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A NEW ICHTHYOSAUR FROM THE UPPER JURASSIC LITHOGRAPHIC LIMESTONES OF BAVARIA

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ABSTRACT—Two ichthyosaurian specimens from the Upper Jurassic lithographic limestones of Bavaria, namely an almost complete skeleton with soft tissue impression and another partial one, are described for the first time. Both belong to the same taxon, which is mainly characterized by a long and slender snout; numerous small, delicate, packed, and well-anchored teeth; a medium size orbit; a reduced triangular squamosal in the cheek region; an angular largely exposed laterally reaching as far anteriorly as the surangular; a humerus with three distal facets for radius, intermedium and ulna; an extrazeugopodial element anterior to the radius; a very reduced hindlimb; packed polygonal paddle elements; and a bipartite pelvis with a distally greatly expanded puboischiatic complex. This combination of characters permits differentiation from all other known genera; moreover, it could be compared to the species inquirendae *Ichthyosaurus leptospondylus* Wagner, 1853a. A new genus, *Aegirosaurus,* is created and proposed as a new combination for this species. *Aegirosaurus* clearly belongs to the clade Ophthalmosauria because of an angular largely exposed laterally and reaching as far anteriorly as the surangular, and the occurrence of an extrazeugopodial element anterior to the radius and the associated digit distal to it. A systematic review of ichthyosaurs from the lithographic limestone of Bavaria (most of them destroyed during World War II) reveals the occurrence of probably three different taxa, namely *Aegirosaurus,* an indeterminate form close to *Ophthalmosaurus* or *Caypullisaurus,* and an indeterminate one possibly close to *Nannopterygius.*

INTRODUCTION

THE UPPER Jurassic lithographic limestones of Bavaria are known worldwide for their excellently preserved fossils, the most famous being *Archaeopteryx.* The lagoonal conditions that prevailed during the Tithonian in the Solnhofen area were favorable to the fossilization of impressive marine and continental floras and faunas, these last ones including both invertebrate and vertebrate representatives (see Barthel et al., 1990; Frickhinger, 1994). The vertebrate fauna consists of a high diversity of bony fish and selachians as well as reptiles, mainly chelonians, lacertilians, crocodilians and pterosaurs. Because of the slightly hypersaline restricted environment, limited from the open-sea by coral-reefs, occurrence of nektonic marine reptiles such as plesiosaurs and ichthyosaurs remains comparatively scarce in the Solnhofen lagoon (Barthel et al., 1990).

Despite the facts that Solnhofen ichthyosaurs have been known since 1852 and that several taxa have been named, they have been only poorly described and figured. This has led to a very confused systematic situation and, probably as a result, Bavarian ichthyosaurs have received little scientific attention.

The aims of this paper are to describe two new specimens and to make a systematic review of the ichthyosaurs from the lithographic limestones of Bavaria.

Institutional abbreviations used are: BMNH (NHM), the Natural History Museum, London; BSPHGM, Bayerische Staatssammlung für Paläontologie und historische Geologie Museum, Munich; SM, Schwegler Museum, Langenaltheim.

HISTORICAL ACCOUNT
(see Appendix for further detail)

The first mention of ichthyosaurs from the lithographic limestones of Bavaria was made by Quenstedt (1852, p. 129), on the basis of a partial skeleton known as the ''Häberlein specimen''. At the same time, Wagner created two specific names: *Ichthyosaurus posthumus,* based on an isolated tooth (Wagner, 1852) and *Ichthyosaurus leptospondylus,* based on a poorly described and figured skeleton, known as the ''Oberndorfer specimen'' (Wagner 1853a, 1853b). These two taxa were only differentiated by their tooth morphology. Then, Wagner succinctly described and figured the Häberlein specimen and referred it to *I. leptospondylus* because of its great similarity with the type specimen (Wagner, 1861). Meyer (1863) described a new fragmentary skull and referred it also to *I. leptospondylus.* Later, Lydekker (1889a) synonymized *I. posthumus,* together with *Ichthyosaurus cuvieri* Valenciennes, 1861a, and *Ichthyosaurus normanniae* Valenciennes, 1861b, both from the Late Jurassic of Normandy (see discussion in Bardet et al., 1997), with *Ichthyosaurus trigonus* Owen, 1840, from the Late Jurassic of England. *Ichthyosaurus leptospondylus* was retained as a valid species, close or identical to *Nannopterygius enthekiodon* (Hulke, 1870) (Lydekker, 1889a). Fraas (1891) was the only author to consider the Häberlein and the Oberndorfer specimens as belonging to different taxa, a view that we share (see Appendix). As a result, he referred the Oberndorfer specimen (type of *I. leptospondylus*; Wagner, 1853a, 1853b) and the specimen described by Meyer (1863) to *I. posthumus.* Indeed, he considered the Häberlein specimen (Quenstedt, 1852; Wagner, 1861) as the new type of *I. leptospondylus.* Because of the short vertebrae and the great number of paddle elements in both *I. posthumus* and *I. leptospondylus,* close affinities with *Ophthalmosaurus* Seeley, 1874, and *Baptanodon* Marsh, 1880, were suggested. The only overview of Late Jurassic Bavarian ichthyosaurs was made by Bauer (1898). The Häberlein, Oberndorfer, and four new specimens were all referred to *I. trigonus* var. *posthumus,* because the differences observed in their respective size and teeth ornamentation were explained in terms of ontogenetic rather than systematic variations. *Ichthyosaurus leptospondylus* was thus synonymized with *I. posthumus.* Moreover, *I. posthumus* and several other taxa, including *Ophthalmosaurus, I. cuvieri* and *I. normanniae,* were considered junior synonyms of *I. trigonus* (Bauer, 1898). Later, the genus *Macropterygius* Huene, 1922 was created for the species *I. trigonus* (Huene, 1922). As the type of *I. trigonus* is a single vertebra, it is suspected that Huene's diagnosis was composite and mainly based on the material from Bavaria and Normandy, previously reassigned to *I. trigonus* by Lydekker (1889a) and Bauer (1898). As suggested by McGowan (1976) and Kirton (1983), *I. trigonus* and thus *Macropterygius* are nomina dubia because they are based on inadequate and composite material. *Ichthyosaurus posthumus* is also considered

TABLE 1—Skeleton measurements (in cm) of *Aegirosaurus leptospondylus.*

Measurements	BSPHGM	SM
L (jaw length)	31.4	56.5
K (skull length)	29.4	56
J (snout length)	19.5	41.5
D (postorbital segment)	1.9?	4.5
H (orbital length)	8.4	10.4
A (orbit center–anterior skull)	23.8	47
C (orbit center–hindmost skull)	5.6	8
I (premaxillar segment)	15.2	31.3
B (prenarial segment)	16	38

a nomen dubium because of inadequate type material and *I. leptospondylus* as a species inquirendae, an available name whose type material is lost (McGowan, 1976).

