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New finds of *Omphalosaurus* and a review of Triassic ichthyosaur paleobiogeography

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With 4 figures and 1 table

Kurzfassung: Triassische Ichthyosaurier sind weit verbreitet und sehr vielgestaltig, aber die meisten Formen sind schlecht bekannt. Neue Funde, wie sie hier beschrieben werden, unterstreichen die erste Feststellung, lassen die zweite aber nur langsam ungültig werden.

Das erste assoziierte Skelett des ungewöhnlichen durophagen Ichthyosauriers *Omphalosaurus, O. wolfi* aus der Mitteltrias (unterstes Ladin) der Salzburger Alpen, wird beschrieben und diskutiert. Die Wirbel haben die für Ichthyosaurier typische Morphologie und belegen damit eindeutig die Zugehörigkeit dieses Taxons zu den Ichthyosauriern.

Ein runder Knochen aus dem fränkischen Muschelkalk wird als linker Humerus von *Omphalosaurus* sp. identifiziert. Diese beiden Funde weiten das Verbreitungsgebiet und das zeitliche Auftreten von *Omphalosaurus* bedeutend aus, da die Gattung bis jetzt nur vom Westrand des nordamerikanischen Kratons und von Spitzbergen bekannt war. Die neuen Funde erlauben außerdem eine Differentialdiagnose der Gattung und eine Revision ihrer Arten, von denen *Omphalosaurus nettarhynchus, O. nevadanus* und *O. wolfi* als gültig erachtet werden, nicht aber *O. nisseri*.

Im Zusammenhang mit diesen neuen Einsichten zur Verbreitung triassischer Ichthyosaurier ist es nötig, die Gültigkeit schlecht bekannter Gattungen, z.B. des mitteltriassischen *Pessosaurus*, zu überprüfen. *Pessosaurus* ist kein valides Taxon, weil ihm diagnostische Merkmale fehlen.

Wenn man den Fortschritt in der Erforschung der Trias-Ichthyosaurier bewertet, stellt man fest, daß die Diversität auf dem Gattungs- und Familienniveau weitgehend bekannt ist, zumindest was prä-norische Vorkommen in Nordamerika, Europa und Ostasien betrifft.

Abstract: Triassic ichthyosaurs are very widespread and diverse but most taxa are poorly known. New discoveries, such as described in this paper, underscore the first statement but only slowy invalidate the second.

The first associated skeleton of the unusual durophagous ichthyosaur *Omphalosaurus* (*O. wolfi*) is reported from the Middle Triassic (earliest Ladinian) of the northern Alps. The vertebrae are of the ichthyosaurian type, firmly establishing the ichthyosaurian affinities of the genus.

A round bone from the Muschelkalk of Franconia, Germany, is identified and described as a left humerus of *Omphalosaurus* sp. These finds greatly extend the paleogeographic and temporal range of *Omphalosaurus* which previously was only known from the western cratonic margin of North America and from Spitsbergen. The new records of *Omphalosaurus* allow a revised differential diagnosis of the genus and a revision of its species. Valid species of *Omphalosaurus* are *O. nettarhynchus, O. nevadanus*, and *O. wolfi*.

In conjunction with such new insights into Triassic ichthyosaur distribution, it is necessary to address the validity of the poorly known genera such as the Middle Triassic *Pessosaurus*. This taxon must be considered invalid because it lacks diagnostic characters.

In assessing progress in research on Triassic ichthyosaurs and their paleobiogeography, it becomes apparent that supraspecific diversity appears largely known, at least for the pre-Norian record of North America, Europe, and East Asia.

Introduction

Ichthyosaurs currently enjoy considerable scientific attention, and a wealth of new discoveries has been made in the last fifteen years. In addition, the focus of research has shifted away from the familiar Jurassic ichthyosaurs to the more poorly known and poorly preserved (as well as commonly more enigmatic) forms that inhabited the Triassic seas.

The paleobiogeography of Triassic ichthyosaurs also continues to elicit interest and our knowledge is rapidly increasing. However, a true understanding of the biogeographic history, i.e. dispersal, is still hampered by the lack of a phylogenetic analysis of this group. At present we are mainly establishing the paleobiogeographic pattern, i.e. the distribution of taxa around the world and in time. This pattern can be altered in two ways: first by the discovery of new occurrences in space and time, and second by restudy of material housed in museum collections, leading to systematic revisions such as synonymy, invalid taxa or recognition of new taxa. We here provide a number of examples for this observation, with the larger goal in mind to assess the status of our knowledge of Triassic ichthyosaur diversity and its implications for phylogenetic studies of these animals.

This review was catalyzed by two seemingly out-of-the-way discoveries of the durophagous ichthyosaur *Omphalosaurus* from the German Muschelkalk

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(*Omphalosaurus* sp.), described in this paper, and from the northern Alps, described by Tichy (1995) as *O. wolfi*. *Omphalosaurus* was hitherto only known from Spitsbergen and Nevada (U.S.A.). This great range extension fits a more general pattern seen in recent research worldwide, i.e. that most Triassic ichthyosaurs were very widespread and that most new finds represent records of known genera and not new genera.

Abbreviations: HBG = Heimatmuseum Burg Golling, Golling near Salzburg, Austria; MHI = Muschelkalkmuseum Hagdorn, Ingelfingen, Germany; PIMUZ = Paläontologisches Institut und Museum der Universität Zürich, Switzerland; PMU = Paleontologiska Museet, Uppsala University, Sweden; UCMP = Museum of Paleontology, University of California at Berkeley, U.S.A.

Omphalosaurus diversity and new finds

One of the most enigmatic of all ichthyosaurs is, no doubt, the Middle Triassic genus *Omphalosaurus*. Indeed, its ichthyosaurian affinities have repeatedly been questioned, an issue that will be considered in more detail below. The animal also is one of the most durophagous of all ichthyosaurs, in fact of all secondarily aquatic tetrapods. Although the anatomy of *Omphalosaurus* is very poorly known, currently four nominal species are recognized whose validity will be addressed below.

In North America, *Omphalosaurus nevadanus* and *O. nettarhynchus* are known from the Prida Formation of the Humboldt Range, Nevada. *Omphalosaurus nevadanus* was collected from the late Anisian beds of the Fossil Hill Member of the Prida (Merriam 1906; Merriam & Bryant 1911), whereas *Omphalosaurus nettarhynchus* was recently described from the Spathian beds of the lower member of the Prida (Mazin & Bucher 1987). *O. nevadanus* is only known from the holotype, a fragmentary skull with the anteriormost cervical vertebrae, and from two referred fragments of dentitions (Merriam 1906; Merriam & Bryant 1911; Mazin 1986a), while *O. nettarhynchus* is based on even scantier remains, a fragmentary lower jaw (Mazin & Bucher 1987).

The genus is also represented in the classical Spitsbergen ichthyosaur faunas. The Spitsbergen material of *Omphalosaurus* was initially called *Pessopteryx* by Wiman (1910). *P. nisseri* was based on isolated dentition fragments and isolated girdle and limb bones, and three additional species were based on three isolated humeri. Similar material from Spitsbergen was also described by Mazin (1983). However, there is no positive evidence that the isolated postcranials, whose ichthyosaurian nature is uncontroversial, belong to the same animal as the dentition fragments. This should be kept in mind when the following discussion touches on any girdle and limb elements of this taxon.

Soon after Wiman's (1910) description of *Pessopteryx* it was pointed out by Merriam (1911) that at least the cranial part of this material should be referred to *Omphalosaurus*. This was accepted by Wiman (1916). The synonymy was formalized by Mazin (1983) who also recognized only one valid species from Spitsbergen, *Omphalosaurus nisseri*. *O. nisseri* occurs in the Spathian/Anisian boundary beds called the Lower Saurian Niveau by Wiman (1910).

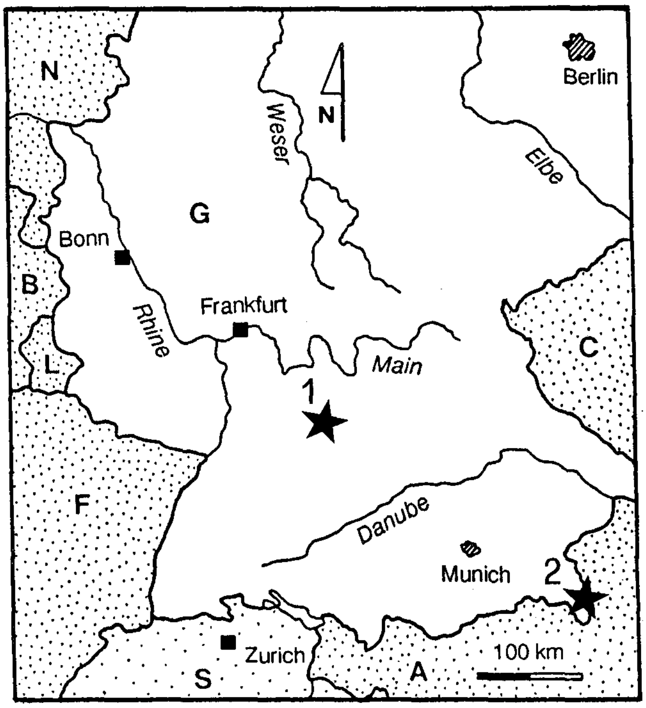


Fig. 1. Localities of *Omphalosaurus* specimens described in this paper. – 1. Garnberg Quarry near Künzelsau, Baden-Württemberg, where the humerus of *Omphalosaurus* sp. was found in the Oberer Hauptmuschelkalk beds of late Ladinian age. 2. Dürrnberg mountain in the Salzburg Alps straddling the German-Austrian border where *Omphalosaurus wolfi* was found in the Lercheck Limestone in a bed of earliest Ladinian age. – A = Austria, B = Belgium, C = Czech Republic, F = France, G = Germany, L = Luxemburg, N = The Netherlands, S = Switzerland.

