Stuttgarter Beiträge zur Naturkunde

Serie B (Geologie und Paläontologie)

Herausgeber:

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart

Stuttgarter Beitr. Naturk.	Ser. B	Nr. 258	27 pp., 5 figs.	Stuttgart, 31. 12. 1997

The cranial osteology of *Ichthyosaurus intermedius* CONYBEARE, 1822 from the Lias of Great Britain

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With 5 figures

Summary

A complete and extraordinarily well preserved ichthyosaurian skull, SMNS 13111, is described in detail. It has been formerly identified as *Stenopterygius hauffianus* v. HUENE, 1922 and was reported to be from the Upper Lias of Whitby. Comparison with the genera *Stenopterygius* and *Ichthyosaurus* shows, however, that the specimen is a representative of the latter, bearing closest resemblance to the type specimen of *I. intermedius* CONYBEARE, 1822 from the Lower Lias of Lyme Regis. It is consequently referred to that species, which is shown to differ from *I. communis*, with which it had been formerly synonymized, mainly in features of its dentition. An emended diagnosis of the species, based mainly on SMNS 13111, is given.

Zusammenfassung

Ein vollständiger und vorzüglich erhaltener Ichthyosaurierschädel, SMNS 13111, wird detailliert beschrieben. Das Stück wurde bislang zu *Stenopterygius hauffianus* v. HUENE, 1922 gestellt. Vergleiche mit den Gattungen *Stenopterygius* und *Ichthyosaurus* zeigen indessen, daß es einem Vertreter der letzteren Gattung angehört, wobei es die größte Ähnlichkeit zum Typusschädel der Art *Ichthyosaurus intermedius* CONYBEARE, 1822 aus dem Unteren Lias von Lyme Regis aufweist. Es wird folglich dieser Art zugewiesen, die sich von *I. communis*, mit welchem sie zuvor synonymisiert wurde, vor allem in Merkmalen der Bezahnung unterscheidet. Eine erweiterte und verbesserte Diagnose dieser Art, die in der Hauptsache auf SMNS 13111 basiert, wird gegeben.

1. Introduction

The ichthyosaurs are one of the most famous and popular groups of fossil tetrapods, second only, probably, to the dinosaurs, and an extensive literature on these enigmatic animals exists. Despite these numerous studies, our knowledge especially of the cranial osteology of the majority of ichthyosaurian taxa is still very limited and systematics within the group is almost entirely based on rather gross morphological differences. No convincing attempt to clarify the in-group relationships of the Ichthyosauria has yet appeared, although MAZIN (1982) provided some useful data, and the systematic position of the entire group within the Tetrapoda is still unknown (Maisch 1997). This situation is clearly caused by our lack of detailed morphological knowledge of most forms.

Systematic approaches in part use an exclusively phenetic methodology (especially Mc Gowan 1974a, b, 1976 and 1979). It often appears to be the only sensibly applicable alpha-taxonomical method when dealing with very compressed specimens, which is the majority of Jurassic ichthyosaur finds. To base systematics practically exclusively on such characters is yet not desirable, in particular because these characters might not always be reliable, a fact already noted by v. Huene (1922) and recently highlighted by the comprehensive studies of Godefroit (1993, 1994).

The existing descriptions of Jurassic ichthyosaur crania are only adequate for *Ichthyosaurus communis* (Sollas 1916; Mc Gowan 1973), *Stenopterygius longifrons* (Owen 1881; Godefroit 1993, 1994), *Baptanodon* (Gilmore 1905) and *Ophthalmosaurus* (Andrews 1910; Appleby 1956, 1961). The purpose of this paper is to give a detailed description of the ichthyosaur skull SMNS 13111, allegedly from the Toarcian of Whitby, but, as it is demonstrated below, more probably from the Lower Lias. Each element of the skull is described in detail and then immediately compared to the two generally most similar genera of Liassic ichthyosaurs, *Ichthyosaurus* and *Stenopterygius*.

2. Comparative cranial osteology of *Ichthyosaurus intermedius*, SMNS 13111

2.1. Previous work

In his classical monograph "Die Ichthyosaurier des Lias und ihre Zusammenhänge" Friedrich v. Huene (1922) introduced the new species *Stenopterygius hauffianus*, based on three skulls from the Posidonienschiefer of the well-known Holzmaden area in South-Western Germany. One of these (GPIT 18287) was later depicted as the lectotype of the species (Mc Gowan 1979). The species was erected to accommodate those specimens of *Stenopterygius* with strikingly short snouts and comparatively very large orbits. v. Huene also referred to this species a skull allegedly from the Upper Lias of Whitby in Yorkshire, which he also figured (v. Huene 1922, pl. 19, fig. 2). Mc Gowan (1978, 1979) mentioned this skull twice, but stated both times that it was impossible to relocate the specimen, assuming that it had been lost. Benton & Taylor (1984), in a review of the Upper Liassic reptiles of the Whitby area, also refer to the specimen as probably lost. Mc Gowan (1978) described, however, three other skulls – comparable in size to v. Huene's specimen and probably all immature – from the Upper Lias of Ilminster, Somerset, which he referred to *Stenopterygius hauffianus* (Mc Gowan 1978). These specimens really appear to belong to *S. hauffianus* as the species is currently understood, providing the only definite record of the taxon from Great Britain so far.

During a revision of the entire ichthyosaur collection of the Staatliches Museum für Naturkunde in Stuttgart (SMNS), I relocated v. Huene's English specimen, which is bearing the number SMNS 13111, identical to the number given in v. Huene (1922) and also well agreeing with v. Huene's figure.

The specimen was received from the commercial fossil and mineral trader F. Krantz in Bonn by the Museum in the year 1912, in exchange for Quaternary mammal material from Steinheim an der Murr (R. WILD, pers. comm.), so there is no doubt that the specimen described here is identical to that figured by v. HUENE.

Because it forms part of the material used by v. HUENE in the original description of *Stenopterygius hauffianus*, SMNS 13111 must be considered a paralectotype of this species. The cranial osteology and general skeletal structure of *S. hauffianus* was in part described by v. HUENE (1922, 1926, 1931b, 1952), MC GOWAN (1978, 1979) and, most recently and quite thoroughly, by GODEFROIT (1994).

2.2. Systematic palaeontology

Order Ichthyosauria DE BLAINVILLE, 1835
Family Ichthyosauridae BONAPARTE, 1838

Type genus: *Ichthyosaurus* DE LA BECHE & CONYBEARE, 1821 = *Eurypterygius* JAEKEL, 1904.

Other genera: ?*Protoichthyosaurus* APPLEBY, 1979 (is very probably synonymous to *Ichthyosaurus* [MAISCH & HUNGERBÜHLER 1997]), probably *Macropterygius* v. HUENE, 1922, too.

Diagnosis (after MC GOWAN 1974b, 1996). – Forefin with no fewer than 4 primary digits, two of which originate from the intermedium, total digital count usually not less than 5, orbit relatively large, ratio diameter of orbit to length of lower jaw > 0.20, aperture of sclerotic ring relatively large, ratio internal diameter of sclerotic ring to diameter of orbit usually > 0.35, maxilla relatively small, ratio length of premaxillary segment to length of lower jaw usually > 0.40, pelvic girdle tripartite, rib articulations predominantly bicipital.

Other diagnostic features include:

– Teeth strongly developed, never reduced, usually with expanded roots, crowns and roots bearing a strong sculpture of apicobasal grooves and ridges, but no carinae are ever developed.

– The fossa dentalis and the fossa praemaxillaris are weakly developed, usually discontinuous structures.

– A separately ossified squamosal between supratemporal and quadratojugal is present but exceedingly delicate and thin, often detached from specimens or crushed beyond recognition and thus appearing to be absent.

– The processus quadratus of the quadratojugal is well-developed, long and clearly offset from the main body of the bone.

– The autopodial fin elements have a very characteristic polygonal shape with well-finished edges, forming a closely fitting mosaic pattern for most of the length of the fins.

– The humerus is very stout, about as wide as long, with a well developed trochanter dorsalis, only two distal facets are present.

– The coracoids are very thick and robust and have well-developed anterior and posterior notches.

– The preflexural vertebral count is low, usually < 80.

– The tailbend is well developed.

Genus *Ichthyosaurus* DE LA BECHE & CONYBEARE, 1821

Type species: *Ichthyosaurus communis* CONYBEARE, 1822.

Other species: *I. intermedius* CONYBEARE, 1822; *I. breviceps* OWEN, 1881; *I. conybeari* LYDEKKER, 1889; *I. janiceps* MC GOWAN, 1996.

Diagnosis. – As for the family, because it is the only genus certainly belonging to it.

Ichthyosaurus intermedius CONYBEARE, 1822
= *Eurypterygius intermedius* (CONYBEARE, 1822) JAEKEL, 1904

Holotype: Original specimen of HOME 1819, pl. 14 and CONYBEARE 1822, pl. 17, incomplete skull and mandible with associated postcrania; the present whereabouts of this specimen are not known.

Referred specimen: SMNS 13111. The specimen has been determined as *Stenopterygius hauffianus* v. HUENE, 1922. This determination of v. HUENE 1922 has been adopted by all subsequent authors (MC GOWAN 1978, 1979; BENTON & TAYLOR 1984; GODEFROIT 1994).

