

Phylogeny, systematics, and origin of the Ichthyosauria – the state of the art

MICHAEL W. MAISCH

Abstract

A historical overview and a synopsis of the current knowledge on the phylogeny, systematics, and phylogenetic position of the Ichthyosauria are presented. All known ichthyosaur taxa are listed, new taxa are discussed and diagnosed. The following new taxa are erected: Thaisauridae n. fam., Wimaniidae n. fam., *Barracudasauroides* n. gen. with *Mixosaurus panxianensis* JIANG et al., 2006 as type species, as well as the species *Omphalosaurus merriami* n. sp. *Merriamosaurus* MAISCH & MATZKE, 2003 is a junior synonym of *Pessopteryx* WIMAN, 1910. “*Ichthyosaurus*” *acutirostris* OWEN, 1840 probably represents a genus of its own.

Based on this summary of our current understanding of the group as a whole, ichthyosaurs are included in two of the largest and more widely used phylogenetic analyses of the Amniota. Character codings and their justifications are discussed. No clear signal on the phylogenetic position of the Ichthyosauria results from these analyses. Instead, they are in one case nested within the Diapsida, but with the anapsid Mesosauria as their sister group. In the other case they are nested within Parareptilia, with Procolophonia (Testudines, Pareiasauria) as sister group. In contrast to previous assumptions, the inclusion of ichthyosaurs in these large-scale analyses always changes the original topology of the resulting cladograms so that turtles and pareiasaurs become sister groups. This underlines the importance of the taxon Ichthyosauria for any future large-scale phylogenetic analyses of amniotes.

At the present state of knowledge, a definite decision on the origin and phylogenetic position of ichthyosaurs is still impossible, but descent from primarily anapsid ancestors and an origin from among the Parareptilia can not be excluded as an alternative to a diapsid origin of the group.

Key words: Ichthyosauria, systematics, taxonomy, phylogeny, origin, phylogenetic analysis, Amniota.

Zusammenfassung

Es wird ein Überblick über die Geschichte und den aktuellen Kenntnisstand der Systematik, Phylogenie und der Diskussion um den Ursprung und die stammesgeschichtliche Stellung der Ichthyosaurier gegeben. Alle bekannten Ichthyosaurier-Taxa werden aufgelistet, neue Taxa werden diskutiert und diagnostiziert. An neuen Taxa werden eingeführt: Thaisauridae n. fam., Wimaniidae n. fam., *Barracudasauroides* n. gen. mit *Mixosaurus panxianensis* JIANG et al., 2006 als Typusart, sowie *Omphalosaurus merriami* n. sp. *Merriamosaurus* MAISCH & MATZKE, 2003 ist ein jüngeres Synonym von *Pessopteryx* WIMAN, 1910. „*Ichthyosaurus*“ *acutirostris* OWEN, 1840 repräsentiert wohl eine eigenständige Gattung.

Basierend auf dieser Zusammenfassung des derzeitigen Verständnisses der Gruppe insgesamt werden die Ichthyosaurier in zwei bestehende groß angelegte Phylogenien der gesamten Amnioten eingefügt. Die Merkmalscodierungen und ihre Begründungen werden im Einzelnen diskutiert. Es zeigt sich, dass aus den Analysen kein einheitliches Signal für die phylogenetische Stellung der Ichthyosaurier im System resultiert. Stattdessen finden sie sich einmal innerhalb der Diapsida, allerdings mit den anapsiden Mesosauriern als Schwestergruppe, ein andermal innerhalb der Parareptilia mit den Procolophonia (Parietasauria, Testudines) als Schwestergruppe. Entgegen anders lautender Vermutungen führt ein Einschluss der Ichthyosaurier in bestehende Analysen zur Amniotenphylogenie zwangsläufig zu einer Veränderung der Topologie, aus der ein Schwestergruppenverhältnis von Testudines und Pareiasauriern resultiert. Dies unterstreicht die Wichtigkeit des Taxons Ichthyosauria auch für künftige großangelegte phylogenetische Analysen der Amniota.