New specimens of *Omphalosaurus* now come from central Europe (Fig. 1), one from the Muschelkalk and one from the northern Alps. The former will be described first.

The Muschelkalk specimen

The specimen (Fig. 2) was collected by H. Hagdorn (MHI) in 1984 from the Garnberg Quarry near Künzelsau, southwestern Germany. The exact stratigraphic horizon is Upper Hauptmuschelkalk (mo_3), Hohenlohe Beds, between clay horizons g and e. These beds belong either to the *praenodosus* Zone or the *nodosus* Zone, indicating a late Ladinian (Longobardian) age for the specimen (Hagdorn 1991).

Description and identification

The specimen MHI 1314 is a flat, roughly circular bone with a greatest width of 100 mm and a maximum thickness of 35 cm (Fig. 2). The perimeter of the bone consists

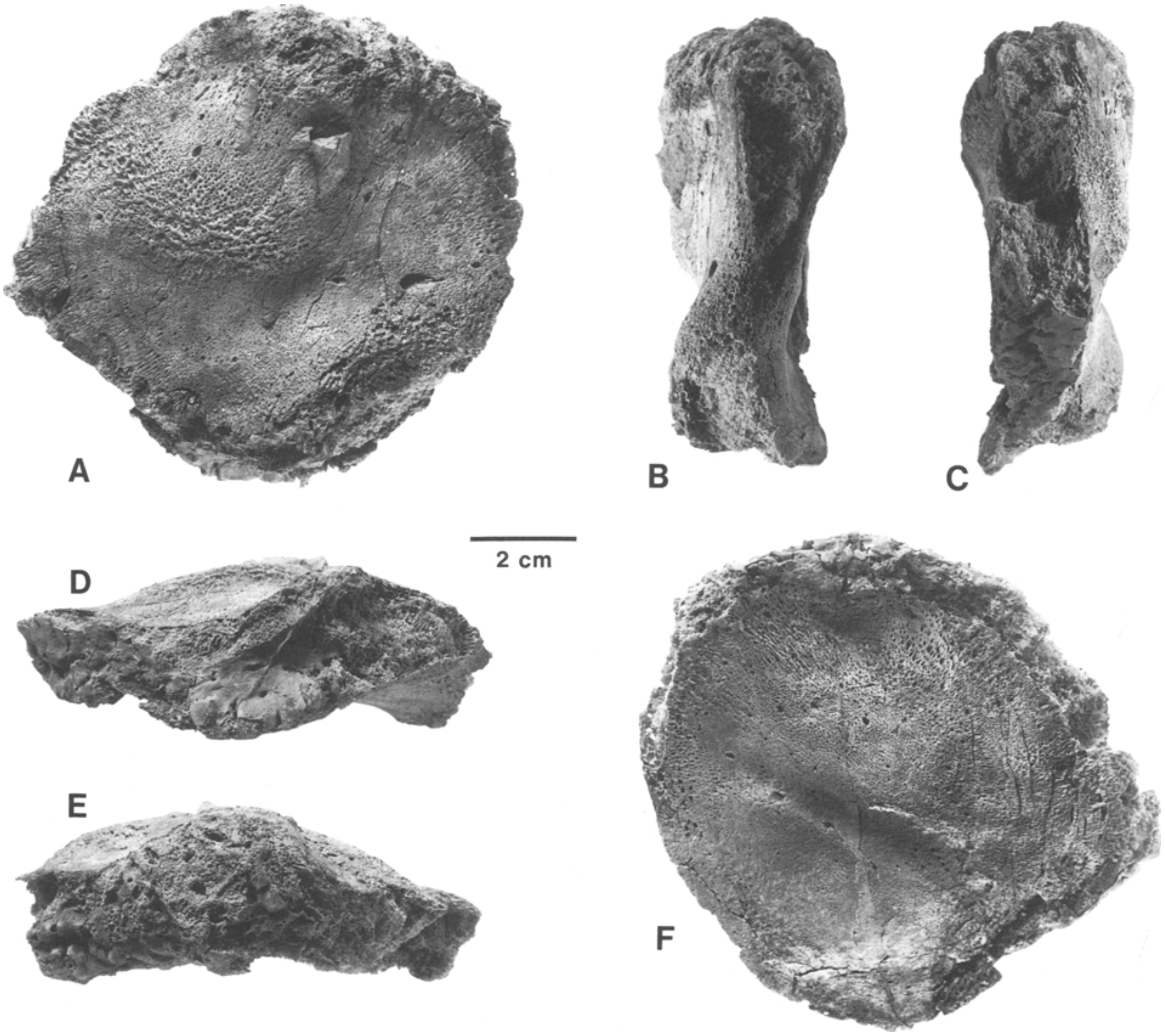


Fig. 2. *Omphalosaurus* sp., MHI 1314, left humerus from the Muschelkalk. – **A:** dorsal view; **B:** posterior view; **C:** anterior view; **D:** distal view; **E:** proximal view, the corroded parts of the margin expose the cancelous bone structure typical for ichthyosaurs; **F:** ventral view.

almost completely of the characteristic, slightly concave pitted surfaces forming the attachment of articular and other cartilages in many ichthyosaurian and sauropterygian bones. Upon closer inspection of the morphology it becomes apparent that the bone is a humerus of ichthyosaurian affinity. Although pectoral and pelvic girdle bones of a number of ichthyosaurs and sauropterygians including placodonts are flattened and roughly circular in shape, none have large tuberosities in the middle of the flat surfaces. The ichthyosaurian affinity of the bone are also clearly evidenced by bone histology (Fig. 2 B, C, D). As can be seen in coroded parts of the margin, the bone structure is entirely cancelous and completely lacks a compacta. This character of bone histology is an adaptation to a completely aquatic mode of life and can be seen in ichthyosaurs, plesiosaurs, mosasaurs, and dolphins (BUFFRÉNIL et al. 1987; BUFFRÉNIL & MAZIN 1990). Of these groups, only ichthyosaurs existed in Triassic times.

Upon closer inspection, the morphology of MHI 1314 (Fig. 2) is very similar to the round bones described as the humeri of *Omphalosaurus* by WIMAN (1910) and MAZIN (1983). More precisely, the MHI humerus is a left one. The proximal end is formed by the gently arched articular surface for the glenoid while the distal end consists of the radial and ulnar facets which are at an angle of about 120°.

In lateral view (Fig. 2 A), the most prominent feature is the deltopectoral crest which is a low hump covered by rugosities close to the middle of the lateral face. Another well developed rugosity is found on the ulnar facet of the humerus. The posterior margin (Fig. 2 B) consists of a finished bone surface but is rather short. The anterior margin of the bone is damaged but seems to have been

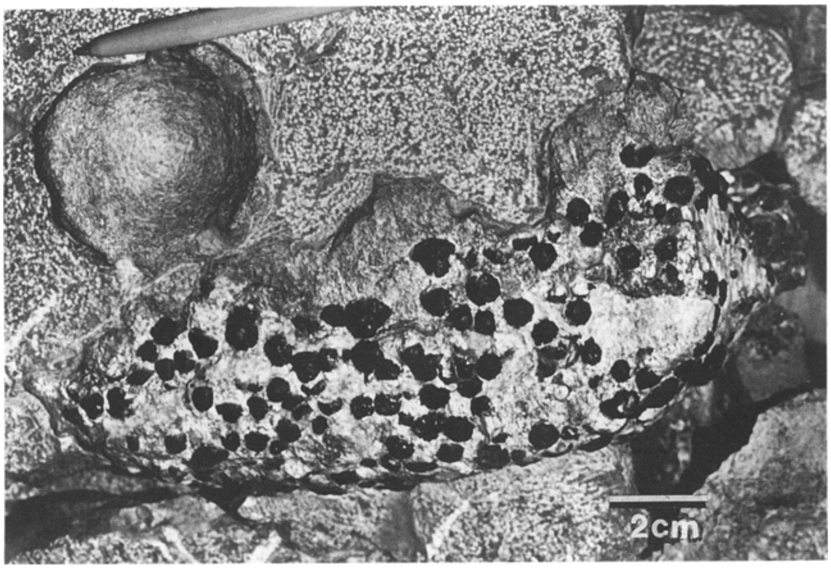


Fig. 3. *Omphalosaurus wolfi* TICHY 1995, HBG uncat. Premaxillary bone, the occlusal surface is covered by irregularly packed, button-like teeth. Note the deeply amphicoelous vertebra below the tip of the pen.

covered completely by cartilage. In medial view (Fig. 2F), the bone is nearly flat with raised edges except for a distinctive groove. This groove is about 9 mm wide and runs from posteroproximal to anterodistal. A similar groove is seen in the humerus of *Shastasaurus osmonti* figured by MERRIAM (1908: pl. 15, fig. 1).