Indeed, with the exception of the Meyer's (1863) skull, kept at London, the ichthyosaur collections from the lithographic limestones of Bavaria (then housed in the Munich State Museum) were completely destroyed during World War II. Recently, new specimens have been unearthed, but remain undescribed until now. Among them are a partial skeleton (BSPHGM 1954 I 608, Munich), referred to as *Macropterygius posthumus* by Barthel et al. (1990), and an almost complete skeleton (SM, Langenaltheim), assigned to *Macropterygius trigonus* by Frickhinger (1994). These two specimens are herein described and systematically reassigned.

SYSTEMATIC PALEONTOLOGY

ICHTHYOSAURIA Blainville, 1835
OPHTHALMOSAURIA Motani, 1999a
Genus AEGIROSAURUS new genus

Type species.—Ichthyosaurus leptospondylus Wagner, 1853a

Diagnosis.—A medium size ichthyosaur less than 2 m long, characterized by a long and slender snout (snout ratio 0.73 to 0.62), not markedly demarcated from the skull; delicate and small packed teeth strongly anchored in the dental groove, with enamel crown minutely ridged or smooth; medium sized orbit (orbital ratio 0.18 to 0.26), filled with 14 sclerotic plates and dorsally bordered by a flange; external naris with a dorsal protuberance; short jugal slightly exceeding anteriorly the orbital margin; postorbital segment of the skull very narrow (postorbital ratio 0.08 to 0.06); postorbital covering quadratojugal; presence in the cheek region of a reduced, triangular and laterally exposed squamosal, which is excluded from the temporal fenestra by a postfrontal-supratemporal bar; angular largely exposed laterally reaching as far anteriorly as the surangular; forepaddle with massive humerus bearing three distal articulations for radius, intermedium (the smallest) and ulna, an extrazeugopodial element and its associated digit distally to the radius, six digits of which the fourth is the longest and comprised 23 elements; short hindlimb with massive femur one half the humerus length and smaller than the puboischiatic complex, articulating distally with two elements, and four digits; both paddles composed of proximally packed polygonal elements becoming more spaced and rounded distally; bipartite pelvis composed of a puboischiatic complex without foramen and with a distal end expanded more than twice the width of the proximal one.

Etymology.—From *Aegir,* God of the oceans and the seashores in the Germanic and Scandinavian mythology and *Sauros,* lizard in Greek.

AEGIROSAURUS LEPTOSPONDYLUS (Wagner, 1853a) new combination
Figures 1–8, Tables 1, 2

Ichthyosaurus leptospondylus WAGNER, 1853a, p. 26;
Ichthyosaurus leptospondylus WAGNER, 1853b, p. 264, pl. 6, figs. 14, 15;
Ichthyosaurus leptospondylus MEYER, 1863, p. 223, pl. 33;
Ichthyosaurus trigonus var. *posthumus* BAUER, 1898, p. 291, pl. 25, figs. 1–5;
Macropterygius posthumus BARTHEL ET AL., 1990, p. 180, fig. 7.74;
Macropterygius trigonus FRICKHINGER, 1994, p. 249, fig. 514;
Brachypterygius extremus FERNÁNDEZ, 1997, p. 483.

Diagnosis.—As for genus.

Types.—Oberndorfer specimen, type of *Ichthyosaurus leptospondylus* Wagner, 1853a, from the lithographic limestones of Borscheim near Kelheim, Bavaria (destroyed during World War II). SM, neotype, an almost complete skeleton with soft tissue impression, Schwegler Museum, Langenaltheim, Bavaria (cast available in the BSPHGM of Munich), from the Solnhofen Formation, Malm Zeta 2b, early Lower Tithonian, uppermost Jurassic (Zeiss, 1977) of the Schrandel quarry district, South of Langenaltheim, Bavaria.

Referred specimens.—BSPHGM 1954 I 608, a partial skeleton, Bayerische Staatssammlung für Paläontologie und historische Geologie Museum (Munich), from the Solnhofen Formation, Malm Zeta 2b, early Lower Tithonian, uppermost Jurassic (Zeiss, 1977) of Steinbruch am Geisberg quarry, Apfeltal, South of Solnhofen, Bavaria; BMNH 42833, a partial skull, Natural History Museum (London), from the lithographic limestones of Eichstätt, Bavaria.

General remarks.—The Schwegler Museum specimen (SM, neotype) is an almost complete articulated skeleton, 1.77 m long, with soft tissue impression on the micritic matrix (Fig. 1). The specimen was found at the lower surface of a lithographic limestone bed and was thus preserved with its dorsolateral surface downward facing. Only the girdles and the left paddles are completely lacking. The skull is exposed in dorsal view, the body in right dorsolateral position and the tail in right lateral exposure. The carcass of the animal probably landed on the sea floor in a dorsal position. As usual in dorsal-down specimens, the vertebral column is quite perfectly articulated (Martill, 1993). The skull may have intruded the sediment first because of its higher density. Then, a right lateral rotation of the body occurred before its complete intrusion in the sediment, a common situation observed in many carcasses that arrive in a dorsal position (Martill,

TABLE 2—Ratios of *Aegirosaurus leptospondylus* and of other Ophthalmosauria (sensu Motani, 1999a, 1999b). Ratios as defined by McGowan (1976) and Kirton (1983): OR = Orbital ratio (H/L), SR = Snout ratio (J/L), PmxR = Premaxillary ratio (I/J sensu Kirton, 1983), PnR = Prenarial ratio (B/L), PoR = Postorbital ratio (D/L), OPI = Orbital position index (C/A). Ratios of *Brachypterygius, Ophthalmosaurus, Caypullisaurus* and *Platypterygius* based on McGowan (1976) and Fernández (1997).