Eine Entscheidung über den Ursprung der Ichthyosaurier ist beim momentanen Kenntnisstand unmöglich, doch kann eine Ableitung von primär anapsiden Formen, insbesondere ein Ursprung innerhalb der Parareptilien, nicht schlüssig zugunsten einer Ableitung von diapsiden Formen widerlegt werden.

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1. Introduction

The work presented here is a result – or rather an intermediate progress report – of ongoing studies, started in 1994, on the most successful and enigmatic group of Mesozoic secondary marine amniotes, the Ichthyosauria. Ichthyosaurs are not known in the fossil record before the Smithian and seem to have become extinct by the end of the Cenomanian (see MAISCH & MATZKE 2000a; MCGOWAN & MOTANI 2003 for recent overviews). Probably they fell victim to one of the smaller global extinction events at the Cenomanian-Turonian boundary, after their diversity had already considerably dwindled since the Middle Jurassic (LINGHAM-SOLIAR 2003).

Generally, the fossil record of ichthyosaurs is very incomplete and patchy (see again MAISCH & MATZKE 2000a; MCGOWAN & MOTANI 2003), a statement which may be surprising with regard to the many virtually complete skeletons on display in museums and collections worldwide. These have, however, all been recovered from a very limited number of fossiliferous localities, most of which are concentrated in Western Europe and North America. This distribution of ichthyosaur fossils serves to explain why these animals have become a focus of palaeontological research from its beginning. Early scientists were significantly puzzled by the aberrant morphology of these animals and struggled to untangle their systematic relationships and to place them properly in existing classifications. The literature on ichthyosaurs has, as a result, become very extensive, with the first descriptions dating back to the 18th century. A couple of pioneers of ichthyosaur research of the 19th and early 20th century stand out with particular prominence. These are GEORG FRIEDRICH VON JÄGER, CARL VON THEODORI, HEINRICH GEORG BRONN, FRIEDRICH AUGUST VON QUENSTEDT, EBERHARD FRAAS, and FRIEDRICH VON HUENE from Germany, THOMAS HAWKINS, Sir RICHARD OWEN, JOHN WHITTAKER HULKE, CHARLES WILLIAM ANDREWS, and HAROLD GOVIER SEELEY from Great Britain, CHARLES WHITNEY GILMORE and JOHN C. MERRIAM from the USA, GEORGES CUVIER, HENRI MARIE DUCROTAY DE BLAINVILLE, and ALBERT GAUDRY from France, VALERIAN KIPRIJANOFF from Russia and CARL WIMAN from Sweden.

Despite these numerous early and a multitude of later studies, our understanding of this group of extraordinary reptiles is still very limited. Only about 10% of its history is represented by adequate or even barely diagnostic findings. Many of the usual and common ichthyosaur fossils, like isolated vertebrae, limb elements and teeth, offer few to no diagnostic characters and are therefore of little value for reconstruction of the evolutionary history of the group. This is particularly true for the morphologically more uniform Jurassic and Cretaceous neochelonians. The few important fossiliferous localities which have yielded about 90% of the available information on the group can be easily enumerated.

In the Lower Triassic, where the record is particularly patchy, these are the Sticky Keep Formation of Svalbard (with *Grippia*, *Pessopteryx*, *Quasianosteosaurus*, *Omphalosaurus* and the questionable *Isffjordosaurus*, as well as two undescribed taxa, none of them known from complete skeletons), the Osawa Formation of Japan (with *Utatusaurus* and another undescribed taxon), the Sulphur Mountain Formation of British Columbia (with *Parvinator*, *Phalarodon*, *Utatusaurus* and probably *Grippia*) and the Nanlinghu Formation (formerly Majiashan Formation, see TONG et al. 2001) in the Chinese Province of Anhui (with *Chaohusaurus*).