Comparisons

The Muschelkalk humerus differs from the Spitsbergen humeri mainly in its proportions. The latter are somewhat longer than wide, usually by about 10 % (figures in WIMAN 1910: pl. 8, figs. 1-4; MAZIN 1983: fig. 3; pl. 2, figs. A-B) while MHI is wider (100 mm) than long (89 mm). The size range of *Omphalosaurus nisseri* humeri is considerable, from 90 to 160 mm long. Thus the Muschelkalk specimen falls within this size range. Apart from the proportions, a comparison of the outlines is of little use as this is rather variable in the Spitsbergen material (figures in WIMAN 1910; MAZIN 1983), probably due to the fact that only the posterior margin of these bones was not continued in cartilage.

Although a humerus of roughly circular outline would appear to be restricted to a single taxon, *Omphalosaurus*, this is not the case and near-circular humeri are rather common in Triassic ichthyosaurs. Thus, the humerus of *Cymbospondylus buchseri* from the Middle Triassic of Monte San Giorgio, Switzerland, is also isometric with an unfinished anterior margin and a rounded, finished posterior edge (SANDER 1989: 171). However, no clear separation into radial and ulnar articular facets can be observed, and both lateral and medial sides are rather flat. Another, unfortunately undescribed, large shastasaurid from Monte San Giorgio in the Zurich collections (PIMUZ uncat.) has a nearly circular humerus as well, but with a large anterior or posterior notch. Again, this bone is very flat. '*Pessosaurus*' humeri from Spitsbergen (WIMAN 1910: pl. 7, fig. 2b) were claimed to be „of the same type“ as the *Omphalosaurus* humeri by WIMAN (1910). Judging from WIMAN's figures, this bone also is rather flat.

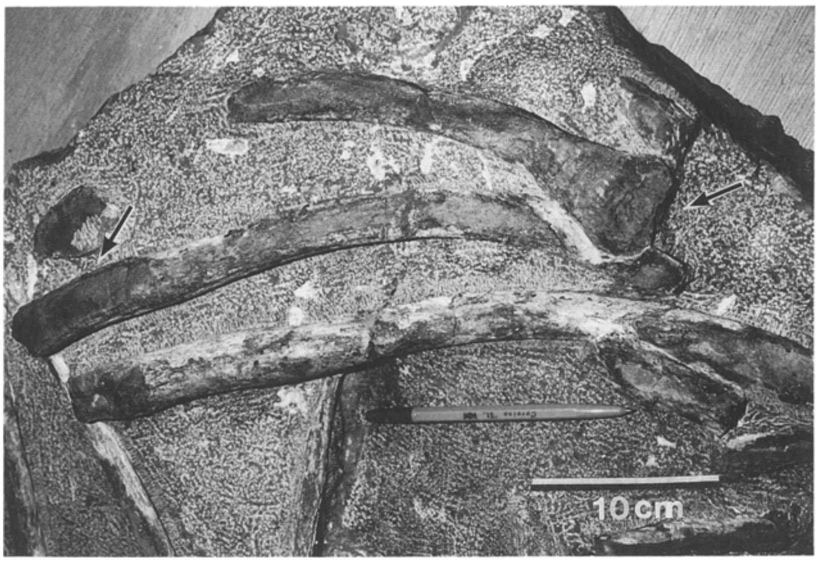
Thus the new Muschelkalk humerus (Fig. 2) still most closely compares to *Omphalosaurus nisseri* (WIMAN 1910; MAZIN 1983), particularly in its unique large rugose deltopectoral crest but also in the separation of the ulnar and radial facets. Again, humeri of this type have not been found in articulation or close association with the cranial material of *Omphalosaurus*, and until their derivation from the same animal is proven, all conclusions must be considered tentative. In the first description of the disarticulated partial skeleton of *Omphalosaurus wolfi*, TICHY (1995) identified a bone as a humerus that has a seemingly different morphology from the round bones. As discussed below, the affinity of this bone remains unresolved at present.

The Alpine *Omphalosaurus*

Bearing in mind the meager state of knowledge about *Omphalosaurus*, the significance of the discovery of a partial skeleton is immediately obvious. Such a find was recently made in the northern Alps near the Austrian city of Salzburg, the excact locality being the Dürrnberg Mountain near Hallein about 15 km S of Salzburg, but on German territory (Fig. 1; TICHY 1995). The bones were discovered in 1991 by an amateur paleontologist, Mr. G. WOLF of Hallein, in the Lercheck Limestone while collecting ammonites. The Lercheck Limestone is part of the Hallstatt Facies. The bed from which the specimen derives is of earliest Ladinian age (Fassanian, TICHY 1995).

TICHY (1995) gave a preliminary description of the specimen and named it *Omphalosaurus wolfi*. Here we offer additional observations and interpretations in the current context, but the detailed description of the specimen requires further preparation.

Fig. 4. *Omphalosaurus wolfi* TICHY 1995, HBG uncat. Several dorsal ribs, rib heads to the right. The rib shafts are round in cross section and have a thickened, swollen appearance in their distal third. The thickened region was once hollow but is now matrix-filled as can be seen in the obliquely truncated middle rib (arrow). The rib head (arrow) is dorsoventrally expanded but forms a single articular surface.



Description

The specimen (Figs. 3, 4) consists of a partial, associated skeleton of a moderately large ichthyosaur which at the time of deposition may have been complete. Some missing bones were destroyed by weathering while others may still remain in the rock at the locality. In addition to the largely complete but disarticulated skull, a number of presacral vertebrae, ribs, and one element identified by TICHY (1995) as the humerus are present. The assignment of the new specimen to *Omphalosaurus* was initially based on the highly characteristic dentition which is nearly identical to that of *Omphalosaurus nisseri*. Other features of the lower jaw are also closely similar to known taxa, in this case to the only other species of which significant skull material is known, *O. nevadanus*.

Skull: In accordance with the extreme crushing dentition, the bones of the skull all are built very massively. Most easily identified are the tooth-bearing bones (Fig. 3). Both premaxillae, to which the maxillae may be fused, are preserved. These bones are dominated by the very powerful dentition which forms two elongate grinding surfaces oriented at nearly right angles to each other. One grinding surface faces ventrally while the other has a parasagittal orientation (Fig. 3). A similar arrangement of teeth, i.e. not only oriented in one plane, is seen in the lower jaw, the dorsal and medial surfaces of which are covered to the very tip by the pavement of teeth.

The anterior portions of the lower jaws, consisting of dentaries and splenials, are fused at the symphysis and gradually taper to a blunt point. The symphysis is ventrally very long because the splenials meet rather far posteriorly along the midline, as is the case in *O. nevadanus*. These bones make up much of the preserved ventral surface of the lower jaws while the dorsal surface consists of the dentaries.

TICHY (1995) suggested that the Salzburg specimen differs in its tapered lower jaw from the supposedly more blunt-snouted skull of *O. nevadanus*. However, the only known skull of this species (UCMP 8121) is truncated about 5 cm anterior to the splenial symphysis. The reconstruction of a short rostrum provided by MAZIN (1986a) is possibly incorrect because it leaves no room for a tooth pavement that is also recorded for the Nevada *Omphalosaurus*, albeit in the shape of two isolated tooth-bearing bone fragments (MERRIAM & BRYANT 1911). *O. nevadanus* may well have had the same kind of snout as the Alpine *Omphalosaurus*.

Dentition: The teeth are arranged in an irregular pavement (Fig. 3) as in the Spitsbergen *Omphalosaurus* and not in distinct rows. Contributing to the irregular appearance, the teeth are exposed in various stages of wear from newly errupted to worn down to the dentin core. The tooth crowns are low and button-like with the orange peel surface typical for the genus. Teeth are only found in the lower jaw and on the marginal bones of the upper jaw. There is no evidence of teeth on the palate.

Axial skeleton: A number of cervical and dorsal vertebrae are present, but these bones seem to have been corroded by long exposure on the sea floor, destroying most of the details. The vertebral centra are of the typical ichthyosaurian type. They are deeply amphicoelous and circular to polygonal in anteroposterior cross section (Fig. 3). Synapomorphic for ichthyosaurs is also their shortness compared to their height and width, which can be observed throughout the preserved part of the column. One dorsal centrum was measured at 50 mm in length at a height and width of 80 mm, the length/height ratio being 0.625.

Rib articular facets could not be discerned due to poor preservation, but the nature of the articulation is indicated by the rib heads (Fig. 4). Numerous dorsal ribs are well exposed. They generally have a dorsoventrally expanded single head. In one instance, a rib seems to be doubleheaded due to a recess in the expanded articular region. As far as can be told, the cervical ribs are single-headed as well.

The shafts of the dorsal ribs have a very unusual morphology and structure. They are rather thick (diameter 2.5 cm) and circular in cross section (Fig. 4) as opposed to the anteroposterior grooves common in other ichthyosaurs. About two thirds down their length, the ribs increase markedly in thickness to form an elongate swelling which may be up to 3.5 cm in diameter (Fig. 4). Natural breaks show the expanded area to be hollow with a thin wall. This cavity in the ribs extends at least halfway towards the rib head.

Discussion

In general, the new find of *Omphalosaurus* supports what has been surmised from the scanty evidence available so far (MERRIAM 1906; MERRIAM & BRYANT 1911; WIMAN 1910; MAZIN 1983, 1986a). *Omphalosaurus* was a moderately large and plump aquatic reptile, extremely adapted to a durophagous mode of life. The complete dentition can be seen for the first time in the Salzburg specimen and is remarkable in its extent and massivness (Fig. 3). Particularly unusual are the two premaxillary grinding surfaces at right angles on the premaxillae, the function of which is rather enigmatic at present.

