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Revision of *Temnodontosaurus nuertingensis* (v. Huene, 1931), a large ichthyosaur from the Lower Pliensbachian (Lower Jurassic) of Nürtingen, South Western Germany

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With 1 figure

Summary

The holotype and only specimen of the large Lower Jurassic ichthyosaur *Leptopterygius nuertingensis* v. Huene, 1931 is redescribed in order to clarify the taxonomic status of this species and its affinities to other known ichthyosaur taxa. It was considered a nomen dubium by Mc Gowan (1979) but the validity of the taxon is confirmed by the morphology of the palate, maxilla and dentition. It shows close affinities to the genus *Temnodontosaurus* Lydekker, 1889 from the Lower Jurassic of Europe. It is, however, clearly different from any hitherto described species of that genus and it is thus referred to the genus as a fourth valid species, *Temnodontosaurus nuertingensis* (v. Huene, 1931) comb. nov.

Zusammenfassung

Der Holotypus von *Leptopterygius nuertingensis* v. Huene, 1931, das einzige bekannte Exemplar dieser Art, wurde neu untersucht, um den taxonomischen Status der Art und ihre Verwandtschaftsbeziehungen zu anderen bekannten Ichthyosauriertaxa zu klären. Die Art, die von Mc Gowan (1979) als nomen dubium aufgefaßt wurde, ist zweifellos valid, was sich an Merkmalen von Gaumen, Maxillare und Bezahnung ablesen läßt. Sie weist die größte Ähnlichkeit zur Gattung *Temnodontosaurus* Lydekker, 1889 aus dem Unterjura von Europa auf. Sie ist indessen deutlich verschieden von allen bisher beschriebenen validen Arten dieser Gattung und wird der Gattung daher als vierte valide Art, *Temnodontosaurus nuertingensis* (v. Huene, 1931) comb. nov., zugeordnet.

1. Introduction

In the marine Lower Jurassic strata of Europe ichthyosaurs are a diverse and numerous group of tetrapods (Owen 1881; Fraas 1891; v. Huene 1922, 1931 a; Mc Gowan 1974 a, 1974 b, 1979). They are known mainly from many finds of articulated skeletons in the pre-Hettangian to Sinemurian strata of Great Britain (Owen

1881; v. HUENE 1922; MC GOWAN 1974 a, 1974 b) and the Toarcian of both Great Britain and Germany (FRAAS 1891; v. HUENE 1922, 1931 a; MC GOWAN 1974 a, 1979; BENTON & TAYLOR 1984). A large gap in the fossil record of European Lower Jurassic ichthyosaurs does, however, exist in the Middle Lias (Pliensbachian). Although there are several specimens, especially from southern Germany (QUENSTEDT 1865–66; FRAAS 1891, 1892; v. HUENE 1922, 1931 b), most of these consist of isolated cranial or postcranial fragments which do not show any diagnostic features. The reason for the rarity of well preserved articulated remains of ichthyosaurs in the Middle Lias of southern Germany lies mainly in the low fossilization potential of the sediments deposited throughout this time interval, at least concerning articulated vertebrate remains. Another reason is the scarcity of outcrops in these strata, which are not of much economic interest and are almost never naturally exposed on a larger scale.

The holotype of *Leptopterygius nuertingensis* v. HUENE, 1931 is a very important specimen that represents the only reasonably well preserved ichthyosaur from the Pliensbachian of Germany. Thus it serves to close the chronological gap between the rich ichthyosaur faunas of the Lower and Upper Lias. Since v. HUENE's original description, a detailed restudy of the specimen has never been done. Because the species was prematurely discarded by MC GOWAN (1979), the first step towards a better understanding of this animal is to address the question of its taxonomic status and systematic affinities. The purpose of this paper is to clarify these problems as far as possible and to provide a short rediscription of the cranial osteology.