In the Middle Triassic there are several important localities that have yielded good material, including complete skeletons. The Tschermafjellet Formation of Svalbard, sometimes considered as Carnian, but with respect to its ichthyosaur fauna typically Middle Triassic (with *Phalarodon*, *Mixosaurus*, *Cymbospondylus*, and *Mikadocephalus*), the Grenzbitumenzone (Besano Formation) of Monte San Giorgio und Besano in the southern Alps (with *Mixosaurus*, *Phalarodon*, *Mikadocephalus*, *Wimanius*, *Besanosaurus*, and *Cymbospondylus*), the Germanic Muschelkalk (with *Contectopalatus*, *Phalarodon*, *Cymbospondylus*, *Phantomosaurus*, *Tholodus*, and *Omphalosaurus*) mostly yielding fragmentary material, though, the Prida Formation of Nevada (with *Phalarodon*, *Omphalosaurus*, and *Cymbospondylus*) and, more recently, the Guanling Formation of Guizhou, China (with *Barracudasauroides* gen. nov., *Phalarodon* and the enigmatic *Xinminosaurus*? = *Tholodus*).

Upper Triassic lagerstätten are sparse. They include the Hosselkus Limestone of California (with *Shastasaurus*, *Toretocnemus*, and *Californosaurus*), the Pardonet Formation of British Columbia (with *Shonisaurus*, *Callawayia*, *Macgowania*, and *Hudsonelpidia*), and the Falang Formation of Guizhou, China (with *Guizhouichthyosaurus* (? = *Shastasaurus*), *Guanlingsaurus*, and *Qianichthyosaurus*).

Lower Jurassic occurrences are even more restricted geographically and almost exclusive to Western Europe. They are mainly concentrated in the early Lower Jurassic of southern England and the late Lower Jurassic of Middle and Northern England (particularly Yorkshire) (with *Ichthyosaurus*, *Leptonectes*, *Temnodontosaurus*, *Excalibosaurus*, *Eurhinosaurus*, *Stenopterygius*, and *Hauffiopteryx*), the Lower Jurassic of Germany, particularly the Posidonienschiefer-Formation of Baden-Württemberg and Bavaria (with, except for *Excalibosaurus*, the same genera plus *Suevoleviathan*), and the Lower Jurassic of France (with *Temnodontosaurus*, *Eurhinosaurus*, *Stenopterygius*, *Suevoleviathan*, mainly from the Toarcian of Normandy and the Paris Basin), Belgium/Luxemburg (with finds from the early, middle and late Lower Jurassic including *Ichthyosaurus*, *Leptonectes*, *Temnodontosaurus*, *Eurhinosaurus*, *Stenopterygius*, and *Hauffiopteryx*) and

Switzerland (early and late Lower Jurassic with *Ichthyosaurus*, *Leptonectes*, *Stenopterygius*, and *Eurhinosaurus*).

In the Middle Jurassic there are only two major fossil-lagerstätten. The Los Molles Formation of Argentina (with *Chacaicosaurus* and *Ophthalmosaurus*/"*Mollesaurus*"), and the English Oxford-Clay (and its equivalents in north-western France) with *Ophthalmosaurus*.

In the Upper Jurassic good finds are restricted mainly to the Sundance Formation of the Central USA (particularly Wyoming, with *Ophthalmosaurus* = *Baptanodon*), the English Kimmeridge-Clay (with *Ophthalmosaurus*, *Brachypterygius*, and *Nannopterygius*), the Russian Volgian (with *Ophthalmosaurus*, *Undorosaurus*, and *Brachypterygius*), the Vaca Muerta Formation of Argentina (with *Caypullisaurus*, and *Aegirosaurus*), and the lithographic limestones of southern Germany (with *Nannopterygius*, *Brachypterygius*, and *Aegirosaurus*).

In the Lower Cretaceous, ichthyosaurs have been found almost all around the globe. The most important concentrations of more complete and relatively well preserved specimens are located in Australia, Russia, Wyoming and Northern Germany. Upper Cretaceous (Cenomanian) finds are rare and usually very fragmentary, with some notable exceptions from Russia.

This very discontinuous fossil record of ichthyosaurs has for a long time hampered any deeper understanding of the evolutionary history and phylogeny of the group, and partially it still does. The phylogenetic origin of these strange animals, the bauplan of which deviates more widely from their terrestrial ancestors than in any other marine reptile group, is to some extent still an unsolved enigma which has puzzled generations of palaeontologists and comparative anatomists.