The swollen, hollow ribs (Fig. 4) are completely unknown in any other ichthyosaur and add to the enigma of *Omphalosaurus*. Swollen ribs would not have been surprising if this swelling were due to pachyostosis, a common adaptation in amniotes returning to the water (e.g. sauropterygians; RICQLÈS 1989). However, the function of such thick hollow ribs is rather unclear at present, suggesting bone histology analysis to help solve the problem. Certainly, the hollowing-out of the ribs did not serve to strengthen and lighten the skeleton of *Omphalosaurus*. In fact, lightening is achieved by a different histologic pathway in aquatic tetrapods as described BUFFRÉNIL et al. (1987) and BUFFRÉNIL & MAZIN (1990). In the most advanced stage of aquatic adaptation as in dolphins, marine turtles, plesiosaurs, mosasaurs, and ichthyosaurs, the bone becomes cancellous throughout and the compacta is lost. This was also observed in *O. nisseri* limb bones (BUFFRÉNIL et al. 1987) making it even more remarkable that the ribs of the Alpine *Omphalosaurus* are hollow and not filled with cancellous bone.

Alternatively, the hollow ribs could be the result of taphonomic processes. A similar hollowing out was observed by COOMBS & DEMÉRÉ (1995) in some bones of a nodosaurid dinosaur carcass discovered in Cretaceous marine sediments in southern California. As ankylosaurs found in terrestrial sediments never have hollow bones, COOMBS & DEMÉRÉ (1995) conclude that the hollow bones are a taphonomic artifact for which „marine organisms may be responsible".

Unfortunatly, the Salzburg specimen cannot provide information about the appendicular skeleton of *Omphalosaurus* as none of its elements appear to be preserved. Although TICHY (1995) described a humerus in the skeleton of *Omphalosaurus wolfi*, we believe that the bone in question cannot be identified with confidence at present. The bone is still largely embedded in the matrix and its shape can only imcompletely observed. It appears to be a massive, rod-shaped element about 19.5 cm long with a slightly bent and constricted central portion and concave surfaces of unfinished bone at either end. The bone shows no similarity with other Triassic ichthyosaur humeri. The position of the bone in the skeleton is directly posterior to the completely disarticulated skull to which it could well belong, considering the generally extremely massive appearance of the skull and lower jaw bones.

The species of *Omphalosaurus*

The description of the Alpine *Omphalosaurus* as a new species by TICHY (1995) invites a review of this and the other species of the genus, based largely on first-hand observation of the specimens but also on published evidence. The species level diversity of *Omphalosaurus* is of great importance for paleobiogeographic considerations. As all nominal species are based on rather incomplete material, it needs to be shown that they are, in fact, distinct from each other, i.e. that they can be diagnosed properly as well as that they are correctly ascribed to the genus. Stratigraphic and geographic separation provides no justification for species validity.

The description of *O. wolfi* by TICHY (1995) will serve as the starting point. Diagnostic characters of this species can potentially only be found in the skull, lower jaw, and dentition which are known to a variable degree in all four nominal species (*O. nettarhynchus*, *O. nevadanus*, *O. wolfi*, *O. nisseri*). However, the skull of *O. wolfi* is currently too poorly known and that of *O. nevadanus* too poorly preserved to serve in a comparison, leaving only lower jaw and dentition characters for the analysis.

O. nettarhynchus is only known from small articulated fragmentary dentaries with teeth of the *Omphalosaurus* type (MAZIN & BUCHER 1987). The holotype and only specimen was not seen by us. There are relatively few and large teeth. The most important character is the symphysial area which is laterally expanded in the lower jaw. This region was believed by MAZIN & BUCHER (1987) to widen into a spatulate snout, hence the species name. The jaw rami enclose an acute angle at the symphysis.

O. nevadanus is only known from a fragmentary, partially articulated skull (MERRIAM 1906) and two isolated tooth-bearing bones (MERRIAM & BRYANT 1911) which one of us (PMS) had the opportunity to study. MERRIAM (1911) noted that there were short limb elements similar to those of *O. nisseri* associated with the type of *O. nevadanus* but that he refrained from describing them at the time because he was not sure of their association with the skull material. These limb elements could not be located in the UCMP collections in 1994 and it is unclear from MERRIAM's writing if they were collected. Little can be added to the descriptions of the type by MERRIAM

(1906) and MAZIN (1986a). Important characters of this species are the large number of small teeth and the round angle enclosed by the lower jaw symphysis dorsally as well as ventrally.

O. wolfi has been described by TICHY (1995) as well by us (see above) and consists of a single incomplete partial skeleton. As opposed to *O. nevadanus*, the lower jaw symphysis in this species is acute-angled in dorsal view where it is formed by the dentaries. In ventral view, where it is formed by the splenials, the symphysis is round-angled and very similar in outline to that of *O. nevadanus*. *O. wolfi* cannot be distinguished from *O. nisseri* based on the number of tooth rows because the teeth are not set in rows but in an irregular pavement. Tooth density appears to be rather similar in *O. nisseri*, *O. nevadanus*, and *O. wolfi*. The skull of *O. nevadanus* cannot be shown to be shorter (smaller) than that of the Salzburg *Omphalosaurus*, contrary to the suggestion by TICHY (1995), because the snout with the dentition is largely unknown in *O. nevadanus*, and the reconstruction of its snout by MAZIN (1986a) is probably too short. *O. wolfi* can be distinguished from *O. nettarhynchus* in its much larger size and its much greater number of teeth.

O. nisseri cranial material consists only of small tooth-bearing fragments too incomplete to assign to specific jaw bones. As noted above, the irregular pavement of densely spaced teeth is very similar to the condition in *O. wolfi* and the referred specimens of *O. nevadanus*. The presumed postcranials of *O. nisseri* can only be compared to the new Muschelkalk humerus.

Thus the two Nevada species and *O. wolfi* appear to be valid but *O. nisseri* cannot be diagnosed properly and must be considered a nomen dubium. This discussion is distilled below into the revised differential diagnosis of the genus *Omphalosaurus* and its valid species.

Systematic paleontology

Reptilia LINNAEUS 1758
Diapsida OSBORN 1903
Ichthyosauria DE BLAINVILLE 1835
Omphalosauridae MERRIAM 1906
Omphalosaurus MERRIAM 1906

Diagnosis: Small to medium-sized durophagous ichthyosaur. Differs from all other ichthyosaurs in the particular arrangement of the teeth forming an irregular pavement and not being set in distinct rows. No other ichthyosaur has maxillary grinding surfaces oriented at right angles to each other. The tooth crowns differ from the other durophagous ichthyosaurs (*Phalrodon, Tholodus*) in that they are lower and more irregular in shape. Instead of longitudinal wrinkles as in the other durphagous ichthyosaurs, the enamel surface has a characteristic orange-peel pitting.

The skull and lower jaw bones are much more massive than in any other ichthyosaur. In no other ichthyosaur have expanded hollow ribs been found. The roundish humeri found in association with *Omphalosaurus* dentitions differ from other roundish ichthyosaur humeri in their prominent deltopectoral crest.

Locality and horizon: Nevada, Spitsbergen, Germanic Basin, northern Alps; late Spathian to late Ladinian.

Referred species: *O. nettarhynchus*, *O. nevadanus*, *O. wolfi.*

Discussion: The genus also has an autapomorphic enamel microstructure discussed in detail elsewhere (SANDER 1996). However, only the enamel of *O. nisseri* was studied but this differed very much from that of the other durophagous ichthyosaurs investigated, *Phalarodon* sp. and *Tholodus schmidi* (SANDER 1996).

Omphalosaurus nettarhynchus MAZIN & BUCHER 1987

Diagnosis: Small species, differs from the other species in the laterally expanded symphysial area of the snout and the presence of relatively few but large teeth.

Omphalosaurus nevadanus MERRIAM 1906

Diagnosis: Differs from the other two species in the rounded posterior margin of the dentary symphysis. Differs from *O. nettarhynchus* in its much larger size and its much greater number of teeth.

Omphalosaurus wolfi TICHY 1995
Figs. 3, 4

Diagnosis: Differs from *O. nevadanus* in the acute angle enclosed by the dentary symphysis. Differs from *O. nettarhynchus* in its much larger size and its much greater number of teeth.

Is *Omphalosaurus* an ichthyosaur?

Although MERRIAM was intimately aquainted with Triassic ichthyosaurs (e.g. MERRIAM 1908), when describing *Omphalosaurus* the ichthyosaurian affinity of this animal were not apparent to him (MERRIAM 1906). They were not championed until much later (MAZIN 1983, 1986a) and have repeatedly been questioned, most recently by MOTANI (1997a) who suggested sauropterygian affinities. However, there are several characters that strongly suggest that *Omphalosaurus* is an ichthyosaur. The most important is the morphology of the cervical and dorsal vertebral centra as seen in *Omphalosaurus wolfi* (see above). The centra are not fused to the neural arches (which are unknown) and distinctly shorter than high. This shortness is combined with a nearly circular to polygonal anterorposterior outline and deeply amphicoelous anterior and posterior faces (Fig. 3). There are no distinct transverse processes, and the ribs must have articulated on dorsoventrally elongate facets on the sides of the centra as indicated by the single, dorsoventrally expanded ribs heads (Fig. 4) that are similar to those of the Triassic ichthyosaur family Shastasauridae.