2. Material

The material investigated for this study includes the following specimens:

SMNS 13488	Holotype of *"Leptopterygius" nuertingensis* v. HUENE, 1931
SMNS 15390	Holotype of *"Leptopterygius" disinteger* v. HUENE, 1926
SMNS 13128	Three dimensional skull of *Temnodontosaurus burgundiae* (GAUDRY, 1892)
SMNS 4966	Skull of *Temnodontosaurus burgundiae* (GAUDRY, 1892)
SMNS 15960	Complete skeleton of *Temnodontosaurus burgundiae* (GAUDRY, 1892)
SMNS 18648	Complete three dimensional skull of *Eurhinosaurus longirostris* (MANTELL, 1851)
GPIT 171/12/2	Complete skull of *Temnodontosaurus burgundiae* (GAUDRY, 1892)
GPIT 1576	Three dimensional skull of *Stenopterygius longifrons* (OWEN, 1881)
GPIT 1796/1	Three dimensional skull of *Ichthyosaurus communis* (CONYBEARE, 1822)
GPIT 328/4/5	Almost complete skeleton of *"Ichthyosaurus" integer* (BRONN, 1844)
WRZD 433	Complete three dimensional skull of *Temnodontosaurus burgundiae* (GAUDRY, 1892)
PB 1 (manuscript number)	Holotype of *"Ichthyosaurus" trigonodon* (v. THEODORI, 1843)

Institutional abbreviations:

WRZD	Museum im Werksforum der Rohrbach Zement AG Dotternhausen
GPIT	Institut und Museum für Geologie und Paläontologie der Universität Tübingen
PB	Petrefaktensammlung Kloster Banz
SMNS	Staatliches Museum für Naturkunde Stuttgart

3. Previous work

The history of research on *Leptopterygius nuertingensis* begins – and practically ends – with the original description published by v. Huene (1931 b). For the standards of the time, v. Huene's osteological treatment of the specimen was very detailed and – as the re-investigation has shown – also very accurate. The specimen was mentioned in the literature at several later occasions (see list of synonyms). In 1939 Kuhn referred an incomplete specimen from the Pliensbachian of Fallstein, Lower Saxony, to v. Huene's taxon, but failed to present evidence for this assignment. Kuhn's specimen is considered here generically and specifically indeterminable.

In 1979 Mc Gowan published a taxonomic revision of the Lower Jurassic ichthyosaurs from southern Germany. He used an almost entirely phenetic methodology, treating qualitative aspects of morphology only in a more superficial manner. The main value of his contribution lies in the elimination of a large array of taxa based on inadequately preserved or fragmentary material. He regarded *Leptopterygius nuertingensis* as such a taxon and considered it a nomen dubium. This conclusion is, however, an artifact of the phenetic methodology Mc Gowan employed, as a qualitative re-assessment of osteological characters shows. The holotype is both excellently preserved and shows the majority of characters considered to be diagnostic on the generic and specific level in ichthyosaurs by earlier workers such as Fraas, v. Huene and Owen. Whether *Leptopterygius nuertingensis* can be referred to any currently recognized ichthyosaur genus, represents a new genus or must remain incertae sedis are questions which have never been properly addressed by means of detailed anatomical comparison so far. The original description of v. Huene is, however, adequate to recognize the specific validity of *Leptopterygius nuertingensis*. What remains to do here is to extend the description of certain morphological features largely already recognized by v. Huene, and to point out their significance more clearly.

4. Description of *Leptopterygius nuertingensis*, SMNS 13488

The following description only refers to the characters considered to be taxonomically important.

Skull. – The premaxilla forms a long and robust rostrum of half-cylindrical shape, broken anteriorly. It bears two parallel rows of foramina and grooves instead of a single continuous fossa premaxillaris.

The maxilla is of unusual shape. It forms a distinctly serrated, vertical suture with the premaxilla, which it partially overlaps. It does not extend anteriorly from its highest point below the naris as far as it does in other temnodontosaurids, such as *Temnodontosaurus platyodon* and *T. burgundiae*. Quantification of this latter character is not possible, since the anterior tip of the snout is missing. The maxilla is comparatively much higher than in most other Liassic ichthyosaurs.

The maxilla is to a large degree overlapped by the anterior extremity of the jugal. On the right side of the skull the maxilla is excluded from the external narial margin by processes of the jugal, premaxilla and lacrimal and this must be considered the "true" state. It can be seen to reach into the narial margin on the left side of the skull (figured by v. Huene 1931 b). However, the left jugal has been lost, so that the lacri-

mal and maxilla are in unnatural contact. HUENE's sketch of the skull in lateral view is obviously reconstructed and combines data from both sides of the skull.