On the other hand, however, the exquisite preservation of numerous specimens from a few selected fossil-lagerstätten has provided unusually deep insights into many aspects of the palaeobiology of a completely extinct group of vertebrates, which is almost unparalleled. Famous examples are found in almost any textbook on palaeontology, including pregnant females with the remains of embryos preserved in the body cavity, specimens with fossilized stomach contents and, most spectacular of all, skeletons with the complete body outline and diverse soft tissues preserved.

These exceptional fossils have provided a reasonable idea of the real appearance of the living animals, their feeding, reproductive and locomotory strategies. One should not forget, though, that with but a few exceptions all these remarkable specimens belong to only two genera of highly derived Lower Jurassic ichthyosaurs, *Stenopterygius* (mainly from southern Germany) and *Ichthyosaurus* (mainly from England). Data gathered from these animals can therefore not be used rather uncritically, as it is often done, to interpret older and more plesiomorphic, and

morphologically much more diverse ichthyosaurs from the Triassic, and they should also be only cautiously used as a basis to interpret the younger and more derived forms.

Apart from the above mentioned exceptionally preserved specimens there are also rather numerous finds of very well preserved skulls and skeletons, mainly from the Jurassic, some of which are three-dimensional and show minutest details of osteology (the finds of *Ophthalmosaurus* from the Middle Jurassic Oxford Clay described by ANDREWS in 1910 may serve as a well-known example). These specimens show many details of anatomy, including courses of nerves and blood vessels and muscle insertions that also serve to gain insight into many palaeobiological questions, as it is impossible for most other fossil reptiles (including the vast majority of nominal dinosaur taxa).

The difficulty in assigning ichthyosaurs their appropriate place in the traditional systema naturae, which has driven numerous systematicists and anatomists to the brink of desperation, also has an unexpected advantage. Since ichthyosaurs are morphologically so distant from any other amniote group, to such an extent, in fact, as to make their entire skeletal anatomy an array of autapomorphies, there was never a major debate about the concept and contents of the group, disregarding some rather trivial exceptions like the discussion around the placement of the fragmentary and aberrant genus *Omphalosaurus* (see MOTANI 2000a; MAISCH & MATZKE 2002a, and SANDER & FABER 1998, 2003 for more recent literature on this subject). There also was never much discussion about the characters that can be used to define the group, and which were in large parts obvious from even the earliest finds and descriptions of the 19th century. This is easily explained, as apart from the cetaceans, ichthyosaurs certainly represent the ecologically most diverse and successful, functionally and morphologically most highly adapted, and thus easily most dramatic attempt made by terrestrial vertebrates to regain the marine realm. These peculiarities have made them almost model organism for the study of evolutionary and functional morphological problems and questions related to the adaptation of animals to a new medium.

The purpose of this paper is threefold. First, it attempts to provide a short overview of the current state of our understanding of ichthyosaur phylogeny in order to make clear what – if any – consensus exists at the moment on the evolutionary history of the group, and on what basis its grundplan (the set of plesiomorphic and apomorphic features characterising the last common ancestor of the group, sensu HENNIG 1950) can be reconstructed. Second, a short review of the valid ichthyosaur taxa is provided to clarify what exactly constitutes the order Ichthyosauria. Third, the problem of ichthyosaur origins is addressed in a more extensive way than it has been done before, by including ichthyosaurs into two of the most extensive and influential analyses of amniote interrelationships, based on

new character codings that have become possible due to the considerable increase of our knowledge on basal ichthyosaur anatomy within the last couple of years.

The “results” of this study, as will be seen from the discussion, nevertheless can not and are in no way intended to be “last words” on any of the ongoing debates concerning ichthyosaurs. In fact it will be seen that our current state of knowledge is blatantly inadequate to elucidate the relationships of ichthyosaurs beyond reasonable doubt. Luckily, there is no end to a historical natural science. Two or three decisive new discoveries may overturn much that is now accepted as “textbook knowledge” and force us to rethink many of our traditional opinions, just as it was necessary between 1997 and 2000 to force the acceptance of new ideas and to establish the basis for a new look on the old fish-lizards. If that happens, it may also become possible to answer some of the old questions, raised again by this study, in a much more satisfactory way.