	OR	SR	PmxR	PnR	PoR	OPI
Aegirosaurus	0.18–0.26	0.62–0.73	0.48–0.55	0.51–0.68	0.06–0.08	0.17–0.23
Brachypterygius	0.18	0.71	0.59	0.60	0.08	0.21
Ophthalmosaurus	0.24	0.65	0.73	0.52	0.05	0.22
Caypullisaurus	0.16	0.68	—	—	0.10	—
Platypterygius	0.11	0.75	—	0.64	0.09	0.18

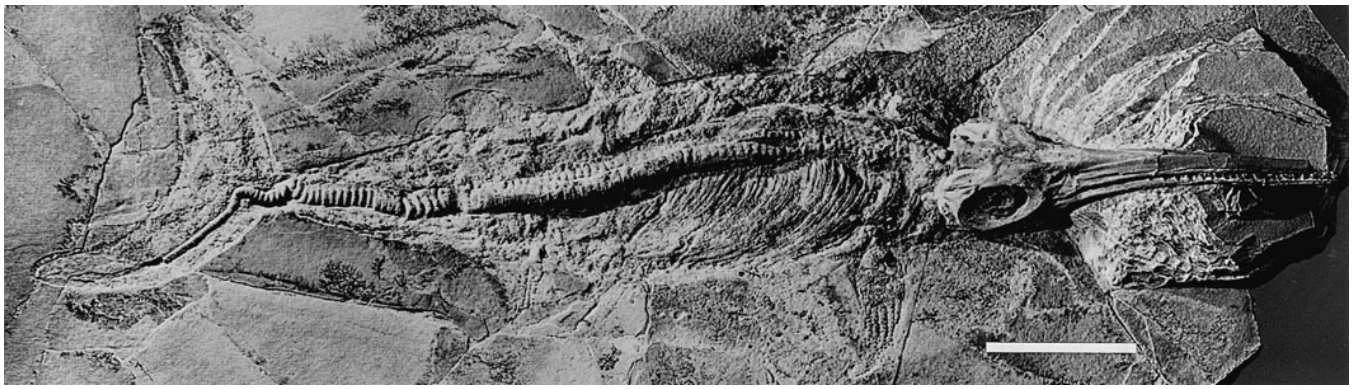

FIGURE *1*—*Aegirosaurus leptospondylus* n. comb., SM (neotype), almost complete skeleton with soft tissue impression, Solnhofen Formation, early Lower Tithonian, Schrandel quarry district, South of Langenaltheim, Bavaria. Global view. Scale equals 20 cm.

1993) and leading to the final buried position mentioned above. The lateral rotation of the body could explain the loss of both the left paddle and girdle. As suggested by Allison (1988), the soft tissues are subject to bacterial degradation whether the water column is oxic or anoxic. Thus, the preservation of soft tissue impression, as well as the complete lack of any scavenger or epifauna activity on the specimen suggest that its burial was rapid.

BSPHGM 1954 I 608 is a partial articulated skeleton, 0.70 m long, exposed on a lithographic slab in left lateral view (Fig. 2). The preserved parts of the skeleton are the completety articulated skull and trunk region with disarticulated girdles and paddles. The tail region is absent. According to Martill (1993), the completeness of the body outline of carcasses that arrive on the sea floor in a lateral position depends on the depth to which they sank. Here, the carcass has probably intruded the sediment by about 50 percent (see Martill, 1993, fig. 6). This specimen, called ''Munich 5'' by McGowan (1976), was erroneously envisaged to be Wagner's more complete skeleton (Häberlein specimen). As previously noted, the old collections from the Munich Museum were completely destroyed and BSPHGM 1954 I 608 was purchased after the war (P. Wellnhofer, personal commun.).

Skull and mandible.—In both specimens the skull and mandible are complete and articulated. The SM skull is 56 cm long and lacks only the anteriormost part of the premaxillae (Fig. 3). The BSPHGM skull is complete and is about 30 cm long (Fig. 4). Both skulls are mainly characterized by a delicate and long snout fitted with numerous teeth, and a medium size orbit. The

FIGURE *2*—*Aegirosaurus leptospondylus* n. comb., BSPHGM 1954 I 608 (referred specimen), partial skeleton, Solnhofen Formation, early Lower Tithonian, Steinbruch am Geisberg quarry, Apfeltal, South of Solnhofen, Bavaria. Global view. Scale equals 20 cm.

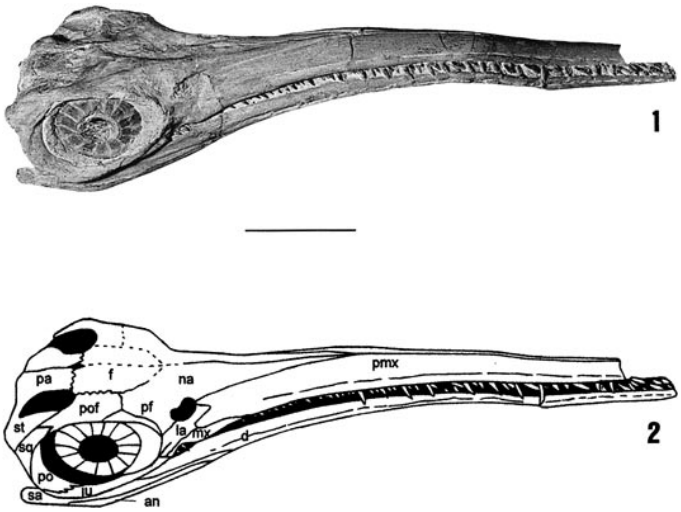

FIGURE 3—*Aegirosaurus leptospondylus* n. comb., SM (neotype), Solnhofen Formation, early Lower Tithonian, Schrandel quarry district, South of Langenaltheim, Bavaria. Skull; *1,* photograph ; *2,* interpretative drawing. Abbreviations: an, angular; d, dentary; f, frontal; ju, jugal; la, lacrymal; mx, maxilla; na, nasal; pa, parietal; pf, prefrontal; pmx, premaxilla; po, postorbital; pof, postfrontal; sa, surangular; sq, squamosal; st, supratemporal. Scale equals 10 cm.