The prefrontal reaches down to the ventral magin of the orbit by means of a smooth lamina of bone pressed onto the posterior surface of the lacrimal along the internal orbital margin. This lamella of the prefrontal is a usual feature observable in most Liassic ichthyosaurs, but it is usually not that long. The lacrimal shows a very distinct knob-like narial process that projects into the naris. The nasal also has a ventrolateral flange protruding into the dorsal narial margin, thus giving the naris a distinctly bilobed appearance. An internasal foramen, mentioned to be present in several other Liassic ichthyosaurs such as *Ichthyosaurus* (MC GOWAN 1973), *Stenopterygius longifrons* (GODEFROIT 1993 b, 1994) and *Temnodontosaurus platyodon* (MC GOWAN 1974 a, 1996 b) is not present in *Leptopterygius nuertingensis*. The nasals are, however, deeply depressed on their dorsal surface anterior to the orbit. In *L. nuertingensis*, the nasals are very thin at the bottom of that depression and partially broken. The same might be a general phenomenon in many ichthyosaur skulls apparently possessing an "internasal foramen".

The jugal is not as complete anymore as at the time v. HUENE saw the specimen. The posteriormost portion figured by v. HUENE (1931 b; fig. 1), which indicates the base of the ascending process and thus the posterior orbital margin, is not present anymore. The jugal is remarkably slender compared to *T. burgundiae*, approaching the condition seen in smaller specimens of *T. platyodon* (MC GOWAN 1994). Anteriorly it extends by means of a distinct process which entirely separates the lacrimal and maxilla – at least superficially – and establishes a point-contact with the subnarial process of the premaxilla at about mid-narial length.

The palatine is very slender in palatal view and does not contribute to the posterior margin of the choana but only forms the lateral border of that opening. It is not even distinctly notched where it enters the choanal margin. Instead, its entire medial margin is straight. The vomer is an unusually extensive element. It forms the anterior, medial and posterior borders of the choana, thus excluding the premaxilla from it. Both anterior and posterior to the choana it is strongly expanded. It, furthermore, sends back a very slender posterior process which appears to be not completely preserved, although it is improbable that more than 5 mm are missing. This process separates palatine and pterygoid for almost their entire preserved length. The choana itself is a rather slit-like opening much smaller than the large elliptical aperture in *Temnodontosaurus burgundiae* (v. HUENE 1931 b; pers. obs.). The parasphenoid, which is only represented by most of the processus cultriformis, is slender but robust and bears a distinct blunt ventral keel in its posteriormost preserved part. The palatal features are illustrated in figure 1.

Dentition. – The dentition was well described by v. HUENE (1931 b). It is completely preserved and shows no signs of reduction. The teeth are closely spaced and large absolutely, but small in relation to the length of the skull. They are distinctly curving posteriorly and laterally. The tips of the crowns are smooth. More basally, the crowns are sculptured by strong grooves and ridges running apicobasally. There are no carinae. The teeth are regularly intermeshing. The premaxillary and maxillary teeth are pointing posteroventrally, whereas the mandibular teeth are equally strongly directed anterodorsally. A comparable phenomenon is described by MC GOWAN (1994) in a juvenile specimen of *Temnodontosaurus platyodon*, where all the teeth are raked back. MC GOWAN explains this as a post mortem effect, arguing convincingly