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2. Phylogeny and system of the Ichthyosauria

2.1. Phylogeny of the Ichthyosauria

The position of ichthyosaurs within amniotes is still debated (see chapter 3), although a certain consensus has emerged among most recent workers that they show similarities and are thus, in some way, related to or even part of the basal diapsids (MOTANI et al. 1998; MAISCH & MATZKE 2002b; MCGOWAN & MOTANI 2003). The difficulty to assign a definite phylogenetic position to the group on one hand, and the spectacular preservation of many ichthyosaur fossils from a handful of fossilagerstätten on the other hand has prompted many scientists to focus onto palaeobiological questions concerning these animals. This has resulted in a remarkable paucity of phylogenetic studies on ichthyosaurs, compared to, e. g. dinosaurs or fossil mammals.

Here I want to provide a review of previous attempts in this field, as the proposal of a new phylogenetic hypothesis is premature, concerning the state of revision in which many ichthyosaur taxa are at the moment. The review is restricted to those studies that in a recognizable way strived to use principles of phylogenetic systematics or cladistics (two terms that are not to be regarded as synonymous, despite of some methodological and terminological overlap).

The first phylogenetic-systematic hypothesis that I am aware of was proposed by MAZIN (1982). It was largely restricted – almost exclusively so – to characters of the anterior limb, reflecting traditional and influential earlier views on ichthyosaur phylogeny like those of KIPRIJANOFF (1881), LYDEKKER (1889a), and VON HUENE (1922a, 1948). These authors subdivided the ichthyosaurs in two subgroups (“suborders”) based on characters of the forefins, called the Latipinnati and the Longipinnati. The Latipinnati were characterized by a normal or supernormal number of digits in the forefin, of which two (via their respective metacarpals and proximal carpals) originate from the intermedium of the proximal carpal row (Latipinnati sensu VON HUENE 1948). The other group was characterized by a subnormal number of digits, of which only one contacted the distal surface of the intermedium (Longipinnati sensu VON HUENE 1948). This classification was almost universally used until the early 1970ies (MCGOWAN 1972a, b, 1974a, b). Papers from the late 1970ies, particularly the important studies of MCGOWAN (1976) and APPLEBY (1979), clearly demonstrated, that this simple scheme was not suitable

to understand the natural phylogenetic relationships within the Ichthyosauria. The numerous papers by MCGOWAN published in the 1970ies to 90ies do not contain, however, any phylogenetic analyses. Instead they concentrate on a variety of other topics, including descriptions of faunas or single specimens, questions of alphataxonomy, and the discussion of a variety of palaeobiological issues (MCGOWAN 1972a, b, c, 1973a, b, 1974a, b, 1978, 1979, 1986, 1989a, b, c, 1990, 1991, 1992a, b, 1993, 1994a, b, 1995, 1996a, b, c, 1997a, b; MCGOWAN & MILNER 1999; MCGOWAN & MOTANI 1999). APPLEBY has not expressed opinions on ichthyosaur phylogeny in any later publication.

Since CHRISTOPHER MCGOWAN'S important but non-phylogenetic working approach dominated ichthyosaur research for almost 20 years, it was not until the early 1990ies before anybody questioned the results of MAZIN (1982). GODEFROIT (1993a, 1994) did so in two important papers. Until then, MAZIN (1982) had been the only author ever to provide a phylogenetic analysis of the Ichthyosauria (which was, rather uncritically, also used by RIESS 1986). The greatest merit of GODEFROIT'S work probably is, that he was the first to use a reasonable amount of data from other parts of the skeleton than the fins to analyse ichthyosaur interrelationships, in this case particularly the cranial and pelvic morphology. Unfortunately, his analysis was restricted to a three-taxon-statement to elucidate the relationships of the three Jurassic genera *Ichthyosaurus*, *Stenopterygius*, and *Ophthalmosaurus*. GODEFROIT demonstrated, and this is the most crucial point, that despite a greater phenetic resemblance of the forefins of *Ophthalmosaurus* and *Ichthyosaurus* (which, as MOTANI 1999a, b elegantly demonstrated, is certainly a result of convergence) the entire set of characters supports a closer relationship of *Ophthalmosaurus* and *Stenopterygius*.