Emended diagnosis (previous ones have been given by CONYBEARE 1822; OWEN 1881; v. HUENE 1922). – A species of small size, skull length probably not exceeding 40 cm, skull proportions rather similar to *I. communis* in SMNS 13111: premaxillary ratio 0.36, snout ratio 0. 61, orbital ratio 0.22, prenarial ratio 0.52, sclerotic ring ratio 0.40); number of maxillary teeth > 20 (possibly > 25), which is by far the highest number in all species of the genus; teeth heavily striated but less than in *I. communis*, crowns very long and slender, roots often expanding rather abruptly, the posterior maxillary teeth situated below the orbit and distinctly recurved; premaxilla and dentary only with rudimentary fossae; fossa surangularis very short; maxilla relatively high with slightly concave ventral border, extremely long and delicate posterior suborbital process reaching up to the middle of the orbit; jugal with dorsoventrally compressed ramus suborbitalis bearing a lateral ridge, as in *Stenopterygius*; quadratojugal shortened dorsoventrally with well developed and characteristically shaped processus quadratus contacting quadrate somewhat dorsal to the condylar area; ascending plate of quadrate very delicately built with narrow, sharp lateral edge.

Comparison of SMNS 13111 (fig. 1, 2) to CONYBEARE's type specimen (fig. 3) strongly suggests that they belong to the same species. Whether this is also true for other specimens that have been referred to *I. intermedius* in the past (OWEN 1881; LYDEKKER 1889; v. HUENE 1922) has yet to be established.

Remarks on the alleged stratigraphic provenance of SMNS 13111

The thought that a typical member of the genus *Ichthyosaurus* should have remained hitherto unnoticed in the well-documented and thoroughly studied ichthyosaurian fauna of the Upper Lias of Western Europe appears very strange. The only primary information available on the origin of the specimen are a note in the inventory book of the SMNS and the original label of the fossil trader F. KRANTZ still preserved in the SMNS. Both equally state that the specimen represents "*Ichthyosaurus trigonodon* CONYBEARE, Upper Lias, Whitby".

The taxonomic determination appears very odd. *Ichthyosaurus trigonodon*, which was thoroughly described by CARL v. THEODORI (1854), is not known to occur in Great Britain at all. It is a gigantic ichthyosaur reaching a skull length in excess of

180 cm. It certainly belongs to the genus *Temnodontosaurus* LYDEKKER, 1889 (pers. obs.) and constitutes a valid species of that genus. It is almost certainly a senior subjective synonym of *Temnodontosaurus burgundiae* (GAUDRY, 1892) and was treated as such by MAISCH (1997).

Stratigraphic and geographic documentation of SMNS 13111 is obviously inadequate. The preservation of the specimen – the bone surface being excellently preserved in rather soft blueish-grey marl, the bone itself being of very dark grey, almost blackish colour – occurs in very similar manner in both Upper and Lower Liassic English ichthyosaurs and thus does not provide adequate evidence to ascertain the origin of the specimen.

A possibility of establishing the age of SMNS 13111 beyond doubt could be to look for microfossils in the matrix still attached to it. There is, unfortunately, so little rock left, that the chance to obtain well enough preserved and determinable specimens of any stratigraphic significance must be considered very low.

Considering the improbability of an Upper Liassic *Ichthyosaurus* one should, of course, bear in mind that at least one species – *Temnodontosaurus acutirostris* (OWEN, 1839) MAISCH 1997 – is known to be restricted to the Toarcian of Great Britain (MC GOWAN 1974b) and another species, "*Leptopterygius*" *disinteger* (v. HUENE, 1926) is restricted to the Holzmaden area (MAISCH, in press a). The latter species, which is in several respects very unusual and certainly represents a genus of its own (MAISCH, in press a), is only known by the holotype skeleton. Both these species are no small or inconspicuous animals, but belong to the largest Upper Liassic ichthyosaurs known. It is therefore evident, that there had been rare and unusual ichthyosaurs of probably restricted occurrence in the Upper Lias of Europe, and that new and surprising discoveries can therefore still be expected in the future

That the genus *Ichthyosaurus* is by no means restricted to the Lower Lias was recently demonstrated by the rather baffling discovery of *Ichthyosaurus janiceps* in Norian strata of British Columbia (MC GOWAN 1996). In spite of this, the extreme morphological similarity of SMNS 13111 to Lower Liassic *Ichthyosaurus* specimens does strongly indicate that the labelling of the specimen by the KRANTZ company was erroneous, although the possibility that it actually is derived from the Toarcian cannot be categorically denied. The geographic assignment may well be correct. Even though the Whitby area is mainly famous for its Lower Toarcian vertebrate fauna, Lower Liassic strata of Sinemurian age (zone of *Oxynoticeras oxynotum*), which have definitely yielded at least one ichthyosaur specimen, are exposed at Robin Hood's Bay near Whitby (BENTON & TAYLOR 1984).

2.4. Description of the skull No. SMNS 13111

Preservation. – The skull described below – No. SMNS 13111 – is practically complete and well articulated, including the entire mandible and three anterior cervical vertebrae. The atlas-axis complex is not visible. It was probably pushed inside the braincase, indicating that SMNS 13111 is a specimen that became embedded "head first", which is corroborated by the many breaks in the snout region.

The entire skull is strongly compressed laterally, exposing its left side, the bones of the snout – premaxilla and maxilla – the circumorbital series, as well as the quadrate and the entire lower jaw are, however, in a truly marvellous state of preservation and show to a large degree their original shape. The nasals as well as the median row of the skull roof and the dorsal temporal region have suffered severe deformation

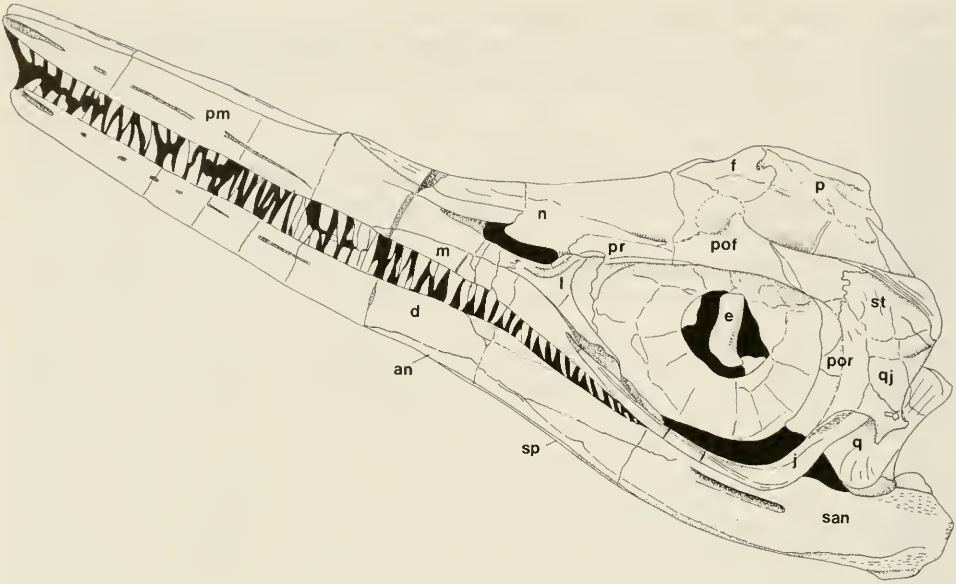

Fig. 1. Skull and mandible of *Ichthyosaurus intermedius* CONYBEARE, 1822, SMNS 13111, from the (probably Lower) Lias of Whitby, Yorkshire (paralectotype of *Stenopterygius hauffianus* v. HUENE, 1922, original of v. HUENE 1922, pl. 19, fig. 2). – x 0,45.
Abbreviations: an = angular, d = dentary, e = epipterygoid, f = frontal, j = jugal, l = lacrimal, m = maxilla, n = nasal, p = parietal, pm = premaxilla, pof = postfontal, por = postorbital, pr = prefrontal, q = quadrate, qj = quadratojugal, san = surangular, sp = splenial, st = supratemporal.

and many breaks are running through the bones, partly obscuring the course of the sutures. The dentition is excellently preserved in both upper and lower jaw, the anterior half of the sclerotic ring is also in a good state. The three cervical vertebrae associated with the skull are exposed from their left sides as well. They are very well preserved but show no noteworthy features.

Preparation of the specimen apparently was done mechanically, but in so excellent manner, that in most regions even finest details of the bone surface are discernible in a way almost never possible in Liassic ichthyosaurs. As it is shown by the remains of the original matrix left in some places, the skull was not extracted from a calcareous nodule, but from very soft marl, which might largely account for its unusual quality.

Premaxilla (Fig. 1). – As usual in all known ichthyosaurs, the premaxilla is an elongated and low bar of bone, forming most of the snout and upper jaw margin. It is in contact with the nasal dorsally, the lacrimal posterodorsally and the maxilla ventrally and posteroventrally. The jugal does definitely not reach the premaxilla. The lateral surface of the bone does not bear the usual deep fossa praemaxillaris seen in most Jurassic ichthyosaurs, where it is expressed as a deep groove that extends from the tip of the snout to the anterior margin of the external narial opening. Instead, in the anterior half of the premaxilla, there are several short, clearly separated furrows which become more or less confluent in the posterior half of the bone, although not reaching up to the anterior narial margin but ending far in front of it.