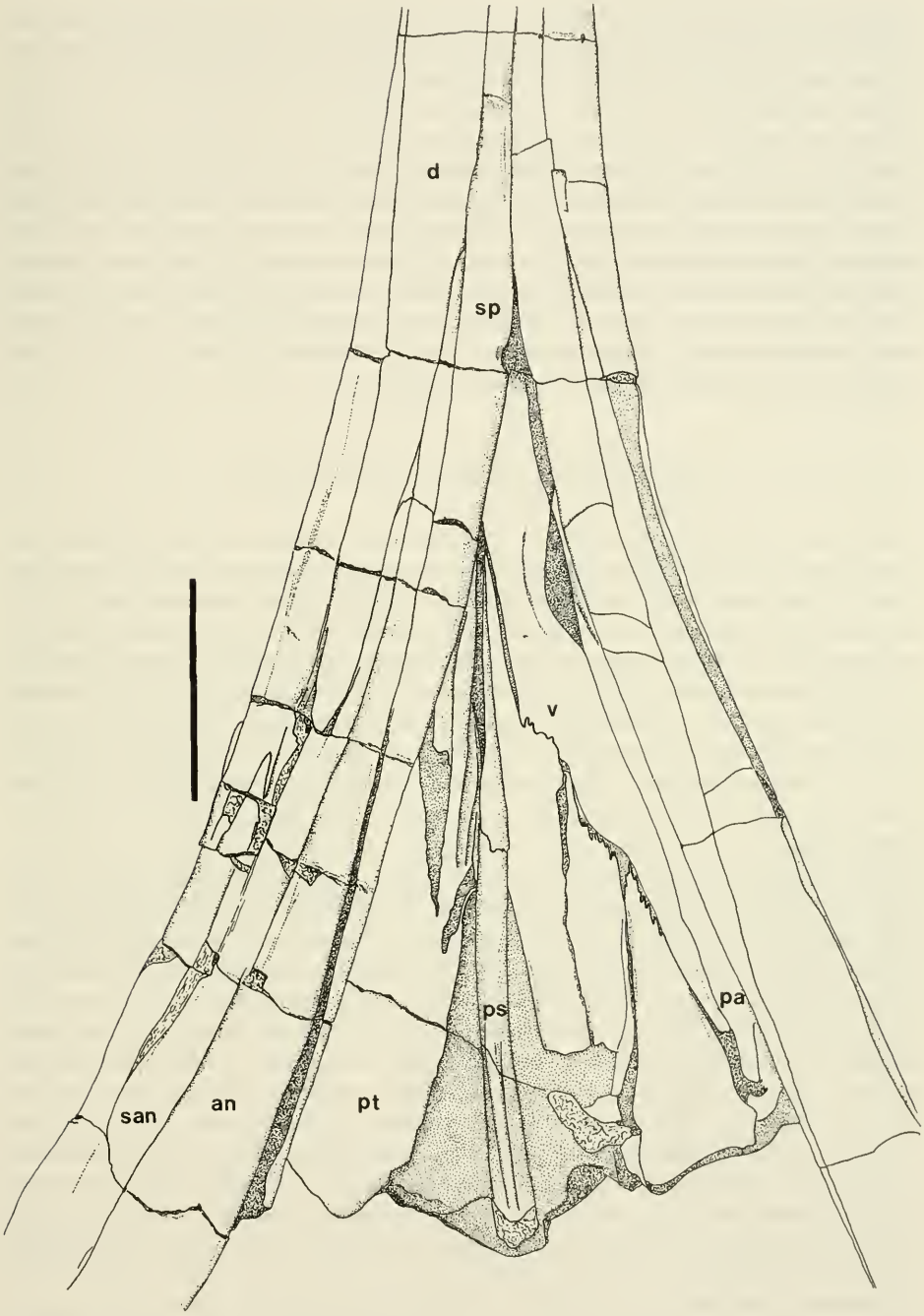

Fig. 1. Holotype skull of *Temnodontosaurus nuertingensis* (v. HUENE, 1931) comb. nov. (SMNS 13488), Lower Pliensbachian (? *jamesoni* or *ibex* Zone), ventral view of the palate, Nürtingen-Enzenhart. The scale bar equals 10 cm.
Abbreviations used in figure: an = angular, d = dentary, pa = palatine, ps = parasphenoid, pt = pterygoid, san = surangular, sp = splenial, v = vomer.

that the teeth would not fit together when the jaws are closed if truly arranged in such a way. The situation in *L. nuertingensis* is different, however, since despite their unusual arrangement, the teeth are closely fitting together and do not show any sign of displacement.