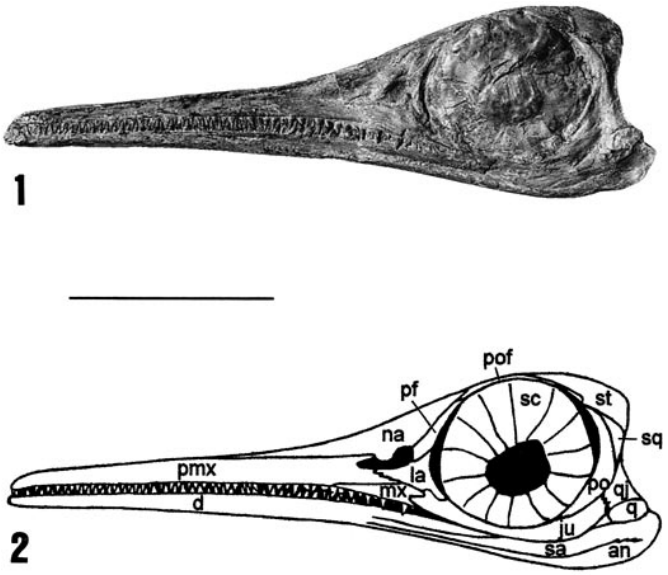

FIGURE 4—*Aegirosaurus leptospondylus* n. comb., BSPHGM 1954 I 608 (referred specimen), Solnhofen Formation, early Lower Tithonian, Steinbruch am Geisberg quarry, Apfeltal, South of Solnhofen, Bavaria. Skull; *1,* photograph; *2,* interpretative drawing. Abbreviations: an, angular; d, dentary; ju, jugal; la, lacrymal; mx, maxilla; na, nasal; pf, prefrontal; pmx, premaxilla; po, postorbital; pof, postfrontal; q, quadrate; qj, quadratojugal; sa, surangular; sc, sclerotic ring; sq, squamosal; st, supratemporal. Scale equals 10 cm.

rostrum is long, slender and not markedly demarcated from the skull. The snout ratios are 0.73 (SM) and 0.62 (BSPHGM) and comparable to other Middle-Late Jurassic ichthyosaurs (see Table 2). The teeth are numerous, small, delicate, closely packed, and strongly anchored in the dental groove; thus, they differ from all other Middle-Late Jurassic genera. In SM, the teeth are less numerous and less packed than in BSPHGM. Moreover, the enamel crown bears minute ridges, whereas it is smooth in BSPHGM. The orbits are of medium size. The orbital ratio of SM (0.18) resembles more *Caypullisaurus* Fernández, 1997, and *Brachypterygius* Huene, 1922, than that of BSPHGM (0.26), which is comparable to *Ophthalmosaurus* (see Table 2). The orbit is oval in SM and the sclerotic ring filled it almost entirely. The orbit is circular and completely filled with the sclerotic ring in BSPHGM. In both specimens the sclerotic rings are well preserved and are composed of 14 largely overlapped thin plates as compared to about 12 in *Brachypterygius* and 15 in *Ophthalmosaurus* (Kirton, 1983). The naris, which bears a diagnostic dorsal lateral protuberance, is oval to rounded in SM, whereas it is more elongate in BSPHGM (as in BMNH 42833), resembling *Ophthalmosaurus.* In both specimens, the bone configuration around the orbit and naris is similar to that observed in *Ophthalmosaurus* (see Kirton 1983, pl. 14). The jugal is short and only slightly exceeds anteriorly the orbital margin. This condition resembles that of *Ophthalmosaurus,* in contrast to *Brachypterygius* in which the jugal is very long and reaches the naris region, contacting the premaxillae (Kirton, 1983). The prefrontal and postfrontal make a supraorbital flange which looks like that of *Ophthalmosaurus.* This structure, which appear to be common in ichthyosaurs (Motani et al., 1998), could have acted as an orbit protector in light of its large size (Kirton, 1983). Sutures of the skull roof are hardly observed in SM and are not available in BSPHGM because of its lateral preservation. As usual, the pineal foramen is located at the frontal-parietal suture. Apparently, the frontal takes part in the anteromedial border of the upper temporal fossa. The postorbital segment of the skull is very short, the ratios being of 0.08 in SM and of 0.06 in BSPHGM. The quadratojugal is almost completely covered by the postorbital, as in *Ophthalmosaurus* (Kirton, 1983). In both specimens, the posterior cheek region exhibits three bones, which are here interpreted as the supratemporal, squamosal and quadratojugal (instead squamosal, supranumeral bone and quadratojugal), following Motani et al. (1998). The squamosal is a small, triangular and laterally exposed bone, which is excluded from the temporal fenestra by an extensive postfrontal-supratemporal contact. In SM, the supraoccipital is preserved and slightly displaced from its original position. It bears the typical ichthyosaurian arch shape.

In both specimens, the mandible is laterally exposed and exhibits the same bone arrangement. The dentary is very long and slender, ending up posteriorly at the orbital level. The most interesting character is that the angular is largely exposed laterally, reaching as far anteriorly as the surangular, an important phylogenetic character (Motani, 1999b) as will be discussed below.

Vertebral column.—In SM, all centra are roughly articulated with neural arches and ribs present (see Fig. 1). The anterior presacral vertebrae are badly preserved and have been estimated as seven. Behind them, there are 45 presacrals more, as well as 40 preflexual, four flexual (preserved as matrix impression) and 61 postflexual (of which about 30 are preserved as matrix impression) caudals. The total number of vertebrae may thus have been about 157 divided into 52 presacrals and 105 caudals. The vertebral count to tail-bend is 92, larger than *Ophthalmosaurus* (69–74), *Ichthyosaurus* De La Beche and Conybeare, 1821 (69–79), *Stenopterygius* Jaekel, 1904 (78–85) and *Leptonectes* McGowan, 1996 (83–85), and is within the range of *Temnodontosaurus* Lydekker, 1889b (88–95). The downturn of the vertebral column after the tail-bend is about 45 degrees. It is lower than the value (about 80 degrees) of two specimens from Solnhofen (Bauer, 1898, pl. 27; Martill, 1995, fig. 2A) and is within the range of *Stenopterygius* from Holzmaden (Martill, 1995, fig. 2B). In contrast to *Nannopterygius,* there is no clear size increase in the posterior presacrals and anterior caudals (Kirton, 1983).

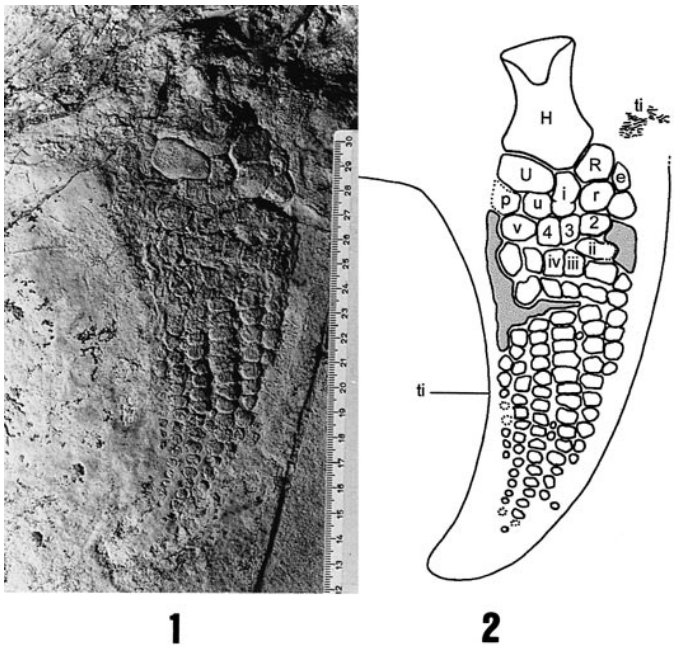

FIGURE 5—*Aegirosaurus leptospondylus* n. comb., SM (neotype), Solnhofen Formation, early Lower Tithonian, Schrandel quarry district, South of Langenaltheim, Bavaria. Forelimb with soft tissue impression, *1,* photograph; *2,* interpretative drawing. Abbreviations: e, extrazeugopodial element; H, humerus; i, intermedium; p, pisiform; R, radius; r, radiale; ti, tissue impression; U, ulna; u, ulnare; 2–4, distal carpals; ii-v, metacarpals; grey zones are covered with matrix; dotted line elements are preserved as matrix impression.