The processus subnarialis of the premaxilla borders at least the anterior half of the ventral margin of the external naris, probably even the anterior two thirds. The subnarial process is well developed and clearly separates the maxilla from the external narial aperture. It is only 5 mm high at maximum, whereas the maxilla reaches its greatest height of 11 mm below the naris. This might be partially due to a slight dorsal displacement of the maxilla. The suture with the lacrimal cannot be seen clearly, but if correctly interpreted is quite strongly interdigitating. The lacrimal probably overlaps the premaxilla for a short distance. The suture with the nasal can largely be seen very clearly, but it is equivocal in the narial region owing to strong deformation. It seems most probable that the premaxilla borders the anterior and the anterior half of the dorsal margin of the external naris. The suture with the maxilla is clear. It is essentially straight without serrations whatsoever. The jaw margin is formed by the premaxilla for 121, 5 mm. 26 teeth are recognizable, but there were probably much more, 35 being a conservative estimate

Comparison. – Mc Gowan (1973) did not give a detailed description of the premaxilla of *Ichthyosaurus*. Owen (1881: pl. 24) and Mc Gowan (1973: pl. 9) provide, however, useful figures of *Ichthyosaurus communis*. Two well preserved skulls of that species (GPIT 1796/1 and GPIT 1796/2) and a good one of the rare *Ichthyosaurus breviceps* (GPIT 1796/3) in the Tübingen collection also provide useful information. The most conspicuous and important resemblance between SMNS 13111 and *Ichthyosaurus* is the discontinuous and shallow fossa praemaxillaris. Godefroit (1993) explicitly uses this character state as an important diagnostic difference to *Stenopterygius*, which always has a continuous fossa which becomes rather deep posteriorly and is only somewhat irregular at the tip of the snout. After examining more than 100 well-preserved skulls of all known species of *Stenopterygius* from embryos to old adults and more than a dozen skulls of three species of *Ichthyosaurus* I have not found a single exception to this rule. The supra- and subnarial processes of the premaxilla are also similar to what is seen in *Ichthyosaurus*, but *Stenopterygius* is not generally different in that respect, the only difference appears to be that the premaxillary-lacrimal contact below the naris is lost in *Stenopterygius longifrons* (Godefroit 1993, 1994; Maisch 1997) and at least some specimens of *Stenopterygius quadriscissus* (A. Hungerbühler pers. comm.; pers. obs.). It should, however, be noted, that the processus subnarialis tends to be more strongly developed and at least as high as the subnarial portion of the maxilla or even higher in *Ichthyosaurus communis* (Owen 1881; pers. obs.) and in *Ichthyosaurus intermedius* (Conybeare 1822; see Figure 3).

The most conspicuous difference to *Stenopterygius hauffianus* is the fact, that in SMNS 13111 the anterior tip of the premaxilla is not unusually slender or low, and also the teeth are not in the least way diminishing in size towards the tip. These features would alone be sufficient to exclude the specimen from any close relationship with *Stenopterygius hauffianus*. Among the several species of *Ichthyosaurus* recognized by Mc Gowan (1974 a) SMNS 13111 would come closest to *Ichthyosaurus communis* in both the general shape and length of the premaxilla. The premaxillary ratio of SMNS 13111 is 0.39, which is remarkably short but within the range given by Mc Gowan for that species (0.38–0.48). In *Ichthyosaurus conybeari* the ratio is > 0.40 (probably considerably higher), in *Ichthyosaurus breviceps* it is 0.33–0.44, so SMNS 13111 is also within the range of the latter, but both species are very different from both *Ichthyosaurus communis* and SMNS 13111 in the shape of the snout.

Whereas it is very low and exceedingly slender in *Ichthyosaurus conybeari* – reminiscent of forms such as *Stenopterygius longifrons* and *Leptonectes tenuirostris* – it is very short and of more or less triangular shape in *Ichthyosaurus breviceps*, with the premaxilla considerably increasing in height posteriorly, reminiscent of "*Temnodontosaurus*" *eurycephalus* and – to a much lesser extent – *Stenopterygius cuneiceps* and the Triassic species *Ichthyosaurus janiceps*. In summary the structure of the premaxilla is much more similar to *Ichthyosaurus communis* and *I. intermedius* than to any other Liassic ichthyosaur.

Maxilla (Fig. 1). – The maxilla is a small element totally excluded from the narial margin by the processus subnarialis of the premaxilla and the processus ventralis anterior of the lacrimal. It is generally very low, but due to the strong convexity of its dorsal margin becomes relatively higher below the external naris. It only reaches anteriorly beyond the anterior narial margin for about one narial length. The lateral surface is essentially smooth without any conspicuous grooves, ridges or foramina. The sutures with premaxilla, lacrimal and jugal are almost totally straight, no interdigitation of any kind is observable. In its posterior portion the maxilla bears a groove-like facet for the reception of the anteriormost spur of the jugal. Because the first 7 mm of the jugal are missing it is visible that this facet is bordered by a thin dorsal and a somewhat broader ventral ridge.

The ventral margin of the maxilla is markedly concave, so that a slight angle is present between the anterior and posterior halves of the main body of the bone. 26 recognizable teeth are present. This might come close to the actual number, because the maxillary teeth are largely situated lateral to the posterior dentary teeth in the specimen, which are therefore not visible, and the maxillary tooth row appears to be practically completely preserved. It must be noted, that the teeth in the specimen show almost no postmortal displacement, which might be due either to rapid burial or to a firm attachment of the teeth in their respective dental grooves. A long posterior suborbital process of the maxilla is present. It is largely covered by the jugal laterally, but clearly visible when looking on the ventral side of the suborbital bar. It is clearly recognizable up to the middle of the orbit. It is edentulous in its posteriormost 15 mm. The presence of this very delicate and long processus suborbitalis is a remarkable feature.

Comparison. – Mc Gowan (1973) gives no detailed description of the maxilla of *Ichthyosaurus*. Judging from the specimens figured by Conybeare (1822), Owen (1881) and Sollas (1916) and the skulls in the GPIT collection, the maxilla of SMNS 13111 is extremely similar to that of *Ichthyosaurus communis* but even more so to that of *I. intermedius* as figured by Conybeare (1822; see Figure 3). The short anterior extension, the marked increase in height below the external naris – as well as the exclusion from that aperture – and even the slight "kink" in the ventral margin of the bone visible at the point of its greatest height are also features which can be observed in Conybeare's specimen. In *Ichthyosaurus breviceps*, the maxilla appears to be smaller than in *I. communis*, being less more than a short triangular plate, visible below the external naris and not reaching much anteriorly beyond the anterior narial border. This is a clear difference to SMNS 13111 and *I. intermedius*.

In *Stenopterygius*, the maxilla is of variable shape. *Stenopterygius hauffianus* also usually has a very small, but rather high maxilla. In *Stenopterygius quadriscissus*, *S. cuneiceps* and *S. longifrons* the anterior extension beyond the external narial aperture is usually more considerable. A similarity between SMNS 13111 and *S. hauffianus* is the fact, that the maxilla is relatively high below the external naris as compared to the premaxilla. This contrasts with the situation usually seen in *Ichthyosaurus*. The very long and delicate suborbital process of the maxilla is not generally developed in *Stenopterygius*. I have only observed it so far in one juvenile specimen (GPIT Re 1297/1) in which the maxilla also reaches back almost to mid-orbital level. The long suborbital process is also lacking in the *Ichthyosaurus* specimens studied in great detail by Sollas (1916) and Mc Gowan (1973) and appears to be a peculiarity of SMNS 13111. Conybeare (1822: pl. 16, fig. 8) does, however, figure a skull referred by him to *Ichthyosaurus communis* which shows the same condition as SMNS 13111. The suborbital process is definitely broken off in his type specimen of *Ichthyosaurus intermedius*. It is therefore, in summary, not sure, whether the long suborbital process of SMNS 13111 can be regarded to be of diagnostic value. More complete and well-preserved material is needed to definitely decide this question, but because it is clearly an unusual feature it was included in the above preliminary specific diagnosis. Generally speaking, the maxilla of SMNS 13111 shows clear resemblances to those of *Ichthyosaurus communis* and *I. intermedius* but is not as different from that of *Stenopterygius hauffianus* as from the other species of this genus.

Nasal (Fig. 1). – The nasal is, as usual, a large bone. Its anteriormost portion – as it is visible because of the deformed state of much of the snout – is clearly merging below the premaxilla for a considerable distance. It reaches the surface of the snout ca. 105 mm behind the anterior tip. The nasal forms the posterior half of the dorsal margin of the external naris. It appears to possess a slightly developed processus narialis in the form of a strongly convex, rounded, ventrolateral emargination protruding into the narial opening, but because the whole region around the external naris is considerably deformed, this might be an artifact. Because of the presence of the processus narialis, the posterior portion of the naris is markedly constricted in SMNS 13111.

Posteroventrally the nasals are in contact with the lacrimals and prefrontals, forming more or less straight sutures with both these elements. It is interesting to note that the nasal hardly appears to reach the lacrimal at all, making only a very short sutural contact with that element. A much more complex suture that shows extreme interdigitation establishes the posterior contact with the postfrontal and frontal bones. The sutures are largely beyond recognition, much more so, as the region is strongly deformed, probably by an underlying bone element on which the skull roof bones were tightly pressed and crushed. It is, nevertheless, clear that the nasal almost reaches the parietal on the left side of the skull, coming close to the condition described by Godefroit (1993, 1994) as characteristic of *Stenopterygius longifrons* (but also observable in specimens of *Stenopterygius cuneiceps* pers. obs.) and the pattern seen in *Temnodontosaurus trigonodon* (pers. obs.), but no direct contact between these bones appears to be established. This can, however, not be determined with absolute certainty.

The left nasal bears a long and narrow depression near its lateral edge at the level of the prefrontal-postfrontal contact zone. It is bordered laterally by a prominent ridge, formed by a triangular shaped projection of the nasal. This feature appears to be natural rather than caused by deformation. Whether the dorsal depression of the nasals characteristically developed in *Stenopterygius* as an elongate and posteriorly deepening groove and in *Ichthyosaurus communis* as a short and well-marked, rounded deep pit (pers. obs.), best called the excavatio internasalis, was present in one way or the other in SMNS 13111 is not visible because of deformation.