Tab. 1. New finds of Triassic Ichthyosauria since 1985 and their geographic distribution. The tabulation is at the genus level. Note the dominance of new records of known genera (n) over the discovery of new genera (G). See text for details.

	Mexico	Nevada	Oregon	Idaho	Wapiti Lake	Williston Lake	Spitsbergen	Muschelkalk	Swiss Alps	Salzburg Alps	Dolomite Mts.	Monte San Giorgio	Thailand	China	Japan	New Caledonia
Utatsusaurus	-	-	-	-	n	-	-	-	-	-	-	-	-	-	+	-
Grippia	-	-	-	-	n	-	+	-	-	-	-	-	-	?	?	-
Thaisaurus	-	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-
Phalarodon	-	+	-	-	n	-	n	-	-	-	-	-	-	-	-	-
Mixosaurus	-	o	-	-	?	-	?	+	-	-	-	+	-	-	-	-
Parvinatator	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-	-
Omphalosaurus	-	+	-	-	-	-	+	n	-	n	-	-	-	-	-	-
Cymbospondylus	-	+	-	n	-	-	n	+	-	-	n	n	-	-	-	-
Shastasaurus	n	?	n	-	-	n	?	n	-	-	o	?	-	-	-	-
Shonisaurus	?	+	-	-	-	?	-	-	n	-	-	-	-	-	-	n
Pessosaurus	-	-	-	-	o	-	o	o	-	-	-	-	-	-	-	-
Besanosaurus	-	-	-	-	-	-	-	-	-	-	-	G	-	-	-	-
Hudsonelpidia	-	-	-	-	-	G	-	-	-	-	-	-	-	-	-	-
Ichthyosaurus	-	-	-	-	-	n	-	-	-	-	-	-	-	-	-	-

+ = known before 1985, - = not present, o = no longer valid, n = new record, G = new genus, ? = questionable occurrence

At the histological level, there is also strong evidence for the ichthyosaurian affinities of *Omphalosaurus*. Using a hand lens, the fractured or worn bone surfaces of *O. wolfi* can observed to show the cancelous bone structure described by BUFFRÉNIL et al. (1987) and BUFFRÉNIL & MAZIN (1990) as typical for ichthyosaurs. The bone of other Triassic marine reptiles shows a well developed outer layer of compact bone (compacta), thus being much closer to the terrestrial pattern. Enamel microstructure also supports ichthyosaurian affinities of *Omphalosaurus*. Several ichthyosaurs including *Omphalosaurus* have an enamel type called microunit enamel which among other reptiles is only found in *Nothosaurus* but not in placodonts (SANDER in press).

Although placodont affinities of *Omphalosaurus* might seem likely, they are contradicted by the lack of a palatal dentition in *Omphalosaurus* and the lack of tooth pavements on the jaw bones as well as microunit enamel in placodonts.

Omphalosaurus paleobiogeography

With the new finds from the Muschelkalk and the Salzburg Alps, the genus *Omphalosaurus* is recorded for the first time in the European Middle Triassic (Tab. 1). It should be noted that there are no finds of the genus in Spain, contrary to the erroneous statement in SANDER & MAZIN (1993). Previously, *Omphalosaurus* has been found in Spitsbergen and Nevada, U.S.A. Thus, the genus is documented for the entire core region of Triassic ichthyosaur finds consisting of the eastern Pacific, the western Boreal realm, and the western Tethys. The occurrences range in age from late Spathian to late Ladinian. Late Spathian are *O. 'nisseri'* from Spitsbergen and *O. nettarhynchus* from Nevada. *O. nevadanus* is late Anisian in age (MAZIN & BUCHER 1987), *O. wolfi* earliest Ladinian, and *O.* sp. from the Muschelkalk beds is late Ladinian, representing the youngest occurrence. This range from the late Spathian to the late Ladinian appears rather long for such a rare and poorly known taxon but mainly serves to illustrate the incomplete state of the fossil record and of our sampling. The oldest occurrence of *Omphalosaurus* in the eastern Pacific and the youngest in the Muschelkalk may hint at patterns of dispersal. However, this question cannot be addressed without a robust phylogenetic hypothesis for the species of *Omphalosaurus*.

Naturally, finds of *Omphalosaurus* in the Muschelkalk and the Alps came as somewhat of a surprise, considering the long history of collecting of marine vertebrates in Europe, particularly in the Muschelkalk. The new finds of *Omphalosaurus* are only the second and third durophagous ichthyosaur records from the region, the only other being *Tholodus* (SANDER & MAZIN 1993). An explanation for this rarity in the western Tethys was recently offered by SANDER & MAZIN (1993) who suggested that the „durophagous marine tetrapod“ role was already taken over by the placodonts. This hypothesis is somewhat undermined by the new finds, although placodonts are still vastly more common in the Middle Triassic of Europe than are durophagous ichthyosaurs. Placodonts also appear to have been very successful in the western Tethys in Late Triassic times, long after the disappearance of all durophagous ichthyosaurs.

Pessosaurus: does it exist?

In considering the paleobiogeography and diversity of Triassic ichthyosaurs, one is repeatedly faced with the unsatisfactory status of the shastasaurid genus *Pessosaurus*. We will here argue that this genus lacks sufficient diagnostic characters or combinations thereof and should be considered a nomen dubium. We will also argue that most material described as *Pessosaurus* should be assigned to Shastasauridae indet. Only rarely such material can be identified as *Cymbospondylus* or *Shastasaurus*. However, pending a formal, critical revision of the Shastasauridae, we will not formalize this synonymy at present.

The Spitsbergen *Pessosaurus*

Some of the first Triassic ichthyosaur remains ever to be described were fossils collected in the 1860's by the Swedish polar explorer A. E. NORDENSKIÖLD in the Ladinian of Spitsbergen (HULKE 1873). Much of the material was later identified as *Mixosaurus nordenskioeldii* (now *Phalarodon nordenskioeldii* according to BRINKMAN et al. 1992a; NICHOLLS et al. in press) and is of no concern here. However, two vertebral series, with eight and three vertebrae respectively, were described as *Ichthyosaurus polaris* by HULKE (1873). This material presumably is, i.e. according to WIMAN (1910), in the Naturhistoriske Riksmuseum, Stockholm, and has never been illustrated and not been studied since HULKE's time (WIMAN 1910). Early on *I. polaris* had a varied taxonomic history as its affinities with shastasaurids were recognized by MERRIAM (1902). The species was formally transferred to *Shastasaurus* by YAKOLEW (1902) and later to *?Cymbospondylus* by MERRIAM (1908: 149) as the anatomy of that genus became better known.

In describing remains of large ichthyosaurs from the Upper Saurian Niveau collected in 1908 and 1909, WIMAN (1910) assigned all the material to the species *polaris*, erecting the new genus *Pessosaurus* for it. From WIMAN's (1910) writing, it appears likely that he did not study the type material of *I. polaris*, however. Although WIMAN (1910) assumed that all material of large ichthyosaurs from the Upper Saurian Niveau belonged to *Pessosaurus polaris*, it is well possible that more than one large ichthyosaur is represented in these beds. Such diversity is the case in most other well documented ichthyosaur faunas from the Middle Triassic (SANDER & MAZIN 1993).

The presence of more than one taxon finds support in paleobiogeographic considerations as well as recent discoveries. As was pointed out by MAZIN (1986b) and SANDER (1992), the lack of *Cymbospondylus* on Spitsbergen represented a distinctive anomaly. It is surprising that the presence of this genus escaped notice until 1992 (SANDER 1992), considering the long history of research on Triassic ichthyosaurs from the region (HULKE 1873; MERRIAM 1908; WIMAN 1910, 1916; MAZIN 1981a, 1981b, 1983, 1984). The suggested explanation, of course, is that *Cymbospondylus* remains were found but not recognized as such and called *Pessosaurus* instead. A similar case already noted above is that of *Pessopteryx nisseri* (WIMAN 1910) which was indentified as *Omphalosaurus* by MERRIAM (1911).

The problems with the Spitsbergen ichthyosaurs stem from the fact that they are rarely found in association, let alone articulation, making identificaton of many remains difficult. This is illustrated well by a look at WIMAN's (1910) figured material of *Pessosaurus polaris* on his plate 7.

The snout fragment in plate 7, fig. 7 could belong to any shastasaurid. The descriptions of the dentition of *C. petrinus* by MERRIAM (1908) and of *Pessosaurus* by WIMAN (1910) are very similar. Both note the infolding at the base of the teeth and the finely but sharpely striated enamel, features which are clearly visible on fig. 7 of WIMAN (1910) as well as in the holotype of *C. buchseri* (SANDER 1989). However, these dental features are only indicative of shastasaurid affinities and not autapomorphic for *Cymbospondylus*. The dorsal vertebra in plate 7, fig. 4, already figured by YAKOLEW (1902), could easily be *Shastasaurus* but it is not diagnostic as the lower half is missing. The limb and girdle bones in plate 7, fig. 2, as well as the femur in fig. 3 could also belong to several shastasaurid taxa as these elements show great plasticity in the family (see also McGOWAN 1994). Their morphology, particularly that of the humerus, is diagnostic at the species level but not at the genus level. However, it seems unwise to erect a new species of unknown generic affinity based on a humerus!