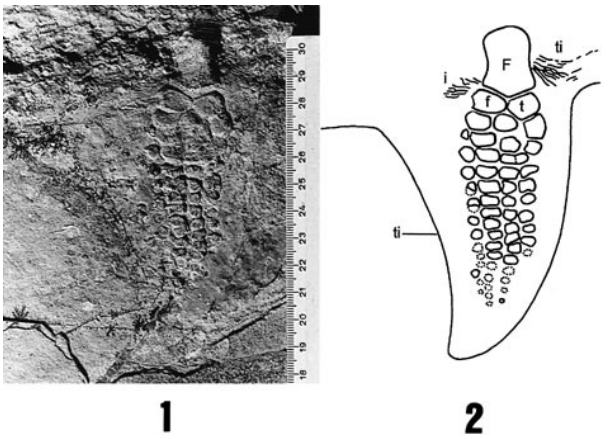

FIGURE 6—*Aegirosaurus leptospondylus* n. comb., SM (neotype), Solnhofen Formation, early Lower Tithonian, Schrandel quarry district, South of Langenaltheim, Bavaria. Hindlimb with soft tissue impression; *1,* photograph; *2,* interpretative drawing. Abbreviations: F, femur; f, fibula; t, tibia; ti, tissue impression; dotted line elements are preserved as matrix impression.

In BSPHGM, only about 34 presacral vertebrae are preserved in articulation (see Fig. 2).

In both specimens, the height of the presacral centra is about twice their length. The neural arches are rather low, rectangular, and slightly posteriorly recurved in the trunk region. They become very low in the caudal region. In BSPHGM, some displaced vertebrae show that the neural canal was large.

Ribs are preserved in articulation with the vertebrae in both specimens. The anterior presacral ribs are short, wide and bear confluent parapophyses and diapophyses located anteriorly. The other ribs are very long and slender, as usual in ichthyosaurs. Some delicate gastralia are preserved disarticulated in BSPHGM.

Limbs.—Right fore- and hindlimbs are completely preserved in articulation and with soft tissue impression in SM (Figs. 1, 5, 6). In BSPHGM, disarticulated elements of possibly both forepaddles and of the right hindlimb are preserved (Figs. 2, 7). In both specimens, the hindlimb is strongly reduced compared to the animal size, and is about half the size of the forelimb.

The humerus is a massive, short element, clearly belonging to the derived 'morphotype 3' of Motani (1999a). As in *Brachypterygius, Ophthalmosaurus, Caypullisaurus* and *Platypterygius,* there are three distal facets. Those for the radius and ulna are similar in size whereas the third facet is smaller and herein interpreted as for the intermedium, like in *Brachypterygius.* The facets are angulated and clearly separated from each other, especially the radial facet which is antero-distally oriented, also like in *Brachypterygius.* The humerus proximal head is almost flat and the distal extremity is wider than the proximal one. Based on the conservative topological features of the primary axis and digital arch as described by Motani (1999a), the homology of the *Aegirosaurus* forefin elements is identified as follows (see Fig. 5.2): the radius is roughly pentagonal; the ulna is trapezoidal and larger than the radius; the radiale is ovoid; the intermediium is wedge-shaped and elongated; the ulnare is quadrangular; there is a pentagonal extrazeugopodial element anterior to the radius and a pisiform posterodistal to the ulna, neither in contact with the humerus; the metacarpal V contacts the ulnare and the distal carpal 4; digit I is considered to be lost; there are three digits anterior to the primary axis (sensu Motani, 1999a), which corresponds to digit IV, the longest one with 23 elements. It should be noted that between digits III and IV there are two small isolated elements that may or not be remains of an additional extra digit. The elements are strongly packed and polygonal in the proximal part of the paddle but become more rounded and spaced in its distal part, as in *Brachypterygius* and *Caypullisaurus.* The epipodial construction of *Aegirosaurus* (intermedium contacting the humerus) is comparable to that of *Brachypterygius* (McGowan, 1997) and is quite different from that of *Ophthalmosaurus, Platypterygius* and *Caypullisaurus* in

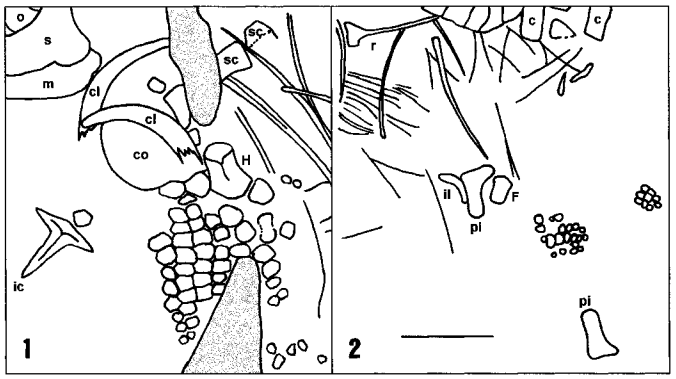

FIGURE 7—*Aegirosaurus leptospondylus* n. comb., BSPHGM 1954 I 608 (referred specimen), Solnhofen Formation, early Lower Tithonian, Steinbruch am Geisberg quarry, Apfeltal, South of Solnhofen, Bavaria. Limb and girdle interpretative drawings; *1,* forepaddle and pectoral girdle; *2,* hindpaddle and pelvic girdle. Abbreviations: c, centra; cl, clavicle; co, coracoid; F, femur; H, humerus; ic, interclavicle; il, ilium; m, mandible; o, orbit; pi, puboischiatic complex; r, ribs; s, skull; sc, scapula. Grey zones indicate cuts on the lithographical slab. Scale equals 5 cm.

which the humerus bears three distal facets for an extrazeugopodial element, radius and ulna (Kirton, 1983; Kuhn, 1946; Fernández, 1997, 1998).