Lower jaw and postcranium. – The surangular is very short and does not reach beyond the anterior margin of the naris in lateral view. On the right side, it is clearly visible that the dentary reached back at least to mid-orbital level, overlapping the surangular with a long tongue-like posterior process, as evidenced by the distinct facet on the lateral surface of the surangular. There is no kink in the surangular-angular suture below the coronoid process. The coracoid, described by v. HUENE (1931 b), but now lost along with all the other postcranial elements, is interesting in that it does not show a posterior, but only a relatively wide anterior notch. In this feature the coracoids clearly approach *T. burgundiae*.

5. Affinities of *Leptopterygius nuertingensis*

Six genera of Liassic ichthyosaurs are currently recognized form Western Europe. These include *Ichthyosaurus* DE LA BECHE & CONYBEARE, 1821; *Temnodontosaurus* LYDEKKER, 1889; *Stenopterygius* JAEKEL, 1904; *Eurhinosaurus* ABEL, 1909; *Excalibosaurus* MC GOWAN, 1986 and *Leptonectes* MC GOWAN, 1996 (introduced to replace the preoccupied *Leptopterygius* v. HUENE, 1922 by MC GOWAN (1996 b)). *Protoichthyosaurus* APPLEBY, 1979 is regarded here as a junior subjective synonym of *Ichthyosaurus*. Even if valid, it cannot be compared, since the skull has never been described in this taxon. Two species from the Lower and Upper Liassic of Great Britain, respectively, *"Leptopterygius" acutirostris* (OWEN, 1839) and *Leptonectes solei* (MC GOWAN, 1993) are too incompletely known to allow a detailed comparison.

Ichthyosaurus is so far exclusively Lower Liassic in Europe (it is also known from the Upper Triassic of Canada, MC GOWAN 1996 a). It differs from *Leptopterygius nuertingensis* by its generally much smaller size – the maximal skull length is about 70 cm – the shorter anterior extension of the much lower maxilla, the shorter lacrimal, the lack of a premaxilla-jugal contact, the lack of the processes of the nasal and lacrimal extending into the narial opening and the arrangement of the palatal bones. In *Ichthyosaurus* the premaxilla forms the anterior border of the choana and the vomer does not reach as far posteriorly. *Ichthyosaurus* shows some similarities in the dentition, which also consists of conical teeth with coarse ridges on the non-carinate crowns, as well as in the general shape of the skull with a relatively high orbital region clearly set off from the snout. Whereas the first feature is probably plesiomorphic, the latter must be considered derived. It should, however, be borne in mind that the skull shape is affected by ontogenetic changes, as shown by MC GOWAN (1994) in *Temnodontosaurus platyodon*.

Stenopterygius, as it is currently understood, shows the same differences to *L. nuertingensis* as *Ichthyosaurus*. Furthermore, it differs in the palatine not extending nearly as far posteriorly as in *Ichthyosaurus, Temnodontosaurus* and *L. nuertingensis* (OWEN 1881; GODEFROIT 1993 b; pers. obs.) due to the development of a processus postpalatinus of the pterygoid, in which respect *Stenopterygius* resembles the Triassic *Shastasaurus alexandrae* (MERRIAM 1902). *Stenopterygius* comprises several

species which show much variation in the dentition, skull proportions and configurations of the skull roof bones (v. HUENE 1922, 1952; GODEFROIT 1993b, 1994).

Leptonectes, Eurhinosaurus and *Excalibosaurus* almost certainly form a natural group (MC GOWAN 1986) which is characterized – among other features – by the dentition consisting of very slender and elongate, small teeth without obvious surface sculpturing, the very gracile, low and slender snout, a very large orbit and a short postorbital region of the skull (which is not known in *L. nuertingensis* but according to the lower jaw was relatively much longer than in these species) and the tendency to develop an overbite of the upper jaw. This latter feature is only incipient in the Lower Liassic *Leptonectes*, but markedly developed in both the Lower Liassic *Excalibosaurus* and the Upper Liassic *Eurhinosaurus*. It is noteworthy, however, that the bilobed shape of the naris is also known to occur in *Eurhinosaurus longirostris* (MC GOWAN 1979). In all other features cited above the *Leptonectes*-group differs considerably from *L. nuertingensis*.