Preparation of the string of dorsal vertebrae and ribs seen in cross section in WIMAN's (1910) pl. 7, fig. 1 would also expose characters of generic significance. The overall proportions of these vertebrae appear very similar to *Cymbospondylus buchseri* (SANDER 1989). A recent visit to the PMU (Uppsala, Sweden) made it clear that no further specimens of *Pessosaurus* than those figured by WIMAN (1910) exist in the collections, and direct inspection of the material led to few advances over WIMAN's published description. Very little further material of '*Pessosaurus polaris*' has come to light since. MAZIN (1984) notes that the animal is very rare and describes the only two specimens collected by a French expedition in 1969, a humerus and a jaw fragment. The humerus is rather round and similar to the one figured by WIMAN (1910).

Thus, none of WIMAN's (1910) material of *Pessosaurus polaris* is diagnostic beyond the family Shastasauridae. However, affinities with *Cymbospondylus* appear likely in view of its established occurrence in the Upper Saurian Niveau of Spitsbergen (SANDER 1992).

The Wapiti Lake *Pessosaurus*

CALLAWAY & BRINKMAN (1989) described an articulated string of five posterior dorsals from the Middle Triassic part of the Sulphur Mountain Formation of the Wapiti Lake area (British Columbia, Canada) as *Pessosaurus* sp. They base their assignment on HULKE's (1873) description of *I. polaris* and on WIMAN's (1910) pl. 7, fig. 5, specifically on the shape of the vertebrae and the diapophysis. The material does not represent *Cymbospondylus* because the otherwise similar diapophysis is located well posterior to the anterior margin of the centrum (SANDER 1989, 1992, 1997; MASSARE & CALLAWAY 1994). Keeping in mind the discussion of the Spitsbergen material of *Pessosaurus*, the Wapiti Lake specimen must be considered Shastasauridae indet. at present, but could well be *Shastasaurus* whose posterior dorsal vertebrae are poorly known.

The Muschelkalk *Pessosaurus*

VON HUENE (1916: 33, pl. 7, fig. 1) described a shastasaurid dorsal vertebra from the Anisian part of the Muschelkalk beds of Swabia (Germany) as *Pessosaurus suevicus* and a caudal vertebra from the same region as cf. *Pessosaurus suevicus*. As already noted by CALLAWAY & MASSARE (1989a), the material is not diagnostic to genus and species and is best considered Shastasauridae indet.

Discussion

In conclusion, the large ichthyosaur fossils described as *Ichthyosaurus polaris* by HULKE (1873), *Pessosaurus polaris* by WIMAN (1910), *Pessosaurus suevicus* by VON HUENE (1916), and *Pessosaurus* sp. by CALLAWAY & BRINKMAN (1989) are not diagnostic beyond the family Shastasauridae. These fossils could easily belong to *Cymbospondylus* or to *Shastasaurus* if not to other shastasaurid genera as well. Because of its uncertain status and affinities, all this material cannot enter genus-level paleobiogeographic considerations.

Published records since 1989

With the areal extension of *Omphalosaurus* records from the eastern Pacific and Spitsbergen to the Middle Triassic of Europe, a pattern is repeated that had been pointed out recently (SANDER 1992; SANDER & BUCHER 1990; SANDER & MAZIN 1993). Triassic ichthyosaurs are well known only from a core area consisting of North America, Europe, and intervening Spitsbergen while the record for the rest of the globe is poor (Tab. 1). This is partially due to the lack of adequate sediments (e.g. South America) and partially due to the much greater density of scientists in the core area than elsewhere. Outside the core area, only the Triassic of East Asia has yielded a significant ichthyosaur fauna. The majority of finds from new localities or new records from already known localities belong to already known genera or even species (Tab. 1). In this way, many genera of Middle Triassic ichthyosaurs and some of Upper and Lower Triassic ichthyosaurs are now known from all paleogeographic regions if not all localities from this core area (Tab. 1; see also SANDER & MAZIN 1993). The pattern of widespread distribution also appears to show up in the sauropterygian record from the Middle Triassic (SANDER et al. 1997).

To illustrate the above remarks, we will take a look at the history of research on Triassic ichthyosaurs during the last decade by reviewing new records of known genera and species, synonymies, and new genera and species. Material that cannot be assigned to genus is not considered. This time span was characterized by a greatly increased interest in Triassic ichthyosaurs which had attracted little attention from about 1930 to 1980. The 1989 tabulation of Triassic ichthyosaurs in time and space by CALLAWAY & MASSARE (1989a) serves as an excellent point of departure for the following consideratons.

This tabulation already incorporated the fauna of the newly discovered British Columbia (Canada) locality of Wapiti Lake which yielded three genera (*Mixosaurus* cf. *M. nordenskioeldii*, *Phalarodon* cf. *P. fraasi*, '*Pessosaurus*' sp.) from the start (CALLAWAY & BRINKMAN 1989); none of them new, however. The recently reported fourth (BRINKMAN et al. 1992b) and fifth genera (NICHOLLS & BRINKMAN 1993) are *Grippia* (*G.* cf. *longirostris*), already known from Spitsbergen, and *Utatsusaurus* (*U.* sp.), already known from Japan. However, recent work of MOTANI (1997b) suggests that *Utatsusaurus* may be a junior synonym of *Grippia*, and it would thus not be surprising if the Wapiti Lake finds pertain only to a single species.

Mixosaurids were once only poorly documented for the North American Middle Triassic (at the time only the Nevada Middle Triassic) which was surprising in view of their common occurrence elsewhere. With exploration in Nevada moving away from pelagic to more coastal deposits, there are now good records in this region (SANDER & BUCHER 1990; SANDER et al. 1994). This material was erroneously ascribed to *Mixosaurus* itself by these authors (as *Mixosaurus* cf. *M. natans* and *Mixosaurus* sp.) but turns out to be postcranial material of the mixosaurid *Phalarodon nordenskioeldii* (NICHOLLS et al. in press). This association is also documented by articulated material recently collected in Nevada.

Cranial remains of this animal from Nevada were described as *Phalarodon fraasi* by MERRIAM (1910). The finds from Wapiti Lake allowed NICHOLLS et al. (in press) to document that *Phalarodon fraasi* is a junior synonym of what traditionally had been called *Mixosaurus nordenskioeldii* from the Middle Triassic of Spitsbergen. While acknowledging that the material is mixosaurid, NICHOLLS et al. (in press) felt that *M. nordenskioeldii* is sufficiently distinct from the European and Chinese *Mixosaurus* species to warrant assignment to a separate genus, *Phalarodon*. This raises the question if there is any true *Mixosaurus* in North America. NICHOLLS et al. (in press) now only cite one specimen from Wapiti Lake (TMP 83.218.6; CALLAWAY & BRINKMAN 1989) as belonging to *Mixosaurus* sp. and the occurrence of the genus in Spitsbergen must also be viewed as questionable.

Concurrently with the first reports on the Wapiti Lake fauna, the first of the non-*Mixosaurus* ichthyosaurs of the diverse Middle Triassic Monte San Giorgio fauna of the southern Alps of Switzerland became known (SANDER 1989) and turned out to be a new species of the genus *Cymbospondylus* (*C. buchseri*), the only good material of which had previously been known from Nevada. *Cymbospondylus* (*C.* sp.) from the Middle Triassic of Spitsbergen followed soon (SANDER 1992). A new record of *Cymbospondylus* is also represented by a specimen from the Dolomite Mountains of the Italian Alps (SANDER 1989) which previously had been identified as *Shastasaurus*.

Turning to the other Shastasauridae, it can be noted that the first good records of *Shastasaurus* from the Middle Triassic of Europe were described just recently from the Muschelkalk beds of central Germany (*S. neubigi*, SANDER 1997). However, isolated vertebrae of *Shastasaurus* recorded from this formation had been identified for some time (CALLAWAY & MASSARE 1989a). Another new find, *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996) from near Besano in northern Italy, belongs to the Monte San Giorgio fauna as well. Although found on Italian territory, the locality is only about 1200 meters away from the nearest Swiss locality (Cava Tre Fontane) in the same beds. The authors of *Besanosaurus* believed it to be intermediate between *Cymbospondylus* and *Shastasaurus* but acknowledge its close similarity to *Shastasaurus*. It would not be surprising if, upon further study of the Besano specimen, it should turn out to belong to *Shastasaurus*. As noted above, there is at least one more undescribed form of medium to large ichthyosaur in the Monte San Giorgio fauna which may also pertain to *Shastasaurus* or may be new (SANDER & MAZIN 1993; COOK 1994).

For the Lower Triassic record, the occurrence of *Grippia* and *Utatsusaurus* at Wapiti Lake in Canada has been discussed already. In addition, as suggested by MOTANI (1994), another Lower Triassic ichthyosaur from East Asia (*Chaohusaurus* with *C. geishanensis* and two other species from China) is very close to if not the junior synonym of *Grippia*. *Grippia* thus is nearly as widespread as *Mixosaurus*, being known from Spitsbergen, Canada, and possibly Japan and China. Among the larger forms, ichthyosaur vertebrae from the Lower Triassic of Idaho are best identified as *Cymbospondylus* (*C.* sp.), extending the record of this genus into the Lower Triassic (MASSARE & CALLAWAY 1994).