Comparison. – In *Ichthyosaurus* and *Stenopterygius* the nasals are generally quite similar. The extent of the nasals onto the skull roof is variable in *Stenopterygius*. In some species it contacts the parietals (*S. longifrons*, *S. cuneiceps*), whereas in others, such as *S. hauffianus*, it does not. A processus narialis is never clearly developed in *Stenopterygius* or *Ichthyosaurus*, so this feature – if not an artifact – is peculiar to SMNS 13111. The suture between nasal and postfrontal, which is extensive in SMNS 13111, is much shorter in the *Ichthyosaurus* specimens figured by Mc Gowan (1973) but has a considerable extent onto the skull roof in the skull described by Sollas (1916), so this feature is evidently variable in that genus. Whether a foramen internasale, which is allegedly present in *Ichthyosaurus* according to Mc Gowan (1973) (although it has not been observed by Sollas 1916 in his serially sectioned specimen, and one of the Tübingen skulls, GPIT 1796/1, which is three-dimensionally preserved and very well prepared in the crucial area does not show it as well, the internasal suture being totally continuous within the excavatio internasalis) as well as in *Stenopterygius longifrons* according to Godefroit (1993, 1994) was developed in SMNS 13111, is not visible. It should be noted that from my own observations on excellently preserved three-dimensional skulls of *Stenopterygius*, including specimens of *Stenopterygius longifrons*, I cannot confirm Godefroit's observation of a foramen internasale in this taxon. I have never seen clear evidence for such an opening in any adequately preserved *Stenopterygius* skull, and – as noted above – I have also strong reason to believe that – if it exists at all – it is not a constant feature of *Ichthyosaurus* as well.

Lacrimal (Fig. 1). – The lacrimal of SMNS 13111 is a stout bone that largely forms the side wall of the skull between naris and orbit, best called the orbito-narial bar. It possesses two ventral extensions, best termed the processus ventralis anterior and posterior. The processus ventralis anterior apparently reaches the middle of the external naris, but – as described above – the suture with the premaxilla is not clear. The processus ventralis posterior takes part in the formation of the suborbital bar and is situated dorsal to the maxilla and jugal. It reaches back at least to the anterior third and possibly up to the middle of the orbit. It is, however, not clear, whether the apparent posterior extension of the process really belongs to the lacrimal or represents some displaced and deformed palatal bone. From the condition in other ichthyosaur specimens investigated I think that the latter is the more likely interpretation.

The lateral surface of the lacrimal is strongly constricted anteroposteriorly behind the external naris. The posterior margin of the lateral surface of the lacrimal is produced into a strong ridge, posterior to which the lacrimal slopes posteromedially to form the ventral half of the anterior orbital margin. The dorsal part of this sloping surface of the lacrimal is overlapped by a descending lamella of the prefrontal, called here the lamina orbitalis descendens. This condition is also seen in adequately preserved skulls of *Stenopterygius*, but mostly figured and described inaccurately in the literature. Mazin (1988) gives, however, an accurate figure. The prefrontal-lacrimal suture can be plainly seen and the lacrimal sends a small process dorsally, which intrudes into the anteroventral portion of the prefrontal. This lacrimal process separates an anterior lateral projection from the main body of the prefrontal, so that the dorsalmost part of the lacrimal appears to be sandwiched between this anterior process and the lamina orbitalis descendens of the prefrontal. Some 20 mm anterior to the posterior lacrimal ridge described above, the lacrimal apparently bears a deep sulcus which runs parallel to the posterior and posteroventral border of the naris. This structure is possibly a deformational artifact.

Comparison. – The lacrimal of SMNS 13111 compares closely to that of *Ichthyosaurus* as described by Mc Gowan (1973). The posterolateral lacrimal ridge and the short anteroposterior extension of the bone are very similar. The main difference is, that Mc Gowan's specimen lacks the processus ventralis anterior, but from personal observations of articulated *Ichthyosaurus* skulls I am inclined to think that it might be incomplete. This is also confirmed e. g. by the figures given by Conybeare (1822), particularly of *I. intermedius*, where the lacrimal is practically identical to that of SMNS 13111 except for the absence of the – probably artificial – sulcus in the anterior part of the bone apparently present in SMNS 13111. The contact between prefrontal and lacrimal can also be seen to be almost identical to SMNS 13111 in the specimen of *Ichthyosaurus communis* figured by Mc Gowan (1973, pl. 9) which was referred to *I. intermedius* by Owen (1881). The prefrontal does not appear to protrude comparably far ventrally in Mc Gowan's (1973) acid-prepared specimens. This might be due to individual or specific variation, incomplete preservation or preparational damage. In *Stenopterygius*, the lacrimal is also quite short anteroposteriorly, the posterolateral ridge is equally seen in most well-preserved specimens, including *Stenopterygius hauffianus*, and the processus ventralis anterior is usually well developed, so the lacrimal does not really help to elucidate the generic affinities of SMNS 13111.

Prefrontal (Fig. 1). – The prefrontal is – as far as it is visible – a rather small element that forms the dorsal half of the anterior and the anterior portion of the dorsal margin of the orbit. Anteriorly it contacts the lacrimal, as described above. The medial suture with the nasal is practically straight. The posterior contact with the postfrontal is more complex. The prefrontal is overlapped dorsally by the latter element for a considerable distance, thus excluding the postfrontal completely from the anterior half of the dorsal orbital margin. The lateral edge of the prefrontal is produced into a prominent shelf overhanging the orbit, which is separated from the main body of the first third of the bone by a slight depression. The external exposure of the prefrontal can be divided – as noted above – into the main body of the bone, best called pars supraorbitalis, a lamina orbitalis descendens which reaches down at least to the middle height of the orbit, and a small processus anterior which intrudes between the lacrimal and the nasal.

Comparison. – The prefrontal is much overlapped by the surrounding bones – mostly the nasal and the postfrontal and therefore appears to be somewhat variable in its externally visible extent on the skull roof – depending on the quality of preservation – in both *Ichthyosaurus* and *Stenopterygius* (Sollas 1916; Mazin 1988; Mc Gowan 1973; Godefroit 1993; pers. obs.). In both genera it usually forms at least nearly the anterior half of the dorsal orbital margin and possesses the lateral orbital shelf described above. What is unusual in SMNS 13111 is the fact, that the prefrontal almost totally excludes the lacrimal from the nasal. A similar condition is, however, rarely observed both in *Ichthyosaurus communis* and *Stenopterygius* (pers. obs.) so this feature cannot be considered as taxonomically important. The ventral extent of the lamina orbitalis descendens is also similar in both genera. It is much more considerable in some other taxa, particularly *Temnodontosaurus nuertingensis* (v. Huene, 1931) (Maisch & Hungerbühler 1997), where it almost reaches the ventral orbital margin.

Postfrontal (Fig. 1). – The size of the postfrontal is considerable. The bone appears much larger than the prefrontal. It forms the whole posterior half of the dorsal orbital margin and the entire anterior and – as far as it can be assessed – the whole anterior half of the lateral border of the fenestra temporalis. As described above, the sutures in the central portion of the skull roof are not clear because of deformation. Nevertheless, there is no doubt that the postfrontal reaches the frontal, although the zone of contact is not extensive. In lateral view, the postfrontal's posterior border apparently forms most of the bar between orbit and fenestra temporalis, but because e. g. in *Stenopterygius* there is generally a considerable overlap between postfrontal and supratemporal (pers. obs.), this must not really be the case. Generally the structure of the postfrontal is very similar to the situation described by Mazin (1988) in *Stenopterygius longifrons*, where the postfrontal also contributes considerably more to the formation of the lateral border of the fenestra temporalis than the supratemporal and is of very considerable extent. The postfrontal-supratemporal suture is clear in SMNS 13111 and shows a very complex interdigitation between these two bones. Contact with the postorbital is established posteroventrally only for a very short distance, the suture being quite simple. Like the prefrontal, the postfrontal also forms a prominent lateral shelf – the two shelves being in fact totally continuous – which laterally overhangs the orbit.

Comparison. – The postfrontal is not as different from Mc Gowan's (1973) acid-prepared specimens as it would seem if one compares his fig. 37. In fact, the bone is practically identical in shape and relationships to what is usually seen in articulated skulls of *Ichthyosaurus*. It is different from the majority of *Stenopterygius* species because of its very diminutive contact-zone with the frontal. *S. longifrons* and *S. cuneiceps* are, however, even more extreme in this respect, because in these species the contact between these two bones is totally lost. No taxonomically relevant information can thus be at present deduced from the postfrontal.

Postorbital (Figs. 1, 2). – The postorbital is incompletely preserved in this specimen. Its ventralmost portion is absent. The remaining portion forms the posterior margin of the orbit. Anterodorsally it is in short contact with the postfrontal and forms a long and posteroventrally curving suture with the quadratojugal and – at least originally – the squamosal, an element which can not be identified unequivocally in the specimen (see below). The prominent ridge that normally marks the dorsal zone of contact with the latter bones is not clearly visible because of the crushing of the whole temporal region. Generally, the postorbital is composed of two portions, a slender, massive bar of bone (pars postorbitalis) at the margin of the orbit and a thin posterior sheet which extensively overlaps the anterior portion of the quadratojugal (lamina posterior). The two parts are almost of equal size and width. It is interesting to note, that the lamina posterior apparently ends at the height of the ventral border of the quadratojugal, the anterior bar of the postorbital extending further ventrally for a considerable distance.

Comparison. – The postorbital confirms totally to Mc Gowan's (1973) description, with the one exception that the lamina posterior is slightly more developed in SMNS 13111. This is, however, the usual condition, as it is confirmed by Sollas (1916), Watson in Romer (1968) and pers. obs. It is noteworthy that Sollas (1916) describes a long posterodorsal process of the posterior lamina of the postorbital in his specimen. A similar shape of the postorbital was described by Sander (1989) in the Middle Triassic shastasaurid *Cymbospondylus buchseri*, and by Mazin et al. (1991) in the presumably Lower Triassic *Thaisaurus chonglakmanii*, in which the postorbital even is said to separate the supratemporal from the postfrontal (a condition otherwise not seen in any ichthyosaur, except for possibly *Grippia longirostris* and – strangely enough – the sectioned *Ichthyosaurus* skull described by SOLLAS in 1916!). It therefore appears to be an unusual and possibly primitive structure in ichthyosaur skulls. It is not mentioned to be present in the material studied by MC GOWAN (1973) and I have not observed anything similar in any *Ichthyosaurus* skull. The posterior lamina is also usually seen in *Stenopterygius*, although the postorbital is generally somewhat more slender, which corresponds to the shortening of the entire postorbital skull segment in this genus relative to *Ichthyosaurus*, and in this respect SMNS 13111 comes a little closer to the latter genus, although this resemblance is not a very important one.