Two species from the Upper Liassic of Germany, *"Ichthyosaurus" integer* BRONN, 1844 and *"Leptopterygius" distinteger* v. HUENE, 1926, currently lack a valid generic designation. The best known specimens of both species were studied for comparison. Both are different in that the jugal is short, as is the maxilla, the entire snout is much shorter and there is no jugal-premaxillary contact. This, apart from the considerably smaller size, clearly distinguishes these taxa from *L. nuertingensis*.

The large size, the long and robust snout, the numerous and strongly sculptured teeth and the general skull shape are all features of *L. nuertingensis* which suggest affinities with *Temnodontosaurus* (MC GOWAN 1996c). The contact between jugal and premaxilla is – amongst all adequately known ichthyosaurs – a feature which only occurs in *Temnodontosaurus burgundiae* and *Leptopterygius nuertingensis*. This most strongly suggests a close relationship between these two species.

At present, the genus *Temnodontosaurus* comprises three valid species (the status of *"Ichthyosaurus" trigonodon* (v. THEODORI, 1843) remains questionable at the moment, pending further investigation, but it is probably a valid senior synonym of *T. burgundiae*). *T. eurycephalus* MC GOWAN, 1974 is characterized by its very short and high snout and a dentition consisting of few but extremely short-crowned, heavily sculptured and carinate teeth (OWEN 1881; MC GOWAN 1974a). It is thus clearly different from *L. nuertingensis*. *Temnodontosaurus platyodon*, the type species, resembles *L. nuertingensis* in the general shape and proportions of the skull and the arrangement of the individual skull bones. Differences lie in the shape of the maxilla, which is very low, the naris not being bilobed, the orbital region of the skull not being that clearly set off from the snout in adult specimens (but in juveniles, see MC GOWAN 1994), the teeth being carinate in adult specimens (but not necessarily in juveniles, see MC GOWAN 1994; HUNGERBÜHLER & SACHS 1997) and the jugal not contacting the premaxilla (OWEN 1881; GODEFROIT 1993a). The palate is not adequately known in *T. platyodon*, even though GODEFROIT (1993a) described some of the elements from incomplete material that does not allow a reliable reconstruction. *T. burgundiae* from the Upper Lias of France and Germany differs in the same respects as *T. platyodon*, except that a premaxillary-jugal contact, which is even more extensive in most individuals than in *L. nuertingensis*, is present in all adequately preserved specimens. The palatal structure, which was well described by v. HUENE (1931b), is much different. The premaxillaries form the anterior and the palatines the posterior borders of the choanae and the vomer is much shorter posteriorly in

T. burgundiae. The rather robust parasphenoid rostrum bearing a strong ventral keel, which is not developed in any other Liassic ichthyosaur in which this feature is known, is however identical, as is the relationship of palatine and pterygoid.

It must be borne in mind that the high orbital region of the skull and the lack of carinae on the teeth are suggested to be juvenile features in both *T. platyodon* (Mc Gowan 1994; Hungerbühler & Sachs 1997) and *T. burgundiae* (pers. obs.). In the latter species, these features are still retained in specimens with an estimated skull length of about 1000 mm, such as WRZD 433, and it is thus not impossible that the holotype of *Leptopterygius nuertingensis* represents an immature specimen. If this hypothesis should be correct, a fully mature *L. nuertingensis* could be estimated to have a skull length of more than 2000 mm. It is also possible, that *L. nuertingensis* shows a trend towards paedomorphosis in these features. Without a larger sample these questions cannot be decided, but it is evident that the lack of carinae on the teeth does by no way hamper the inclusion of the species in the genus *Temnodontosaurus*. Consequently *Leptopterygius nuertingensis* v. Huene, 1931 is referred to the genus *Temnodontosaurus* Lydekker, 1889.

6. Systematic Palaeontology

Ichthyosauria de Blainville, 1835

Temnodontosauridae Mc Gowan, 1974 [1974 a]

Genus *Temnodontosaurus* Lydekker, 1889

Type species: *Ichthyosaurus platyodon* Conybeare, 1822.

Temnodontosaurus nuertingensis (v. Huene, 1931) comb. nov.