The femur is half the humerus length and in BSPHGM it is smaller than the puboischiatic complex. It articulates distally with two bones. The tibia is pentagonal. The fibula is rectangular with a posterior notch and is larger than the tibia. There are four digits, versus three digits in *Ophthalmosaurus* and five in *Caypullisaurus.* As in the forelimb, the posterior paddle is composed of packed polygonal elements which distally become more rounded and spaced.

Girdles.—Girdles are completely lacking in SM. They are preserved in BSPHGM, disarticulated but only slightly displaced from their original position (see Figs. 2, 7).

The pectoral girdle preserves interclavicle, the two clavicles and scapulae, as well as one coracoid (Fig. 7.1). The interclavicle is stout and typically T-shaped. The clavicles are robust, curved elements, bearing interdigitating surfaces in their junction zones, as in *Ophthalmosaurus.* Only the dorsal rami of the scapulae are preserved. The preserved coracoid is large and rounded.

The pelvic girdle is bipartite (Fig. 7.2). One ilium and both puboischiatic complexes are preserved. The ilium is a recurved stick of bone. Ischium and pubis are completely fused. No foramen marking the suture between the two bones is visible, unlike *Ophthalmosaurus* and *Stenopterygius.* In ichthyosaurs, pubis and ischium are usually wider distally than proximally, but in *Aegirosaurus* the distal end of the complex is diagnostically expanded, being more than twice the width of the proximal extremity (1.7 cm versus 0.7 cm).

Ontogenetic variation.—Using Johnson's (1977) criterion for the shape of the humeral head, both specimens are probably immature, as they have very flat humeral head surfaces. However, SM was probably older than BSPHGM, because of its greater size. It should be noted that the orbital and snout differences observed between the two specimens of *Aegirosaurus* are here interpreted in terms of ontogenetic rather than taxonomic differences. The differences in ratios are within the interval expected from a intraspecific growth series [see McGowan, 1994 for *Temnodontosaurus platyodon* (Conybeare, 1822)]. The difference in tooth form and ornamentation could also be related to ontogenetic variation (Kiprijanoff, 1881).

Soft tissue impression.—In SM, soft tissue impression is preserved all around the body, except the skull (see Fig. 1). The caudal fin is perfectly preserved and bears the typically lunate form. The soft tissue impression also reveals important details concerning the limb shape. The forelimb outline follows closely the skeleton anteriorly, distally and posteriorly, revealing that the forepaddle was long, narrow and deeply concave posteriorly (see Fig. 5). It differs from an *Ichthyosaurus* specimen from England, in which the outline is almost straight and extends distally well beyond the limb bones (Owen, 1841). In the hindlimb, the outline extends anteriorly, distally and posteriorly beyond the limb skeleton, indicating that the hindpaddle was short and very broad (see Fig. 6).

With grazing lighting, three different types of soft tissue impression, interpreted here as skin impression, have been recognized: 1) longitudinal rippled-like texture along the back, the base of the paddles and the pelvic region (see Figs. 5, 6, 8), looking like some already described in the litterature (Lydekker, 1889c; Martill,1993, pl. 5, figs. 2, 4); 2) straight fibers perpendicular to the rippled-like texture, at the abdomen and back levels producing a ''cross-hatched'' pattern (Fig. 8) which could be comparable with that described by Martill (1993, pl. 5, figs. 5, 6); and 3) rounded millimeter-scale structures in the dorsal part of the lunate tail. These last impressions have not been produced by epifaunal activity and are here tentatively interpreted as minute scales covering the ichthyosaurian skin, an opposite opinion to Martill (1995). The occurrence of such a skin structure on at least this ichthyosaurian taxon must be confirmed by detailed microscopic analysis.

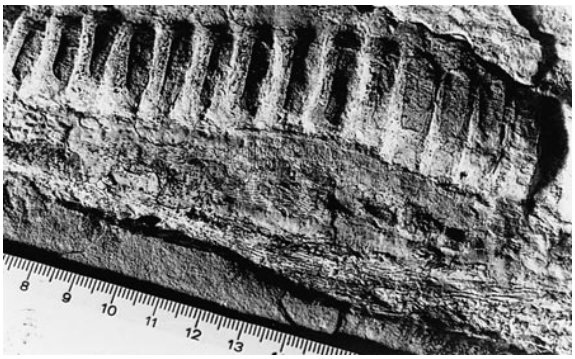

FIGURE 8—*Aegirosaurus leptospondylus* n. comb., SM (neotype), Solnhofen Formation, early Lower Tithonian, Schrandel quarry district, South of Langenaltheim, Bavaria. Soft tissue impression back to the pelvic region. Note the rippled textures and the perpendicular straight fibers in the area located between the ruler and the vertebrae. When combined, they produce a ''cross-hatched'' texture.

DISCUSSION

According to the descriptions given by Wagner (1853a, p. 28–29) and Bauer (1898, p. 291–294) of its type specimen (Oberndorfer specimen), the species *I. leptospondylus* was mainly characterized by a long and slender snout fitted with numerous, small teeth; a rather large orbit filled almost completely by the sclerotic ring; elongated and narrow nares; small, short vertebrae with a diameter about twice the length, bearing diapophyses confluent with neurapophyses and parapophyses anteriorly located on the centra; a narrow scapula expanded at both extremities and medially slender; and polygonal paddle elements without a notch. These characters are also shared by the two specimens described in this paper. It thus can be assumed that the Oberndorfer specimen, SM and BSPHGM belongs to the same species, namely *I. leptospondylus.* As the Oberndorfer specimen has been destroyed, *I. leptospondylus* is a species inquirendae (McGowan, 1976) and SM is here proposed as the neotype of this species. Concerning the two generic names commonly combined with *leptospondylus*, none of them applies: *Ichthyosaurus* is not appropriate because of significant diagnostic differences (see McGowan, 1974; Godefroit, 1994b) and *Macropterygius* is a nomen dubium, as previously noted (see McGowan, 1976; Kirton, 1983). Moreover, the combination of characters exhibited by the Oberndorfer specimen, SM and BSPHGM, differentiates them from all other known genera. As a result, the new genus *Aegirosaurus* is here proposed as a new combination for the species *leptospondylus.*