Jugal (Fig. 1, 2). – The jugal is the usual slender bar of bone forming most of the ventral margin of the orbit. As described above, it contacts the maxilla and lacrimal anteriorly. It is a dorsoventrally compressed bar for most of its length but flares out somewhat dorsoventrally at the posteroventral corner of the orbit. It then curves upwards at an angle of 75° to 80° to the long axis of the skull and thereby forms a prominent "corner" very characteristic of most ichthyosaur skulls. For most of its length, the jugal bears a lateral ridge which divides into a dorsal and ventral ridge on the bone's broadened posterior portion. The ascending postorbital ramus of the jugal bears an anterior facet for the postorbital, the posterodorsal end of the bone is not preserved. The jugal is clearly in contact with the quadratojugal. The nature of this contact is, however, not completely obvious in the specimen, because the jugal appears to have slightly been displaced posteroventrally. It was by no means very extensive.

Comparison. – The jugal of SMNS 13111 is remarkable for its extremely slender and fragile build, in which respect it even surpasses most *Stenopterygius* skulls examined. The most considerable difference lies in the region where the ramus suborbitalis merges into the ramus ascendens (postorbitalis). This region is normally somewhat expanded in *Stenopterygius*, often by means of a small posteroventral flange, which is most conspicuous in fully adult individuals (MAISCH 1997). In SMNS 13111 this expansion is almost totally absent, which is more reminiscent of the situation in *Ichthyosaurus*, although a similar expansion can occur in large specimens of *Ichthyosaurus communis* (cf. e. g. CONYBEARE 1822). The dorsoventral compression of the jugal is, however, as GODEFROIT (1993) also noted, a feature normally distinguishing *Stenopterygius* from *Ichthyosaurus* and in this respect SMNS 13111 comes closer to the former. It is, however, not as considerable a difference as GODEFROIT assumes. The suborbital portion of the jugal in *Ichthyosaurus* e. g. cannot be described adequately as being "laterally compressed", because it is rather a more or less circular rod of bone for most of its length (cf. the cross-sections in SOLLAS 1916). The jugal figured by CONYBEARE (1822) in his type skull of *Ichthyosaurus intermedius* appears – judging from his illustration – extremely similar to that of SMNS 13111 (compare Figures 1 and 3), except that it has a much shorter anterior extension and ends below the anterior third of the orbit. This is almost certainly a misinterpretation, because in all other *Ichthyosaurus* skulls examined the jugal reaches at least to the level of the anterior orbital margin.

It is very noteworthy, that in *Stenopterygius* the jugal usually clearly extends a considerable distance beyond the anterior orbital margin and reaches at least the middle of the orbito-narial bar, whereas in *Ichthyosaurus* it does normally not extend beyond the orbit (this is, however, a variable feature the value of which is further limited because the jugal is one of the bones most easily displaced in compressed or even slightly disarticulated ichthyosaurian skulls). In this respect SMNS 13111 is clearly more similar to *Ichthyosaurus*. The very considerable depth of the jugal-quadratojugal notch brought about by the peculiar shape of the clearly offset, bar-like processus quadratus of the latter bone in *Ichthyosaurus*, and even more amplified in SMNS 13111 because of the dorsoventral shortening of the quadratojugal and the long and slender ramus ascendens of the jugal, which is almost perpendicular to the ramus suborbitalis, are further important features of SMNS 13111 which show its close affinities to *Ichthyosaurus*. Nothing similar was observed by me in any well-preserved *Stenopterygius* skull. It is, however, clearly approached by *Ichthyosaurus communis*, a fact that is well shown by articulated skulls of that species, and particularly the type skull of *Ichthyosaurus intermedius*, where the origin of the processus quadratus of the quadratojugal is equally situated at mid-orbital height (cf. CONYBEARE 1822, see Fig. 3). In summary it is therefore clear that the jugal of SMNS 13111 speaks much in favour of assigning the specimen to *Ichthyosaurus*.

Frontal (Fig. 1). – The frontals are small elements situated at the level of the anterior end of the fenestra temporalis or at half the length of the orbit respectively. They are much mutilated by lateral compression and it is not even unequivocal where the foramen parietale and the median suture are situated. Generally, most sutures in the whole region are difficult to discern. The naso-frontal suture is satisfactorily visible and the suture with the parietal appears to be represented by a rather straight line that curves gently in an anterolateral-posteromedial direction. The frontals taken as a unity send a lanceolate process anteriorly which separates the nasals for a considerable distance. The latter in turn extend backwards in the form of triangular processes which intrude between frontals and postfrontals.

Comparison. – As with the prefrontal, the extent of the frontal on the dorsal side of the skull roof in both *Ichthyosaurus* and *Stenopterygius* depends on how much of the overlapping bones is preserved, because the frontal is more or less considerably covered by the surrounding bones (SOLLAS 1916; MC GOWAN 1973; GODEFROIT 1993). In some specimens of *Stenopterygius longifrons*, the frontals are almost invisible on the dorsal skull roof, because they are reduced to extremely narrow strips of bone (GODEFROIT 1993, 1994; pers. obs.). Normally, however, the frontals are small, more or less lanceolate elements in that genus, forming the anterior and in many cases the lateral borders of the foramen parietale. This is especially true for *Stenopterygius hauffianus* and *Stenopterygius quadriscissus*, where the frontals are of "normal" size and establish a comfortable contact with the postfrontals (GODEFROIT 1994 and pers. obs.). In *Ichthyosaurus* the extent of the frontals is also variable, but usually they appear as very small rounded elements practically surrounding the entire foramen parietale. The investigations of both SOLLAS (1916) and MC GOWAN (1973) are very instructive concerning the discrepancy between the apparent and the real extent of the interorbital skull roof bones in *Ichthyosaurus*. An important difference between *Ichthyosaurus* and *Stenopterygius* is, that in the latter genus the frontals are normally elevated considerably above the general surface of the interorbital skull roof. This can only be seen adequately in three-dimensionally preserved specimens. SMNS 13111, which is strongly compressed laterally, shows small frontals which are, however, not strip-like but rounded. The parietals, which are better preserved, appear to have a totally continuous median suture which indicates that the foramen parietale was situated entirely within the frontals, as usual in *Ichthyosaurus*, but similar specimens of *Stenopterygius* – particularly *Stenopterygius quadriscissus* – do exist (e. g. SMNS 51515, a three-dimensional skull which also shows the frontal elevation in a perfect manner) and evidence is therefore rather equivocal.

Parietal (Fig. 1). – The parietals are large elements which form most of the medial borders of the fenestrae temporales. Both the left and the medial portion of the right parietal are visible. The median parietal suture is very distinct. It is bordered by slightly raised margins and takes a rather strongly sigmoidal course. The parietals are very compressed and numerous cracks run through the bones, so the suture with the ramus medialis of the supratemporal is not completely clear, but can be guessed at with a great degree of certainty from the general shape of the bones. It appears as if the supratemporals reach far towards the midline of the skull, as it is also the case in specimens of *Stenopterygius longifrons* investigated (such as SMNS 9130 and SMNS 18012 determined by me and herewith referred to this species) but not recorded in *Ichthyosaurus* by either SOLLAS (1916) or MC GOWAN (1973). One of the skulls of *Ichthyosaurus communis* in the GPIT collection (1796/1) shows, however, also a remarkably long ramus medialis. In lateral view the parietal is a more or less triangular, posteriorly inclined plate. A conspicuous ridge is visible at about the half of its length on the portion of the left parietal forming the medial temporal wall. This might be a preservational artifact. As described above, the parietal forms a small medial anterior process which is almost reaching the nasal.

Comparison. – Although they are not too well preserved, the parietals of SMNS 13111 are clearly relatively short and broad elements. The parasagittal ridges along the suture, which is not essentially straight but rather somewhat interdigitating and curved, are considerably roughened. The bone does not reach far forwards alongside the frontal, but is ending in a rather straight transversal suture anteriorly. All these features are found in *Ichthyosaurus* and *Stenopterygius* specimens, but the parietal appears to be generally a little more slender and elongate in dorsal view in the majority of *Stenopterygius* skulls investigated, than it probably was in SMNS 13111, and the median suture is generally straighter. This is especially true for well preserved specimens of *Stenopterygius hauffianus*. These features do, however, not appear to be of great taxonomic value, as they are rather variable. The shape of the bones and the apparent course of the suture in a compressed specimen such as SMNS 13111 are at any rate not very reliable characters, anyway.

Supratemporal (Fig. 1). – The supratemporal in SMNS 13111 is a large element that forms part of the posterior and posterolateral border of the fenestra temporalis. Its sutures with the postfrontal and postorbital are completely clear and have been described above. The ramus medialis is stout in its lateral, but slender and rodlike in its medial portion. The ramus anterior is practically non-existing in external view. The bone is probably largely overlapped by the postfrontal. The extent and shape of the posteroventral part and ramus occipitalis of the supratemporal are impossible to determine with certainty and the ventral suture of the bone cannot be followed unequivocally because the entire dorsal cheek region is practically destroyed, because it was pressed onto a displaced bone of the braincase, possibly a stapes or opisthotic, the contours of which are clearly visible through the dermal skull bones. It is therefore also not possible to tell unequivocally whether SMNS 13111 originally possessed a separately ossified squamosal. The presence of this bone which has now been identified in a large number of Triassic and post-Triassic taxa, e. g. *Stenopterygius longifrons* (Owen 1881; Fraas 1891; v. Huene 1952; Godefroit 1993, 1994; Maisch 1997) and *Ophthalmosaurus icenicus* (Maisch in press b) has yet to be unequivocally demonstrated in *Ichthyosaurus*. In SMNS 13111 no clear traces of it are seen, but it is clearly present e. g. in the well preserved skull GPIT 1796/1, so that there is little doubt that a separate squamosal was also usually present in *Ichthyosaurus*. The bone labelled "squamosal" in SMNS 13111 by v. Huene (1922) is in fact the lamina posterior of the postorbital.