Similar trends obtain for the Late Triassic: A new large ichthyosaur from Mexico belongs to *Shastasaurus* (CALLAWAY & MASSARE 1989b; *S.* cf. *altispinus*), a genus best known from California (MERRIAM 1908). MOTANI (1997c) believes this specimen to be closer to *Shonisaurus*, however. A new species of *Shastasaurus* (*S. neoscapularis*) was also reported „up the coast“, from the recently discovered Norian locality of Williston Lake, Canada (MCGOWAN 1994). An additional recent record of *Shastasaurus* (*S.* cf. *S. osmonti*) comes from the Wallowa Mountains of Oregon (ORR 1986). The occurrence of *Shastasaurus* in the Middle Triassic of Nevada is still not established although it appears likely (SANDER & MAZIN 1993). New remains of an even larger ichthyosaur from the Swiss Alps belong to *Shonisaurus* (CALLAWAY & MASSARE 1989a; *Shonisaurus* sp.) which was first described from Nevada (CAMP 1976, 1980; *S. popularis* and two additional species) and is also recorded from New Caledonia (MAZIN 1985; *S.* sp.). A new twist to the paleobiogegraphy of Triassic ichthyosaurs was added by MCGOWAN (1996) when he described a new record of a well-known Jurassic genus from the Norian of Williston Lake. This is *Ichthyosaurus janiceps* which is about 8 million years older than the other species of *Ichthyosaurus* which are best known from the Early Jurassic of England.

The reduction in diversity of Triassic ichthyosaurs by the recently suggested synonymies also adds to the pattern of a limited number of very widespread forms. The junior synonyms of *Grippia* as proposed by MOTANI (1994, 1997b, c) have been discussed above. With *Pessosaurus* a nomen dubium as advocated in this paper, a reduction in diversity results for Middle Triassic ichthyosaurs, although not accompanied by a gain in areal extent of another genus as is the case for *Grippia*. Further candidates for nomina dubia because of non-diagnostic type material clearly are the Lower Triassic *Svalbardosaurus crassidens* (MAZIN 1981b) and the Upper Triassic *Tibetosaurus tingjensis* (YOUNG et al. 1982), both of which are primarily based on large conical teeth. Such teeth are very common among ichthyosaurs, after all.

To test this pattern of a few widespread to cosmopolitan genera (Tab. 1), the publication of new genera since 1989 has to be reviewed. *Besanosaurus* (DAL SASSO & PINNA 1996) and the other new taxon from the Monte San Giorgio fauna have already been discussed. MAZIN et al. (1991) announced the discovery of *Thaisaurus chonglakmanii* from the Triassic of southern Thailand. Although this animal is poorly known and its age poorly constrained (see MOTANI 1997c) it may well turn out to belong to the *Grippia*-*Utatsusaurus* clade. NICHOLLS & BRINKMAN (1996) recently added a sixth member to the Wapiti Lake fauna, *Parvinatator wapitiensis*, which shows the same generalized forefin structure as *Utatsusaurus*, *Grippia*, and *Thaisaurus*. The age of *Parvinatator*, however, cannot be constrained beyond Lower to Middle Triassic because it was collected from scree. A new genus from the Late Triassic is the small *Hudsonelpidia brevirostris* described by MCGOWAN (1995) from the Norian of Williston Lake. Another new taxon, as yet unnamed, from Williston Lake is very large and shares characters with *Shonisaurus* from the Nevada Upper Triassic but also with *Leptopterygius* from the central European Lower Jurassic (MCGOWAN 1997).

In conclusion, some new genera have been erected in the last decade (Tab. 1) but most are based on such poor material or so poorly diagnosed that their validity is not beyond doubt, making it difficult to establish the number of new genera.

Implications for Triassic ichthyosaur paleobiogeography

Research trends since the CALLAWAY & MASSARE (1989a) survey can thus be characterized as follows (Tab. 1): despite a flurry of new discoveries, not many new genera (*Besanosaurus*, *Hudsonelpidia*, *Parvinatator*, *Thaisaurus*) were described (and most of those are poorly characterized) whereas the range of most established genera is continually expanding by new occurrences and synonymy (*Grippia*, *Phalarodon*, *Omphalosaurus*, *Cymbospondylus*, *Shastasaurus*, *Shonisaurus*). Only the range of *Mixosaurus* shrank to the 'benefit' of *Phalarodon*. A special case is represented by the record of *Ichthyosaurus* from the Norian of British Columbia because it is so much older than the other records of this genus.

These trends, of course, have implications for the utility of studying Triassic ichthyosaur paleobiogeography and for future directions of research in the field. Obviously, the very widespread and roughly contemporaneous occurrence of most genera in the core area of North America, Spitsbergen, and Europe leaves little room for the study of dispersal. If dispersal studies are to be successful, two conditions have to be met: first, determinable specimens of ichthyosaurs have to be collected from other coastal and shallow marine sediments of Triassic Pangea, and second, we need robust hypotheses of relationships within the Ichthyosauria as well as of the entire group.

In a worst case scenario, Smithian to Carnian ichthyosaur evolution and dispersal was too swift to register in the fossil record. In more positive terms, the diversity largely would be known today, providing a firm basis for phylogenetic analysis, leading in turn to a better understanding of ichthyosaur evolution. The Norian record, mainly based on the Williston Lake locality in British Columbia (Canada), appears to be rather different, indicating gradual evolution towards the ichthyosaurian diversity observed in the Jurassic (MCGOWAN 1991, 1994, 1996, 1997).

If, however, more detailed exploration of pre-Norian rocks in Sibiria, Africa, and Australasia would produce entirely new forms, dispersal and biogeography could fruitfully be studied (after phylogenetic analysis) from the fossil record of Triassic ichthyosaurs. Only future field work will tell.

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References

BRINKMAN, D. B.; NICHOLLS, E. L. & CALLAWAY, J. M. 1992a. New material of the ichthyosaur *Mixosaurus nordenskioeldii* from the Triassic of British Columbia, and the interspecific relationships of *Mixosaurus*. – North American Paleontological Convention V, Abstracts with Program: 37, Chicago.

BRINKMAN, D. B.; XIJIN, Z. & NICHOLLS, E. L. 1992b. A primitive ichthyosaur from the Lower Triassic of Brithish Columbia, Canada. – Palaeontology **35**: 465-474, Lawrence.

BUFFRÉNIL, V. DE & MAZIN, J.-M. 1990. Bone histology of the ichthyosaurs: comparative data and functional interpretation. – Paleobiology **16**: 435-447, Lawrence.

BUFFRÉNIL, V. DE; MAZIN, J. M. & RICQLÈS, A. DE 1987. Caractères structuraux et mode de croissance du fémur d'*Omphalosaurus nisseri*, Ichthyosaurien du Trias moyen de Spitsberg. – Annales de Paléontologie **73**: 195-216, Paris.

CALLAWAY, J. M. & BRINKMAN, D. B. 1989. Ichthyosaurs (Reptilia, Ichthyosauria) from the Lower and Middle Triassic Sulphur Mountain Formation, Wapiti Lake area, British Columbia, Canada. – Canadian Journal of Earth Science **26**: 1491-1500, Ottawa.

CALLAWAY, J. M. & MASSARE, J. A. 1989a. Geographic and stratigraphic distribution of the Triassic Ichthyosauria (Reptilia; Diapsida). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen **178**: 37-58, Stuttgart.

— 1989b. *Shastasaurus altispinus* (Ichthyosauria, Shastasauridae) from the Upper Triassic of the El Antimonio district, northwestern Sonora, Mexico. – Journal of Paleontology **63**: 930-939, Lawrence.

CAMP, C. L. 1976. Vorläufige Mitteilung über große Ichthyosaurier aus der oberen Trias von Nevada. – Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Sitzungsberichte, (I) **185**: 125-134, Wien.

— 1980. Large ichthyosaurs from the Upper Triassic of Nevada. – Palaeontographica, (A) **170**: 139-200, Stuttgart.

COOK, D. H. N. 1994. A new ichthyosaur genus from the Middle Triassic of Monte San Giorgio, Switzerland (Abstract). – Journal of Vertebrate Paleontology **14**: 21A-22A, Lawrence.

COOMBS, W. P. & DEMÉRÉ, T. A. 1995. A Late Cretaceous nodosaurid ankylosaur (Dinosauria: Ornithischia) from marine sediments of coastal California. – Journal of Paleontology **70**: 311-326, Lawrence.

Dal Sasso, C. & Pinna, G. 1996. *Besanosaurus leptorhynchus* n. gen. n. sp., a new shastasaurid ichthyosaur from the Middle Triassic of Besano (Lombardy, N. Italy). – Paleontologia Lombarda, Nuova serie **4**: 1-23, Milano.

Hagdorn, H. 1991. Muschelkalk - A Field Guide. – 80 pp., Korb (Goldschneck-Verlag).

Huene, F. von 1916. Beiträge zur Kenntnis der Ichthyosaurier im deutschen Muschelkalk. – Palaeontographica **62**: 1-68, Stuttgart.

Hulke, I. W. 1873. Memorandum on some fossil vertebrate remains collected by the Swedish expeditions to Spitzbergen in 1864 and 1868. – Bihang till K. Svenska Vetenskapsakademiens Handlingar **1**: 1-11, Stockholm.

Massare, J. A. & Callaway, J. M. 1994. *Cymbospondylus* (Ichthyosauria: Shastasauridae) from the Lower Triassic Thaynes Formation of southeastern Idaho. – Journal of Vertebrate Palaeontology **14**: 139-141, Lawrence.