Until recently no global phylogenetic analysis of Ichthyopterygia has been made, so that the relationships within this group remain poorly known. Preliminary analyses of post-Triassic ichthyopterygian phylogeny have been performed by Kirton (1983), Godefroit (1994a) and Maisch (1998) and a comprehensive phylogenetic analysis has been carried out recently by Motani (1999b). According to this analysis, *Aegirosaurus* clearly belongs to the Ophthalmosauria because of the following synapomorphies: 1) the angular is largely exposed laterally, reaching as far anteriorly as the surangular; and 2) the occurrence of an extrazeugopodial element anterior to the radius and the associated digit distal to it (Motani, 1999a, 1999b). This clade includes

at least *Ophthalmosaurus, Brachypterygius, Caypullisaurus* and *Platypterygius* (Motani, 1999a, 1999b). Within the Ophthalmosauria, *Ophthalmosaurus, Caypullisaurus* and *Platypterygius* differ from *Aegirosaurus* by their epipodial arrangement (extrazeugopodial element + radius + ulna). *Aegirosaurus* shares with *Brachypterygius* the same forefin construction and especially the humerus-intermedium contact, but differs from it in several cranial characters such as the delicate snout fitted with numerous small teeth, the number of sclerotic plates and the short jugal.

Pending a more precise description and illustration of several taxa, notably from Russia (Arkhangelsky, 1997, 1998, 1999; Efimov, 1998, 1999a, 1999b) and a detailed comparative study of the taxa included into the Ophthalmosauria, precise phylogenetic relationships of *Aegirosaurus* among Ophthalmosauria cannot be traced yet.

CONCLUSION

A systematic review of the ichthyosaurs from the Late Jurassic of Bavaria, based on the bibliographical revision of old collections (most destroyed during World War II—see Historical account and Appendix) and the description of two new specimens, reveals that three different taxa were probably present during Tithonian times during deposition of the lithographic limestones of the Solnhofen area: *Aegirosaurus leptospondylus* (Wagner, 1853a) new combination, an indeterminate form close to *Ophthalmosaurus* or *Caypullisaurus* (Häberlein specimen—see Appendix) and an indeterminate one possibly close to *Nannopterygius* (Solhnofen specimen—see Appendix). This study shows that ichthyosaurs from the lithographic limestones of Bavaria were not as scarce as previously thought and that during Tithonian time, ichthyosaurs were more diversified worldwide than classically assumed.

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APPENDIX

Review of lithographic limestones ichthyosaurs from Bavaria (old collections)

One tooth (Munich State Museum, destroyed during WWII).—An isolated tooth from the *Diceras* Chalk near Kelheim, part of the Oberndorfer collection (Kelheim) and type of the species *Ichthyosaurus posthumus* Wagner, 1852. It was slightly recurved and bore a short, rounded enamel crown, ornamented by longitudinal striations, with a robust, oval, strongly ridged root. This tooth is typically ichthyosaurian but does not exhibit any specific diagnostic character so that it is assigned to an indeterminate ichthyosaur.

Oberndorfer specimen (Munich State Museum, destroyed during WWII).—A partial skeleton from the Oberndorfer collection, type of *Ichthyosaurus leptospondylus* Wagner, 1853a, partially figured by Wagner (1853b, pl. 6, figs. 14, 15) and Bauer (1898, pl. 25, figs. 1–5). It consists of fragments of both jaws, a sclerotic ring, a quadrate, six teeth, a scapula, several vertebrae, ribs and paddle elements, of a single individual found during mining works in the lithographic limestones of Borscheim.

According to the descriptions given by Wagner (1853a, p. 28–29), Fraas (1891, p. 73–74) and Bauer (1898, p. 291–294), this specimen was a medium size (about 2 m), but not an adult. It was mainly characterized by a long, slender snout fitted with numerous small, striated teeth (height between 1.2 and 2 cm); a large orbit filled almost completely by the sclerotic ring (diameter about 7 cm); a large postorbital (height about 6 cm); long and narrow nares; a massive reniform quadrate (height about 5.5 cm) bearing an oval stapedial facet; a powerful mandible; small and short, biconcave vertebrae with a diameter about twice the length (diameter about 3 cm, length about 1 cm), with diapophyses confluent with neurapophyses and parapophyses located anteriorly on the centra; a narrow scapula, expanded at both extremities and slender medially; and finally irregular penta- or hexagonal paddles elements without any notch.

The only character used by Wagner (1853a, p. 29) to justify the creation of this new species was the extraordinary difference in teeth with *I. posthumus.* According to Fraas (1891, p. 74), the short vertebrae and great number of paddle elements indicate a species close to *Ophthalmosaurus* or *Baptanodon.* This specimen roughly shares the same character combination that the two new skeletons here described. The specific name *leptospondylus* is thus kept as valid and newly combined to *Aegirosaurus* (see discussion for more details).

Häberlein specimen (Munich State Museum, destroyed during WWII).—This first ichthyosaurian specimen to have be found in the lithographic limestones of Bavaria was mentioned as 'an exemplar found with polygonal bones in the flippers and draughtboard-shaped vertebral centra' (Quenstedt, 1852, p. 129). It was assigned to *I. leptospondylus* by Wagner (1861) and later considered by Fraas (1891, p. 74) as the new type of this species. This small and rather well preserved specimen came from Solnhofen and was part of the Häberlein collection (Pappenheim). This specimen was 90 cm long and included the skull and mandible, teeth, vertebrae, ribs, pectoral girdle and paddle elements.

Following the description given by Wagner (1861, p. 120–121), Fraas (1891, p. 74–75) and Bauer (1898, p. 295–299), this individual was estimated to have been about 1.5 m long, of which the skull occupies 35 cm. It was mainly characterized by a large orbit (compared to the animal size) filled entirely by the sclerotic ring; numerous, small, slender and almost smooth teeth (height about 1.2 cm) weakly anchored in the jaws (they were all preserved separately); a robust mandible; short vertebrae with a diameter more than twice the length (diameter about 2.3 cm, length about 0.8 cm); a pectoral girdle composed of slender scapula, rounded and unnotched coracoid and pointed interclavicle; and a pelvic girdle represented only by an elongated ilium (pubis of Wagner, 1861; Bauer, 1898, p. 299). The most diagnostic elements described by Bauer (1898, p. 299) were those of the paddle. The humerus (basiphenoid of Wagner, 1861) was described as short and robust (length =

3.2 cm, proximal width = 2.4 cm, distal width = 3.2 cm) with three distal facets. The two largest for radius and ulna were almost equal in size (1.6 cm and 2 cm) and at 131 degrees to each other; whereas the smallest (few mm) for the pisiform was dorsally oriented. The femur was preserved as an impression in the matrix. It was described as short (length = 1.9 cm, proximal width = 1 cm, distal width = 1.5 cm) with two distal facets (0.9 cm and 0.7 cm). Finally, about 100 paddle elements, ranging from 1.5 cm to 0.3 cm were preserved, the largest being penta- or hexagonal whereas the smallest being rounded.