The lateral rim of the fenestra temporalis is considerably roughened and forms a conspicuous ridge that overhangs the lateral wall of the cheek. This is a general feature of well preserved *Stenopterygius* and *Ichthyosaurus* skulls. The ridged portion of the bone was interpreted as the entire supratemporal in SMNS 13111 by v. Huene (1922) and a suturelike crack is actually visible below the anterior end of the ridged area, but it cannot be followed posteriorly so it is concluded that no division is actually present.

Comparison. – SMNS 13111 differs from most specimens of both *Ichthyosaurus* and *Stenopterygius* in the extreme shortness of the externally exposed ramus anterior of the supratemporal. The long and slender process described by Mc Gowan (1973) to be present in that position in *Ichthyosaurus* is not developed. In *Stenopterygius* the anterior extent of the supratemporal is rather variable, as is the exact course of the anterior suture of that bone, but it also usually extends much further anteriorly than in SMNS 13111, which in this respect comes closest to the species currently known as "*Leptopterygius*" *integer* (Bronn, 1844) and particularly some specimens of *Stenopterygius longifrons* (Mazin 1988; pers. obs.). The strong development of the dorsolateral supratemporal ridge also is a remarkable feature and I cannot recall having seen it so well developed in any other Liassic ichthyosaur skull. Therefore, in summary, the structure of the supratemporal appears to be quite peculiar in SMNS 13111 and might even prove to be a diagnostic feature when more material becomes available.

Quadratojugal (Figs. 1, 2). – It cannot be made out whether the lower part of the cheek region is made up of one or two bones in SMNS 13111, so the entire area is here described under the heading "quadratojugal". The extent of this bone cannot be determined completely in SMNS 13111, but its suture with the postorbital is clear. The bone possesses an unusually strong and markedly curved posteroventral process that is situated at the level of the preserved dorsal end of the ramus ascendens of the jugal and protrudes 5 mm beyond the posterior margin of the main body of the quadratojugal. This process establishes contact with the quadrate anterodorsal to the latter's condylar area, the contact surface is concave on the quadratojugal. The processus quadratus is situated far more dorsal than in most other ichthyosaurs, at about mid-orbital height. Dorsal to the processus quadratus the posterior rim of the quadratojugal, which forms the anterior margin of the foramen quadrati between quadratojugal and quadrate, is strongly concave, indicating that the foramen was of considerable size. The ventral border of the bone, as far as it is visible, is slightly concave anterior to the processus quadratus, so that the latter is clearly set off from the main body of the bone as a short posteroventrally directed strut. The entire quadratojugal is very short dorsoventrally and its area of contact with the ramus ascendens of the jugal cannot have been extensive.

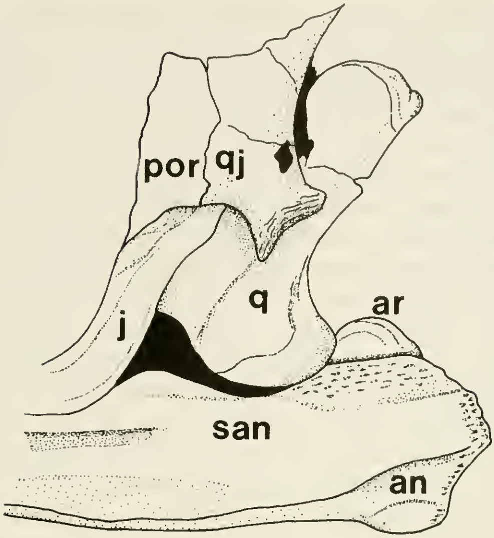

Fig. 2. Sketch of the cheek region of SMNS 13111 in more detail and under a slightly different angle. Not to scale. Abbreviations: ar = articular, otherwise as in fig. 1.

Comparison. – The very short quadratojugal with its strut-like and clearly offset, totally posteroventrally directed processus quadratus, which bears a distinct, somewhat concave facet for contact with the quadrate, and the extreme depth of the jugal-quadratojugal notch are all features which most clearly indicate a close relationship between this specimen and *Ichthyosaurus*. Except for its extreme shortness, the quadratojugal of SMNS 13111 agrees well with the descriptions of WATSON in ROMER (1968) and MC GOWAN (1973), and personal observation as well as the literature (OWEN 1881) show, that articulated skulls of *Ichthyosaurus communis* possess a cheek region which is virtually identical to that of SMNS 13111. The best figure of an isolated quadratojugal of very characteristic shape, showing all the peculiarities of this bone in *Ichthyosaurus* in almost overexaggerated form, is given by SOLLAS (1916), but already CONYBEARE (1822) and OWEN (1881) have provided very good figures. The type specimen of *Ichthyosaurus intermedius* comes even closer to the condition exhibited by SMNS 13111 than *Ichthyosaurus communis* in that the processus quadratus is also situated at half orbital height in that specimen. This is a peculiarity shared by the two specimens which I consider to be of diagnostic value at the specific level.

Stenopterygius – in contrast to this – has a quadratojugal which is much narrower anteroposteriorly than in *Ichthyosaurus* and SMNS 13111 because of the shortening of the postorbital skull segment. The processus quadratus is generally similar but different in detail from that in *Ichthyosaurus*. It is directed more posteromedially instead of posteroventrally and is not as clearly set off from the rest of the bone, because the ventral margin of it is not more or less concave as in *Ichthyosaurus* but quite straight or even somewhat convex, an important feature already noted by v. HUENE (1951). The process in both genera rests in a well-marked facet on the anterolateral surface of the quadrate, which is not far above the condylar area. Contact must have been established further dorsally in SMNS 13111 and probably also in Conybeare's skull of *Ichthyosaurus intermedius*. In *Stenopterygius*, the processus quadratus is in its entirety rather hook-shaped with a concave dorsal border (see Maisch 1997, fig. 4), and not so strut- or bar-like as in *Ichthyosaurus*, coming closer to what is seen in *Temnodontosaurus* and *Eurhinosaurus*, although shorter – in correlation to the narrower occipital width of the skull in *Stenopterygius* – and weaker – which might be correlated to absolute size. All these features have in large parts already been recognized by v. Huene (1951). The shape and relationships of the quadratojugal in SMNS 13111 are, in summary, strongly indicative of the specimen belonging to the genus *Ichthyosaurus*.

Quadrate (Figs. 1, 2). – The quadrate is not visible in its entirety. It is partly covered by the jugal and quadratojugal, but because of posteroventral displacement most of it can be seen, more in anterior than in lateral view. It is a more or less flat plate of bone with a slightly thickened dorsal and a considerably thickened ventral edge, the latter representing the condylar area. The dorsal flange is quite broad and short. The articular surface is situated on both the ventral and posteroventral edges of the bone, but as Mc Gowan (1973) has demonstrated in *Ichthyosaurus*, probably only the posterior portion was in contact with the articular. The condyle itself is convex anteroposteriorly and more or less flat mediolaterally, being clearly separated from the anterior and posterior surfaces of the bone. The lateral edge of the quadrate is very thin and sharp-edged, and the whole dorsal blade slightly curves posteriorly, thus forming the posterior margin of the foramen quadrati. This curvature is, however, far less considerable than in most other ichthyosaur skulls examined. The quadrate of SMNS 13111 is very similar to the left quadrate described and figured by E. Fraas (1891, p. 14, pl. 5, fig. 5) from the Upper Lias of Whitby as belonging to "*Ichthyosaurus quadriscissus*" and later referred to as "Ichthyosauria gen. et sp. indet." by Mc Gowan (1978, p. 1155).

Comparison. – The quadrate of SMNS 13111 clearly differs from that described and figured by Mc Gowan (1973) in having a somewhat more expanded dorsal blade and a very narrow lateral edge. In this respect, as well as in its general gracile build and little posterior curvature, it is also quite different from all *Stenopterygius* specimens investigated, in which the lateral edge of the bone is also rather broad and bluntly rounded. The thin and fragile dorsal flange of the quadrate is therefore a peculiarity of SMNS 13111 and considered here as a diagnostic character.

Epipterygoid (Fig. 1). – None of the occipital, brain case and palatal bones are visible or identifiable in SMNS 13111 except for a fragment of bone lying within the interior aperture of the sclerotic ring. This is very probably the ventral portion of the left epipterygoid which in that case would have been rotated for 180°, showing its medial surface. It is practically identical to the epipterygoid figured by Mc Gowan (1973) in *Ichthyosaurus* and clearly differs from the epipterygoid of *Stenopterygius longifrons*, described by v. Huene (1949) by the lack of a pronounced posteroventral heel.

Dentary (Figs. 1, 2). – The dentary – which is by far the most extensive and longest bone of the mandible in lateral aspect – possesses a series of longitudinal furrows similar to those seen in the premaxilla. The first, right at the anterior end of the bone, is rather a groove 12 mm long, but there follow three much shorter depressions which have much more the appearance of foramina, and there can be little doubt that they served for the transmission of nerve fibres and/or blood vessels. Behind these, there are three more grooves of 3, 8 and 20 mm in length respectively. The third of them ends 103 mm behind the anterior tip of the dentary. Further posteriorly there is no furrow or depression at all and the lateral surface of the dentary is completely smooth. The dentary bears 30 visible teeth, but the posterior part of the tooth row is obscured by the maxillary teeth, and probably more than 45 are actually present. They are in a truly excellent state of preservation. The posterior sutures with the surangular and angular, which are somewhat serrated, are perfectly visible. The dentary reaches back to the level of the middle of the orbit with a posterodorsal spur that overlaps the anterodorsal edge of the surangular. The dentary terminates at exactly the same point where the maxilla ends in the upper jaw.