1919	*Ichthyosaurus* n. sp. – E. Fraas, p. 63.
1922	*Leptopterygius* aff. *margaritatus* n. sp. – v. Huene: 21, pl. 14, fig. 1 a–b.
1926	*Ichthyosaurus bellicosus* n. sp. – E. Fraas, p. 54 (nomen nudum).
1930	*Leptopterygius nürtingensis* v. Huene, p. 108–109, fig. 2 (nomen nudum).
*1931	*Leptopterygius nürtingensis* n. sp. – v. Huene, p. 305–313, fig. 1–6. – [1931 b]
1934	*Leptopterygius nürtingensis* v. Huene, 1930. – Kuhn, p. 58.
1938	*Leptopterygius nürtingensis* v. Huene, 1931. – Berckhemer, p. 151, 156.
1939	*Leptopterygius nürtingensis* v. Huene, 1931. – Kuhn, p. 136–137.
1956	*Leptopterygius nürtingensis* v. Huene, 1931. – v. Huene, p. 133, fig. 174 d.
1968	*Leptopterygius nürtingensis* v. Huene, 1931. – Kuhn, p. 50, fig. 20. 4.
1979	*Leptopterygius nurtingensis* v. Huene, 1931. – Mc Gowan, p. 128.
1992	*Leptopterygius nurtingensis* v. Huene, 1931. – Godefroit, p. 167.
1997	*Leptopterygius nuertingensis* v. Huene, 1931. – Hungerbühler & Sachs, p. 35–36, fig. 7/4.

Holotype: SMNS 13488, incomplete three-dimensional skull and mandible in excellent state of preservation. Acquired by the Museum in 1914, donated by director Schott. The entire postcranial material from the same individual is lost.

Locus typicus: The former Schott Cement Quarry, Nürtingen-Enzenhart, Baden-Württemberg.

Stratum typicum: Lias gamma = Lower Pliensbachian. From the matrix attached to the specimen probably from the zone of *Uptonia jamesoni* or *Tragophylloceras ibex*.

Nomenclatorial note: The specimen was given the name *Ichthyosaurus bellicosus* by Eberhard Fraas (published posthumously in 1926). Fraas obviously intended to describe the new find, but his untimely death in 1915 did not allow him to do so. Unfortunately the bi-

nomen *Ichthyosaurus bellicosus* must be considered a nomen nudum, since it was not connected with a description of the specimen, and it is therefore not available. The oldest available name is thus *Leptopterygius nürtingensis* v. HUENE, 1931. It was first published by v. HUENE in 1930, no adequate description being given and only a figure of some undiagnostic pathological thoracal ribs being provided. The first fully illustrated specific description was provided by v. HUENE in 1931 (1931 b). According to the ICZN (Art. 32 c) the specific name has to be emendated to *nuertingensis*, not *nurtingensis*, as MC GOWAN (1979) proposed erroneously (HUNGERBÜHLER & SACHS 1997).

Diagnosis (based on v. HUENE 1931 b and pers. obs.). – Possibly small species of the genus, estimated lower jaw length < 130 cm; long and robust rostrum which is clearly set off from the high-crowned orbital skull region; maxilla high, overlapping premaxilla and showing complexly serrated suture with the latter, relatively short anteriorly, not entering into border of external naris; probably no internasal foramen but deep depression along internasal suture anterior to orbit; prefrontal large, reaching ventral margin of orbit internally; lacrimal and nasal with distinct narial processes, naris thus of bilobed shape; jugal extending far anteriorly below naris by means of a slender process that establishes sutural contact with premaxilla; ventral exposure of palatine narrow, palatine only forming lateral margin of choana in ventral view; vomer very large, excluding premaxilla from choanal margin and extending far posteriorly, almost separating pterygoid and palatine; parasphenoid with slender but strong processus cultriformis bearing a distinct ventral keel posteriorly; teeth relatively small, with rounded cross section, no carinae, tip smooth, basal two thirds of crown bearing pronounced furrows and ridges; lower teeth pointing anteriorly, upper teeth pointing posteriorly in characteristic intermeshing manner; surangular very short in external view, not reaching beyond level of external naris; coracoid with distinct anterior but no posterior notch.

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