, a hand-book to the gallery of organic remains of the British Museum. – 1. Aufl., 496 pages; London (H. G. Bohn).
- Maisch, M.W. (1998): Kurze Übersicht der Ichthyosaurier des Posidonienschiefers mit Bemerkungen zur Taxonomie der Stenopterygiidae und Temnodontosauridae. – Neues Jahrbuch für Geologie und Paläontologie 209: 401-431; Stuttgart.
- Maisch, M.W. (2001): Neue Exemplare der seltenen Ichthyosauriergattung Suevoleviathan Maisch 1998 aus dem Unteren Jura von Südwestdeutschland. – Geologica et Palaeontologica 35: 145-160; Marburg.
- Maisch, M.W. (2008): Revision der Gattung *Stenopterygius* Jaekel, 1904 emend. Von Huene 1922 (Reptilia: Ichthyosauria) aus dem unteren Jura Westeuropas. – Palaeodiversity 1: 227-271; Stuttgart.
- Maisch, M.W. & Ansorge, J. (2004): The Liassic ichthyosaur *Stenopterygius* cf. *quadricissus* from the lower Toarcian of Dobbertin (northeastern Germany) and some considerations on lower Toarcian marine reptile palaeobiogeography. – Paläontologische Zeitschrift 78: 161-171; Stuttgart.
- Maisch, M.W. & Matzke, A.T. (2000): The Ichthyosauria. – Stuttgarter Beiträge zur Naturkunde 298: 1-159; Stuttgart.
- Maisch, M.W. & Matzke, A.T. (2003): The cranial osteology of the ichthyosaur *Leptonectes* cf. *tenuirostris* from the Lower Jurassic of England. – Journal of Vertebrate Paleontology 23: 116–127; Abingdon.
- Martin, J.E.; Fischer, V.; Vincent, P. & Suan, G. (2012): A longirostrine *Temnodontosaurus* (Ichthyosauria) with comments on Early Jurassic ichthyosaur niche partitioning and disparity. – Palaeontology 55: 995-1005; UK.
- Maxwell, E.E. (2012): New metrics to differentiate species of *Stenopterygius* (Reptilia: Ichthyosauria) from the Lower Jurassic of southwestern Germany. – Journal of Paleontology 86: 105-115; Cambridge.
- Maxwell E.E.; Fernández M.S. & Schoch R.R. (2012): First diagnostic marine reptile remains from the Aalenian (Middle Jurassic): a new ichthyosaur from southwestern Germany. – PLoS ONE 7 (8): e41692; international.

- McGowan, C. (1973): Differential Growth in Three Ichthyosaurs: *Ichthyosaurus communis*, *I. breviceps*, and *Stenopterygius quadriscissus* (Reptilia, Ichthyosauria). – Life Sciences Contribution Royal Ontario Museum 93: 1-21; Ontario.
- McGowan, C. (1974): A Revision of the Longipinnate Ichthyosaurs of the Lower Jurassic of England, with Descriptions of Two New Species (Reptilia: Ichthyosauria). – Life Sciences Contributions Royal Ontario Museum 97: 1-37; Ontario.
- McGowan, C. (1979): A Revision of the Lower Jurassic Ichthyosaurs of Germany with Descriptions of two new Species. – *Palaeontographica* 166: 93-135; Stuttgart.
- McGowan, C. (1991): *Dinosaurs, spitfires, and sea dragons*. – 1. Aufl., 365 pages; Cambridge (Harvard University Press).
- McGowan, C. (1995): *Temnodontosaurus risor* is a juvenile of *T. platyodon* (Reptilia: Ichthyosauria). – *Journal of Vertebrate Paleontology* 14: 472-479; Abingdon on Thames.
- McGowan, C. (1996): The taxonomic status of *Leptopterygius* Huene, 1922 (Reptilia: Ichthyosauria). – *Canadian Journal of Earth Sciences* 33: 439-443; Ottawa.