Comparison. – The dentary of SMNS 13111 is clearly most similar to that of *Ichthyosaurus communis* and *Ichthyosaurus intermedius*. It differs considerably from *Stenopterygius* in the lack of a continuous fossa dentalis. This fossa is – as the fossa praemaxillaris – a well-developed deep groove in *Stenopterygius*; a feature which does not exhibit any considerable variation. The fossa dentalis reaches back almost to the posterior end of the dentary and is therefore nearly confluent with the fossa surangularis in *Stenopterygius*. This condition is not shown in any *Ichthyosaurus* skull known to me or described in the literature, instead there is a more or less discontinuous system of short and often somewhat anastomosing grooves, furrows and foramina in the dentary of that genus, usually arranged more or less roughly in a row. This was already well illustrated by OWEN (1881).

The dentary of SMNS 13111 is very different from that of *Stenopterygius hauffianus* in that it is not nearly as gracile and slender in its anteriormost portion as it is typical of this species, and the anterior dentary teeth are not considerably smaller than those in the more posterior sections of the lower tooth row. All this evidence taken together with the similar situation concerning the premaxilla (see above) provides the strongest arguments against any close relationship of SMNS 13111 to *Stenopterygius* in general and *Stenopterygius hauffianus* in particular (it should be noted that immature specimens such as GPIT Re 1297/1, probably referable to *Stenopterygius quadriscissus*, show an anterior snout region totally similar to what is typically seen in *Stenopterygius hauffianus*, they are, however, easily distinguishable by their proportionally much longer snouts).

Splenial (Fig. 1). – In lateral view the splenial, which is a very large element on the medial side of the ichthyosaurian mandible in general, is only visible as a narrow spur of bone on the ventral edge of the jaw from about the middle of the orbit to the anterior edge of the naris.

Angular (Figs. 1, 2). – The angular is seen in lateral view as a rather thin strip of bone which forms the ventral jaw margin from about mid-orbital length to the posterior extremity of the mandible. Anteriorly it – externally – contacts the dentary and splenial, dorsally the surangular. In its posteriormost portion the angular becomes somewhat higher in lateral view, but forms far less than one third of the height of the posterior portion of the lower jaw. There is also no strong curvature of the surangular-angular suture at about the level of the coronoid process. Instead, the suture merely takes a somewhat sigmoidal course in that area. The angular appears to form a slight ventrolateral projection of 15 mm in length at its posterior end, which might be a preservational artifact. The posterior and posteroventral edges of the angular are roughened, probably due to insertion of the musculus pterygoideus.

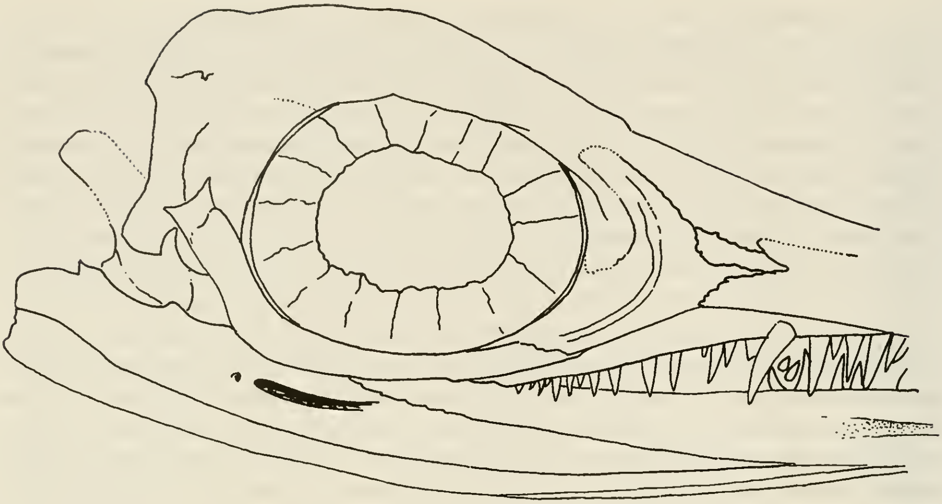

Fig. 3. Sketch of the holotype skull of *Ichthyosaurus intermedius* CONYBEARE, 1822; redrawn from CONYBEARE (1822). – x 0,45 (teste CONYBEARE).

Comparison. – A very conspicuous difference between *Ichthyosaurus* and *Stenopterygius* in the morphology of the lower jaw is the fact that the surangular-angular suture in the latter genus curves strongly dorsally at about the level of the coronoid process, so that in the posteriormost portion of the lower jaw practically the entire ventral half of the lateral mandibular surface is formed by the angular. In *Ichthyosaurus* the angular-surangular suture more or less parallels the ventral margin of the mandible for its entire length and curves dorsally only very slowly, so that even at the posterior end of the lower jaw the angular usually forms half of the lateral mandibular surface at maximum. At any rate, the conspicuous kink of the suture so characteristic of *Stenopterygius* – it appears to be present in all adequately preserved specimens investigated, which are more than 100, independent of the stage of ontogenetic development – is never developed in *Ichthyosaurus*. It is evident, that in this respect SMNS 13111 is much more similar to *Ichthyosaurus* than to *Stenopterygius*.

Surangular (Figs. 1, 2). – The surangular of SMNS 13111 is excellently preserved. It is remarkable that the lateral deep groove usually present in ichthyosaurs – best termed the fossa surangularis – which is situated at probably half the height of the laterally exposed surface of the bone, is very short, only 30 mm in length, in the present specimen. It starts at the mid-orbital level where contact with the posterodorsal spur of the dentary is established, and ends very abruptly posteriorly. It is demarcated for its entire length by a conspicuous dorsal ridge and a ventral lateral convexity of the surangular. The function of this groove is not clear. It was probably no area of muscle attachment since the dorsal ridge which borders it does also overhang it to some degree and the muscle fibres approaching it dorsally would have to wrap around that ridge. There are also no scars or roughenings visible. The fossa surangularis is pierced by foramina in *Ichthyosaurus* (MC GOWAN, 1973), but this is not generally the case. Foramina of this kind do not appear to be found in *Stenopterygius*, as well as in *Ophthalmosaurus*, but they definitely occur in *Temnodontosaurus*

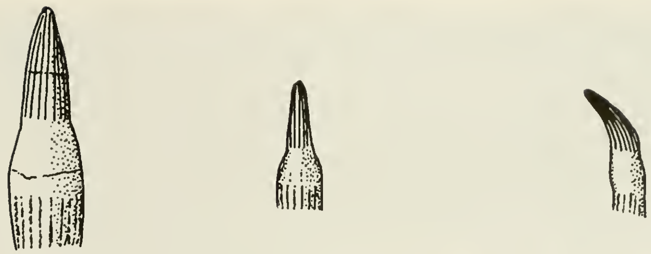

Fig. 4. SMNS 13111. A: premaxillary tooth, B: middle maxillary tooth, C: posterior maxillary tooth. About twice natural size.

trigonodon (pers. obs.). The posterior – retroarticular – portion of the surangular is strongly roughened in a similar way as the posteroventral portion of the angular, indicating an area of muscle attachment, probably of the musculus depressor mandibulae. The coronoid process of the surangular is not visible, because it is covered by the expanded posteroventral portion of the jugal, but it is obvious that the dorsal contour of the surangular is markedly ascending in its direction, indicating that it was well developed.

Comparison. – The surangular of SMNS 13111 is more similar to *Ichthyosaurus* than to *Stenopterygius* because of the presence of a very short fossa surangularis which is practically confined to the middle third of the lateral exposure of that bone and is deepest below the processus coronoideus. The same is described for *Ichthyosaurus* by Mc Gowan (1973) and was already well figured by Conybeare (1822) and Owen (1881). In *Stenopterygius* the fossa surangularis extends usually much further anteriorly. It is often not very clearly demarcated in its posterior part but becomes gradually shallower. This must, however, not be the case. It is almost confluent with the fossa dentalis in all specimens examined. The posterior extent of the fossa surangularis is comparable in both genera. Unfortunately it is not visible in SMNS 13111 if there were any foramina piercing the fossa surangularis. The small foramen posterior to the fossa which is shown in the type skull of *Ichthyosaurus intermedius* (Fig. 3) is clearly absent.

Articular (Figs. 1, 2).- Only a slight dorsal portion of the articular is visible. It shows a slightly concave lateral surface and a roughened and narrow dorsal and posterodorsal edge.

Sclerotic plates (Fig. 1). – The enormous sclerotic ring which appears to be practically entirely filling the orbit (which is, however, an incorrect impression caused by flattening, cf. Mazin 1988) is quite well preserved, but its posterior half is somewhat distorted and its anterior half completely flattened. It consists of at least 15 plates, probably more, the exact number is not determinable because the dorsal and posterodorsal plates are too damaged to count reliably. Inside the sclerotic ring there is a slender rod of bone 21 mm long and 8 mm broad, identified above as the left epipterygoid. The internal opening of the sclerotic ring is of moderate size, about one third the diameter of the orbit. The sclerotic plates themselves are of the usual

Fig. 5. Photograph of SMNS 13111. Scale bar 100 mm.

form bearing fine radial striations. They considerably overlap each other and show serrated sutures.