Mazin, J.-M. 1981a. *Grippia longirostris* Wiman, 1929, un Ichthyopterygia primitif du Trias inférieur du Spitsberg. – Bulletin du Muséum national d'Histoire naturelle, Paris **3**: 317-340, Paris.

— 1981b. *Svalbardosaurus crassidens* n. g. n. sp., un Ichthyopterygien nouveau du Spathien (Trias inférieur) du Spitsberg. – Comptes Rendus de l'Académie des Sciences, Paris, (II) **293**: 111-113, Paris.

— 1983. *Omphalosaurus nisseri* (Wiman, 1910), un ichthyoptérygien à denture broyeuse du Trias moyen du Spitsberg. – Bulletin du Muséum national d'Histoire naturelle, Paris **5**: 243-263, Paris.

— 1984. Les Ichthyopterygia du Trias du Spitsberg – Descriptions complémentaires à partir d'un nouveau matériel. – Bulletin du Muséum national d'Histoire naturelle, Paris **6**: 309-320, Paris.

— 1985. Les Ichthyopterygia du Trias supérieur de Nouvelle Calédonie. Implications paléobiogéographiques. – Revue de Paléobiologie **4**: 177-182, Geneva.

— 1986a. A new interpretation of the type specimen of *Omphalosaurus nevadanus* Merriam 1906. – Palaeontographica, (A) **195**: 19-27, Stuttgart.

— 1986b. Paleobiogeography of Triassic ichthyopterygian reptiles; some working hypotheses. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen **173**: 117-129, Stuttgart.

Mazin, J.-M. & Bucher, H. 1987. *Omphalosaurus nettarhynchus*, une nouvelle espèce d'Omphalosauridé (Reptilia, Ichthyopterygia) du Spathien de la Humboldt Range (Nevada, U.S.A.). – Comptes Rendus de l'Académie des Sciences, Paris, (II) **305**: 823-828, Paris.

Mazin, J.-M.; Suteethorn, V.; Buffetaut, E.; Jaeger, J.-J. & Helmcke-Ingavat, R. 1991. Preliminary descriptions of *Thaisaurus chonglakmanii* n.g. n.sp., a new ichthyopterygian from the Lower Triassic of Thailand. – Comptes Rendus de l'Académie des Sciences, Paris, (II) **313**: 1207-1212, Paris.

McGowan, C. 1991. An ichthyosaur forefin from the Triassic of Brithish Columbia exemplifying Jurassic features. – Canadian Journal of Earth Sciences **28**: 1553-1560, Ottawa.

— 1994. A new species of *Shastasaurus* (Reptilia: Ichthyosauria) from the Triassic of British Columbia: the most complete exemplar of the genus. – Journal of Vertebrate Paleontology **14**: 168-179, Lawrence.

— 1995. A remarkable small ichthyosaur from the Upper Triassic of British Columbia, representing a new genus and species. – Canadian Journal of Earth Sciences **32**: 292-303, Ottawa.

— 1996. A new and typically Jurassic ichthyosaur from the Upper Triassic of British Columbia. – Canadian Journal of Earth Sciences **33**: 24-32, Ottawa.

— 1997. A transitional ichthyosaur fauna. – [In:] Callaway, J. M. & Nicholls, E. L. [eds.] Ancient Marine Reptiles: 61-80, San Diego (Academic Press).

Merriam, J. C. 1902. Triassic Ichthyopterygia from California and Nevada. – University of California Publications - Bulletin of the Department of Geology **3**: 63-108, Berkeley.

— 1906. Preliminary note on a new marine reptile from the Middle Triassic of Nevada. – University of California Publications - Bulletin of the Department of Geology **5**: 5-79, Berkeley.

— 1908. Triassic Ichthyosauria, with special reference to the American forms. – Memoirs of the University of California **1**: 1-155, Berkeley.

— 1910. The skull and dentition of a primitive ichthyosaurian from the Middle Triassic. – University of California Publications – Bulletin of the Department of Geology **5**: 381-390, Berkeley.

— 1911. Notes on the relationships of the marine saurian fauna described from the Triassic of Spitzbergen by Wiman. – University of California Publications - Bulletin of the Department of Geology **6**: 317-327, Berkeley.

Merriam, J. C. & Bryant, H. C. 1911. Notes on the dentition of *Omphalosaurus*. – University of California Publications – Bulletin of the Department of Geology **6**: 329-332, Berkeley.

Motani, R. 1994. Computer aided comparisons among Early Triassic ichthysosaurs reveals smaller taxonomic diversity than was believed. – Journal of Vertebrate Paleontology **14**: 39A, Lawrence.

— 1997a. Phylogeny of the Ichthyosauria (Amniota: Reptilia) with special reference to Triassic forms. – Journal of Vertebrate Paleontology **17**: 66A, Lawrence.

— 1997b. Redescription of the dentition of *Grippia longirostris* (Ichthyosauria) with a comparison with *Utatsusaurus hataii*. – Journal of Vertebrate Paleontology **17**: 39-44, Lawrence.

— 1997c. Temporal and spatial distribution of tooth implantations in Ichthyosaurs. – [In:] Callaway, J. M. & Nicholls, E. L. [eds.] Ancient Marine Reptiles: 81-103, San Diego (Academic Press).

Nicholls, E. L. & Brinkman, D. B. 1993. A new specimen of *Utatsusaurus* (Reptilia: Ichthyosauria) from the Lower Triassic Sulphur Mountain Formation of British Columbia. – Canadian Journal of Earth Science **30**: 486-490, Ottawa.

— 1996. A new ichthyosaur from the Triassic Sulphur Mountain Formation of British Columbia. – [In:] Sarjeant, W. A. S. [ed.] Vertebrate fossils and the evolution of scientific concepts: 521-535, London (Gordon and Breach Publishers).

Nicholls, E. L.; Brinkman, D. B. & Callaway, J. M. [in press]. New material of *Phalarodon* (Reptilia: Ichthyosauria) from the Triassic of British Columbia and its bearings on the interrelationships of mixosaurs. – Palaeontographica, (A), Stuttgart.

Orr, W. N. 1986. A Norian (Late Triassic) ichthyosaur from the Martin Bridge Limestone, Wallowa Mountains, Oregon. – U.S. Geological Survey, Professional Paper **1435**: 41-47, Washington.

Ricqlès, A. de 1989. Les mécanismes hétérochroniques dans le retour des tétrapodes au milieu aquatique. – Géobios, Mémoire Spécial **12**: 337-348, Lyon.

Sander, P. M. 1989. The large ichthyosaur *Cymbospondylus buchseri*, sp. nov., from the Middle Triassic of Monte San Giorgio (Switzerland), with a survey of the genus in Europe. – Journal of Vertebrate Paleontology **9**: 163-173, Lawrence.

— 1992. *Cymbospondylus* (Shastasauridae: Ichthyosauria) from the Middle Triassic of Spitsbergen: filling a paleobiogeographic gap. – Journal of Paleontology **66**: 332-337, Lawrence.

— 1996. The microstructure of reptilian tooth enamel: terminology, function, and phylogeny. – Habilitation Thesis, University of Bonn. – 191 pp., Bonn.

— 1997. The paleobiogeography of *Shastasaurus*. – [In:] CALLAWAY, J. M. & NICHOLLS, E. L. [eds.] Ancient Marine Reptiles: 17-43, San Diego (Academic Press).

— [in press]. Prismless enamel in amniotes: terminology, function, and evolution. – [In:] TEAFORD, M. F.; FERGUSON, M. W. J. & SMITH, M. M. [eds.] Development, Function and Evolution of Teeth: New York (Cambridge University Press).

SANDER, P. M. & BUCHER, H. 1990. On the presence of *Mixosaurus* (Ichthyopterygia: Reptilia) in the Middle Triassic of Nevada. – Journal of Paleontology **64**: 161-164, Lawrence.

SANDER, P. M. & MAZIN, J.-M. 1993. The paleobiogeography of Middle Triassic ichthyosaurs: The five major faunas. – Paleontologia Lombarda, Nuova serie **2**: 145-152, Milano.

SANDER, P. M.; RIEPPEL, O .C. & BUCHER, H. 1994. New marine vertebrate fauna from the Middle Triassic of Nevada. – Journal of Paleontology **68**: 676-680, Lawrence.

— 1997. A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of plesiosaurs. – Journal of Vertebrate Paleontology **17**: 526-533, Lawrence.

TICHY, G. 1995. Ein früher, durophager Ichthyosaurier (Omphalosauridae) aus der Mitteltrias der Alpen. – Geologisch-Paläontologische Mitteilungen Innsbruck **20**: 349-369, Innsbruck.

WIMAN, C. 1910. Ichthyosaurier aus der Trias Spitzbergens. – Bulletin of the Geological Institution of Upsala **10**: 124-148, Upsala.

— 1916. Notes on the marine Triassic reptile fauna of Spitzbergen. – University of California Publications - Bulletin of the Department of Geology **10**: 63-73, Berkeley.

YAKOLEW, N. 1902. Neue Funde von Trias-Sauriern auf Spitzbergen. – Verhandlungen der Kaiserlichen Mineralogischen Gesellschaft, (2) **40**: 179-203, Petersburg.

YOUNG, C. C.; LIU, D. & ZHANG, M. 1982. Ichthyosauria from Xizang Zhong. – Monograph on Mount Xixia, Bangma, Scientific Expeditions 1964: 350-355, Peking.

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