- McGowan C. (1997) A transitional ichthyosaur fauna. – In: Callaway, J. M. & Nicholls E. D. (eds.): *Ancient Marine Reptiles*: 61-80; Cambridge (Academic Press).
- McGowan C. (2003): A new specimen of *Excalibosaurus* from the English Lower Jurassic. – *Journal of Vertebrate Paleontology* 23: 950-956; Abingdon.
- McGowan, C. & Motani, R. (2003): *Ichthyopterygia*. – *Handbook of Paleoherpptology* 8: 1-175; Munich.
- Motani, R. (1999): Phylogeny of the Ichthyopterygia. – *Journal of Vertebrate Paleontology* 19: 473-496; Abingdon on Thames.
- Motani, R., Rothschild, B. M. & Wahl, W. J. (1999): Large eyeballs in diving ichthyosaurs. – *Nature* 402: 747; London.
- Motani, R., You H. & McGowan C. (1996): Eel-like swimming in the earliest ichthyosaurs. – *Nature* 382: 347-348; London.
- Nicholls E.L. & Manabe M. (2004): Giant ichthyosaurs of the Triassic—a new species of *Shonisaurus* from the Pardonet Formation (Norian: Late Triassic) of British Columbia. *Journal of Vertebrate Paleontology* 24: 838-849; Abingdon on Thames.
- Pearce, J.C. (1846): Notice of what appears to be the embryo of an *Ichthyosaurus* in the pelvic cavity of *Ichthyosaurus (communis?)*. – *Annals & Magazine of Natural History* 17: 44-46; London.
- Pollard, J.E. (1968): The gastric contents of an ichthyosaur from the Lower Lias of Lyme Regis, Dorset. – *Palaeontology* 11: 376-388; London.
- Riegraf, W. (1985): Mikrofauna, Biostratigraphie und Fazies im Unteren Toarcium Stidwestdeutschlands und Vergleiche mit benachbarten Gebieten. – *Tübinger Mikropaläontologische Mitteilungen* 3: 1-232; Tübingen.

- Riegraf, W.V.; Werner, G. & Lörcher, F. (1984): Der Posidonienschiefer. Biostratigraphie, Fauna und Fazies des südwestdeutschen Untertoarciums (Lias $\overline{\text{II}}$). – 1. Aufl., 195 pages; Stuttgart (Ferdinand Enke)
- Röhl J. & Schmid-Röhl, A. (2005): A Lower Toarcian (Upper Liassic) Black Shales of the Central European Epicontinental Basin: A Sequence Stratigraphic Case Study from the SW German Posidonia Shale. In the Deposition of Organic-Carbon-Rich Sediments: Models, Mechanisms, and Consequences. – SEPM Special Publication 82: 165–189; Tulsa.
- Romer, A.S. (1948): Ichthyosaur ancestors. – American Journal of Science 246: 109-121; USA.
- Sander, P.M. (2000): Ichthyosauria: their diversity, distribution, and phylogeny. – Paläontologische Zeitschrift 74: 1-35; Stuttgart.
- Storrs, G.W.; Arkhangelskh, M. S. & Efimov, V. M. (2000) Mesozoic marine reptiles of Russia and former Soviet republics. – In: Benton, M. J.; Shishkin, M. A.; Unwin, D. M. & Kurochkin, E. N., (eds.): The age of dinosaurs in Russia and Mongolia: 187-210; Cambridge (Cambridge University Press).
- Whitear, M. (1956): On the colour of an ichthyosaur. – Annals and Magazine of Natural History 9: 742–744; London.
- Zellmer, H. (2014) Stratigraphie (Schichtenfolge) und Paläogeographie des Unterjura (Lias) und Mitteljura (Dogger) im Geopark Harz . Braunschweiger Land . Ostfalen. – In: Kosma, R. (ed.): Jurameer. Niedersachsens versunkene Welt: 4-6; München (Dr. Friedrich Pfeil).