Comparison. – The internal diameter of the sclerotic ring in relation to the length of the lower jaw is about 0.89 in SMNS 13111. This is in excess of what is seen in practically all specimens of *Stenopterygius* and at the extreme margin of variability recorded for *Stenopterygius hauffianus* (0.084 +/– 0, 0043) by Mc Gowan (1973). It is, however, a normal value for a specimen of the genus *Ichthyosaurus*. In *Ichthyosaurus communis* e. g. the ratio can far exceed 0.095 (Mc Gowan 1974a).

Dentition (Figs. 1, 4). – The teeth of SMNS 13111 are closely spaced in both upper and lower jaws. The tooth rows appear to be totally complete. Replacement teeth are frequently seen. Most teeth are not displaced in any way, thus not the least sign of tooth reduction can be recognized. In the posterior part of the maxilla the upper teeth considerably diminish in size. They are only half as big as the anterior premaxillary teeth and also strongly recurved (Fig. 4 C), whereas the more anterior teeth in both jaws are essentially straight, showing only a slight lingual curvature (Fig. 4 A-B). The enamel of the crowns is heavily crenulated, but there is no development of mesial or distal carinae. There is a distinct smooth, unsculptured "neck" between the striated crown and the equally striated root. The roots appear to be slightly, but sometimes, especially in the maxillary dentition, rather abruptly expanded (Figure 4 B). The dentition of SMNS 13111 obviously represents an almost ideal device to catch slippery and actively struggling prey.

Comparison. – The teeth of *Ichthyosaurus* have been well described by numerous authors (e. g. Conybeare 1822; Owen 1881; v. Huene 1922; Mc Gowan 1973, 1974 a). In *Ichthyosaurus communis* and *I. breviceps* they are rather stout and conical in shape, bear very heavy striations and have considerably expanded roots. They are somewhat more slender and delicate in the tenuirostrine *Ichthyosaurus conybeari*. The very long and slender teeth of SMNS 13111 with their only slightly but rather abruptly expanded roots and their well-marked but not unusually heavy striations are therefore not typical of the genus. They are admittedly more typical of teeth seen in some species of *Stenopterygius*, particularly *S. longifrons* and juveniles of *S. quadriscissus*, although these tend to be less coarsely sculptured. The dentition is – as already noted – very different from that of *S. hauffianus*, however, because the teeth do not decrease markedly in size towards the tips of the jaws, as it is characteristic of that species.

The shape of the teeth definitely is practically identical to those described, figured and considered diagnostic of *Ichthyosaurus intermedius* by CONYBEARE (1822), and they provide a strong argument for identification of SMNS 13111 with that species. The very high number of maxillary teeth – 26 – is, according to MC GOWAN (1974a) by far in excess of what is known of all hitherto described species of *Ichthyosaurus*, except for *Ichthyosaurus conybeari* which is known to have more than 18 teeth in the maxilla, the maximum number recorded in *I. communis* (MC GOWAN 1974a). In *Stenopterygius hauffianus* I have personally never observed more than 15 maxillary teeth, and this might come close to the maximum number present in that species. MC GOWAN, however, appears to have overlooked the fact that CONYBEARE's figure (1822, pl. 17, compare Fig. 3) of *Ichthyosaurus intermedius* shows 18 maxillary teeth still in place and – judging from the gaps present in the tooth row of that specimen, which shows a dentition far more disturbed than does SMNS 13111 – it is evident that at least seven more teeth must have been present originally (compare Figure 3). This would provide CONYBEARE's specimen with a maxillary tooth count of certainly > 20 (some of the smaller teeth actually might only represent replacement teeth), which is much closer to SMNS 13111 than that of any other *Ichthyosaurus* specimen I know. It is therefore not only the shape, but also the number of teeth which link the two specimens. It should be noted that CONYBEARE's specimen shows the same abrupt size decrease of the suborbital teeth, which also appear to be slightly recurved, as in SMNS 13111 (cf. Fig. 3).

3. Discussion

From the above description and comparison of SMNS 13111 it is obvious that the specimen has much more in common with *Ichthyosaurus* than with *Stenopterygius*. Only the dorsoventral flattening of the ramus suborbitalis of the jugal and the relatively high maxilla can be cited as features more similar to the latter genus. In contrast to this, the discontinuous and short fossa dentalis and fossa praemaxillaris, the short anterior portion and long processus suborbitalis of the maxilla, the slenderness, anterior extent and general shape of the jugal, the structure of the entire cheek region of the skull, particularly the quadratojugal and its characteristically shaped processus quadratus, the shortness of the fossa surangularis and the lowness of the posterior portion of the angular as well as the course of the angular-surangular suture and the shape of the teeth are all features which do occur very similarly in Lower Liassic specimens of *Ichthyosaurus* but are not known in *Stenopterygius*.

The assignment of the specimen to *Stenopterygius hauffianus*, as originally proposed by v. HUENE (1922) must be rejected because of the above general and the following more specific differences: both the dentary and the premaxilla are quite robust bones throughout their entire length, their tips are not particularly slender or low, the teeth in the tips of the jaws are not remarkably diminished in size and are far bigger than one half the size of the more posterior dentary or upper jaw teeth, the orbital ratio as defined by GODEFROIT (1994) is less than 0.37 (0.36), the maxillary tooth count is 26, which is far in excess of any known specimen of *S. hauffianus*. It appears therefore highly probable that SMNS 13111 is a representative of the genus *Ichthyosaurus* DE LA BECHE & CONYBEARE, 1821.

Other valid ichthyosaur genera known from the Lias of Europe are *Leptonectes* Mc Gowan, 1996, *Excalibosaurus* Mc Gowan, 1986, *Eurhinosaurus* Abel, 1909, constituting the family Leptonectidae (fam. nov. in Maisch, in press a), and *Temnodontosaurus* Lydekker, 1889 of the family Temnodontosauridae Mc Gowan, 1974. All these genera are so considerably different from SMNS 13111 as to totally exclude any possibility of identification. All leptonectids are characterized by their extremely long and slender snouts, their extremely shortened postorbital skull segment, very small temporal fenestrae and their absolutely very large round orbits, amongst other features. SMNS 13111 is obviously very different from these animals.

Temnodontosaurus is still a rather heterogeneous assemblage. The typical forms – as exemplified by *T. platyodon* and *T. trigonodon* – are characterized by their relatively small orbits, their long and very robust snouts, extremely robust lower jaws, very long postorbital skull segment and bi- to quadricarinate teeth in adult individuals, amongst other features. The aberrant *Temnodontosaurus eurycephalus* is even more different from SMNS 13111 because of its extremely high and strongly built snout with very few strong and large teeth, which is unparalleled in other ichthyosaurs. It is therefore obvious that SMNS 13111 can, amongst Liassic ichthyosaurs, only be referred to *Ichthyosaurus*.

Four species of *Ichthyosaurus* are currently recognized. Two of these, the Triassic *I. janiceps* Mc Gowan, 1996 and the Lower Liassic *I. breviceps* Owen, 1881 are readily distinguishable from SMNS 13111 because of their much higher and more robust snouts which give the entire skull an almost triangular outline in lateral view. *I. breviceps* is furthermore distinguished by its few maxillary teeth (never exceeding 15 to my knowledge). The number of maxillary teeth is not known in *I. janiceps*, but Mc Gowan's (1996) figures show 5 still in place and it is hardly imaginable from the size of these and the length of the entire maxilla that more than 15 teeth were originally present in the type and only known specimen of that species. *I. conybeari* has a higher maxillary tooth count than the other species, the number of maxillary teeth exceeding 18, but it differs from SMNS 13111 considerably in its very slender, tenuirostrine snout with longer premaxillary segment and smaller internal sclerotic ring diameter. SMNS 13111 is within the range of *Ichthyosaurus communis* as given by Mc Gowan (1974a) considering all important skull proportions, but differs considerably from that species by its very high maxillary tooth count of 26, the maximum recorded in *I. communis* being 18. It is also different from this – and probably the other, inadequately described, species – in the very short and reduced quadratojugal that reaches just downwards to half orbital height, the shape of the long and slender, relatively gently sculptured teeth and – possibly – the extremely long processus suborbitalis of the maxilla that reaches to mid-orbital length (but see Conybeare 1822). Bearing these differences in mind and considering the exact resemblances between SMNS 13111 and the type-skull of *Ichthyosaurus intermedius* Conybeare, 1822, it appears justified not only to reestablish that species, which was sunk into *Ichthyosaurus communis* by Mc Gowan (1974a) without a precise discussion of the dental and cranial characters of the two species, but also to refer SMNS 13111 to that taxon. Appleby (1979) equally argued – along a different line of reasoning – for the retention of *Ichthyosaurus intermedius*. Should the specimen ever prove to come from the Toarcian of Whitby, it would be the most geologically recent representative of the family Ichthyosauridae, and it would then possible represent a distinct species. Yet, because information on the provenance of the specimen is so scanty, as discussed above, I prefer to take a conservative course and assume that the Upper Liassic age has been mistakenly assigned to it.

Acknowledgements

I greatly acknowledge the friendliness of Dr. Rupert Wild, Stuttgart who made the entire ichthyosaur collection of the SMNS accessible for this study, as well as Dr. Olivier Rieppel, former director of the museum, who tolerated me for months dealing with the valuable specimens. Dr. Wild helped with literature – and much more. Dr. Ronald Böttcher was also very helpful due to his long ichthyosaurological experience and always had an open ear for discussion. Dipl. Geol. Rainer R. Schoch, Martin Rücklin, Andreas Matzke and Matthias Kröner (all Tübingen) and especially Dipl. Geol. Axel Hungerbühler (Bristol) contributed much to this study either directly or indirectly. Dr. Rupert Wild and Dr. Gert Bloos (Stuttgart) critically read earlier drafts of this manuscript. Andreas Matzke kindly took the photograph.

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