The analysis of GODEFROIT was also used with good success by FERNÁNDEZ (1999) in connection with the description of a new taxon from Argentina which she named *Mollesaurus* (arguably a basal species of *Ophthalmosaurus*), but she also added a whole set of additional characters of her own to the original analysis. GODEFROIT'S results were corroborated, as they were also in an even more inclusive analysis published recently by the same author (FERNÁNDEZ 2007) in connection with a redescription of the Upper Jurassic genus *Caypullisaurus*.

All these analyses mentioned so far, with exception of the original one by MAZIN (1982), concentrated, however, usually practically exclusively, on the relatively well-known post-Triassic ichthyosaurs. It was not until 1996 that anybody re-investigated the ingroup phylogeny of Triassic ichthyosaurs. This was done by DAL SASSO & PINNA (1996), who tried to place the newly described Middle Triassic *Besanosaurus leptorhynchus* from Italy in a phylogenetic context. Their analysis mainly included large Middle to Upper Triassic ichthyosaurs (of the "shastasaur-

grade" of evolution), which were at that time still widely regarded as a monophyletic assemblage. Most of the data used by DAL SASSO & PINNA (1996) were actually taken from the unpublished Ph. D. thesis of the late JACK M. CALLAWAY. Apart from *Grippia*, a genus from the Lower Triassic of Svalbard, no other more plesiomorphic ichthyosaurs were included in the analysis of DAL SASSO & PINNA (1996), and they also ignored all the post-Triassic taxa. It is thus no wonder that the "shastasaurids" emerge as a monophylum from that analysis. Just like the analyses of GODEFROIT (1993a) and FERNÁNDEZ (1999) that of DAL SASSO & PINNA also takes only a small fraction of the ichthyosaurs into account.

The first more inclusive attempt to untangle ichthyosaur phylogeny, including both some well-known Triassic and post-Triassic taxa, was the study of MAISCH & MATZKE (1997b), in connection with the description of the Middle Triassic genus *Mikadocephalus* from Monte San Giorgio (Switzerland). This analysis also had some shortcomings. Some of the characters used were uninformative autapomorphies, and two of the characters have since been recognized as correlated (MOTANI 1999b). The codings for *Mixosaurus*, which was still very little known at that time, have since also been demonstrated to be partially incorrect. The osteology of *Mixosaurus* is now much better understood (MAISCH & MATZKE 1997a, 1998c; BRINKMANN 1998a, b, 2004; MOTANI 1999c).

Despite these shortcomings, this was also the first analysis of ichthyosaur ingroup phylogeny that took all parts of the skeleton and particularly cranial characters into account on a large scale. Its results were highly unexpected, but have since then been corroborated many times by later and more inclusive studies. It was shown that the post-Triassic ichthyosaurs are monophyletic, with the Triassic genera included, *Mikadocephalus*, *Cymbospondylus* and *Mixosaurus*, as successive sister groups. No evidence was found for a monophyletic Shastasauridae including *Cymbospondylus* and *Mikadocephalus*, as would have been expected from their phenetic similarity. The traditional subdivision of the Jurassic taxa into latipinnate and longipinnate forms was rejected. The longipinnate *Temnodontosaurus* was found to be the most basal post-Triassic ichthyosaur, overturning the traditional view that the latipinnates like *Ichthyosaurus* were the more basal forms. This has since been corroborated by MOTANI'S (1999a) detailed investigations on the evolution of the ichthyosaurian forefins. The results of GODEFROIT (1993a, 1994) were once again reproduced, and accordingly the longipinnate *Stenopterygius* was grouped into the same family as the latipinnate *Ophthalmosaurus*.