According to Wagner (1861), this specimen belongs to the same species as the Oberndorfer one and differs from it only in its relative size and mandible height. On the contrary, for Fraas (1891, p. 74–75), the Häberlein specimen was clearly different from the Oberndorfer one and considered as the new type and only specimen referable to *I. leptospondylus*. Finally, Bauer (1898), considered these two specimens as belonging to the same species, the Häberlein one being considered as a juvenile. Bauer (1898) also noted that the humerus of the Häberlein specimen looks like that of *Ophthalmosaurus cantabrigiensis* and that its hindlimb was very reduced compared to the forepaddle.

For Fraas (1891), the short vertebrae and great number of paddle elements suggest a species close to *Ophthalmosaurus* or *Baptanodon*. We confirm here his view, arguing that the Oberndorfer and Häberlein specimens belong to different taxa. The above mentioned characters, namely a large orbit, small teeth all preserved out of the jaws (which seem thus edentulous), the humerus shape and the important reduction of the hindlimb, indicate that the Häberlein specimen has possible affinities with *Ophthalmosaurus* or *Caypullisaurus*. Nevertheless, the very poor illustration of the material prevents any accurate identification. It is considered as an indeterminate form, possibly close to *Ophthalmosaurus* or *Caypullisaurus*.

BMNH 42833 (London).— An incomplete skull from the lithographical limestones of Eichstätt, part of the Krantz collection (Bonn), referred to *I. leptospondylus* (Meyer, 1863, p. 222) and later to *I. posthumus* (Fraas, 1891, p. 73).

This portion of skull, 31.2 cm long, preserved the snout back to the nares. Its total length was estimated to about 42 cm (Meyer, 1863). The snout is long, slender (length about 28 cm) and not markedly demarcated from the skull in lateral view. It bears numerous minutely ridged or smooth, small teeth, well anchored in the dental groove and extending almost under orbit. The nares is elongated (2.7 cm) and tapers anteriorly. On the basis of these combination of characters, this specimen is here referred as to cf. *Aegirosaurus leptospondylus*.

One tooth and two vertebrae (Munich State Museum, destroyed during WWII).—An isolated tooth from Eichstätt (Fraas, 1891, pl. 11, fig. 18) and a vertebra from Solnhofen (Fraas, 1891, pl. 12, fig. 5) were attributed to *I. posthumus*. Another vertebra from Kelheim (Fraas, 1891, pl. 12, fig. 6) was referred to as *I. leptospondylus*. These three specimens do not show any diagnostic character permitting a precise identification and they are assigned to indeterminate ichthyosaurs.

Solnhofen specimen (Munich State Museum, destroyed during WWII).—An incomplete skeleton unearthed from the lithographic limestones of Solnhofen, including skull elements, vertebrae, ribs, parts of pectoral and pelvic girdles. The description given by Bauer (1898, p. 300–309) was extensive but the illustrations were very poor.

The specimen was 1.45 m long (estimated length about 2–2.5 m) and mainly characterized by a long and slender skull about 41 cm long; large orbits (diameter about 7 cm) completely filled by the sclerotic ring; elongated nares tapering anteriorly as in the Meyer specimen; premaxillae long and slender, forming part of the lower narial opening; maxillae excluded from the nares; jugals located above the maxillary and forming the lower orbital margin; triangular nasals taking part in the nares and articulating with premaxillae and lacrymals; pterygoids bearing two branches at an angle of 50–60 degrees; basicranium robust; teeth small (height about 0.7 to 1.5 cm) and very variable in crown ornamentation, being either smooth or striated; mandible about 37.5 cm long with a powerful dentary; fifty short vertebrae (diameter about 2 cm, length about 1.2 cm) with diapophyses confluent with neurapophyses; short and robust femur (height = 2 cm) with two articular facets; polygonous paddle elements (2 mm to 2 cm); pectoral girdle including elongated coracoids (length = 6.54 cm, width = 4.4 cm) with an anterior notch, scapulae (length = 7.5 cm) and clavicle (length = 11 cm); and a tripartite pelvic girdle composed of rodlike ilium (length = 4.24 cm), bootlike ischium (length = 2.93 cm) and sticklike pubis (length = 1.98 cm).

This specimen was assigned by Bauer (1898) to *I. trigonus* var. *posthumus* along with all the ichthyosaurs from the Late Jurassic of Bavaria. Some characters exhibited by the Solnhofen specimen such as a slender skull, a medium size orbit (ratio estimated to about 0.19), small teeth, small and short thoracic vertebrae, an elongated and anteriorly notched coracoid, a tripartite pelvis and finally a femur with two distal facets, tend to exclude *Brachypterygius* and *Ophthalmosaurus* but are comparable to *Nannopterygius*. However, because of the scarcity of the illustrations given by Bauer (1898) it is not possible to assign the Solnhofen specimen with certainty to this genus and it is thus only considered as an indeterminate ichthyosaur, possibly close to *Nannopterygius*.

Tail (Munich State Museum, destroyed during WWII).—The lunate tail 90 cm high, with soft tissue impression, was from a large specimen estimated to be about 4 m long, referred to *I. trigonus* var. *posthumus* (Bauer, 1898; Merriam, 1908). It comes from the lithographic limestones of an indeterminate locality in Bavaria. The angle of downturn (about 80 degrees) was very high. There were about 12 vertebrae preserved before the tail-bend and 70 after, the last one being elongated with bulged borders. This specimen does not exhibit characters permitting a precise identification and may be only assigned to an indeterminate ichthyosaur.

Rib and vertebrae (Munich State Museum, destroyed during WWII).—A slab from Kelheim mentioned by Bauer (1898, p. 295) included about 8 abdominal ribs and 12 vertebrae. As no description was given and as the material is poorly diagnostic, it could only be assigned to an indeterminate ichthyosaur.

Paddle elements (Munich State Museum, destroyed during WWII).—A slab from Solnhofen mentioned by Bauer (1898, p. 300) consisted of articulated paddle elements exhibiting four primary digits (radial, ulnar, intermedium and pisiform). No detailed description was given of this material. The limb construction and especially the occurrence of an intermedium suggests either *Aegirosaurus* or *Brachypterygius* but it is impossible to determine in this specimen, which is referred as an indeterminate ichthyosaur.