A small analysis of the post-Triassic forms, on the occasion of the description of the new Lower Jurassic genus *Suevoleviathan*, was published by MAISCH (1998a). It used only a very limited amount of characters, some of

them again uninformative autapomorphies, and could not completely resolve the phylogeny of the included taxa. Important results were that, again, *Temnodontosaurus* turned out to be the most basal post-Triassic genus, that the monophyly of the Stenopterygiidae (*Stenopterygius* and *Ophthalmosaurus*) was corroborated, and that a third monophylum could be clearly identified among the post-Triassic taxa, the Leptonectidae (*Leptonectes* and *Eurhinosaurus*). The Leptonectidae was founded on and diagnosed by a suite of autapomorphies. This monophylum has been found in all subsequent analyses. The status of the Cretaceous genus *Platypterygius* was, however, misinterpreted by MAISCH (1998a). The results of the analysis apparently corroborated previous suggestions by VON HUENE (1922a) and MCGOWAN (1972b) who interpreted this genus as relatively basal. This result was without doubt an artefact of the choice and limited number of characters employed. Homoplasies of the two large growing genera *Temnodontosaurus* and *Platypterygius* were therefore given too much weight.

MOTANI (1998) published another small analysis of basal Lower and Middle Triassic ichthyosaurs to resolve the relationships between *Utatsusaurus*, *Grippia* and *Mixosaurus*. Working only with characters of the forefin he could nonetheless demonstrate that *Grippia* and *Mixosaurus* are more closely related to each other than any of the two is to *Utatsusaurus*. MOTANI's results were reproduced by later, more inclusive analyses (MOTANI 1999b; MAISCH & MATZKE 2000a), underlining the quality of the characters he identified as well as the usefulness of forefin features for ichthyosaur phylogeny, particularly in the plesiomorphic taxa.

MOTANI (1999b) was the first to publish a very inclusive analysis of ichthyosaur ingroup phylogeny. Based on 105 characters from all parts of the skeleton the relationships between the majority of well-known ichthyosaur taxa were investigated. The results of this analysis and many characters that MOTANI first recognized became an important basis for the final version of the originally independently developed analysis by MAISCH & MATZKE (2000a), that incorporated many of his suggestions with due credit. In summa, it is no wonder that many of the characters used by MOTANI (1999b) and MAISCH & MATZKE (2000a) are identical, although codings are sometimes slightly different. The choice of taxa is also similar. The two analyses can therefore be compared to each other very easily. MOTANI (1999b) uses 105 characters and 27 ingroup-taxa. The basal diapsids *Petrolacosaurus* (Araeoscelidia), *Hovasauros*, *Thadeosaurus* (Eosuchia), and *Claudiosaurus*, as well as the aberrant, superficially ichthyosaur-like, marine (?) archosauromorph *Hupehsuchus* from the Middle Triassic of China serve as outgroups.

Compared to MAISCH & MATZKE (2000a), MOTANI did not include the following genera: *Thaisaurus*, *Wimanius*,

Qianichthysaurus, *Phantomosaurus*, *Mikadocephalus*, *Callawayia*, *Aegirosaurus*. However, all of these, except *Thaisaurus*, *Wimanius* and *Mikadocephalus* were erected after the publication of his paper (LI 1999; MAISCH & MATZKE 2000a; BARDET & FERNÁNDEZ 2000). There was not much information available to MOTANI on *Mikadocephalus* or *Wimanius* because he had not seen any of the specimens of these genera. His choice of taxa is thus acceptable. Irritatingly, no credit is given by MOTANI to some of the important previous attempts (GODEFROIT 1993a, 1994; MAISCH & MATZKE 1997) to resolve ichthyosaur phylogeny.

The mixosaur genera *Mixosaurus*, *Phalarodon* and *Contectopalatus*, clearly separated by MAISCH & MATZKE (2000a), are united in a single genus *Mixosaurus* by MOTANI (1999b), corresponding to his taxonomic view (MOTANI 1999c). Since he uses the type species of these genera as different operational taxonomic units, this makes no difference, however. The separate treatment of two species of *Cymbospondylus*, *C. petrinus* and *C. buchseri* by MOTANI (1999b) is remarkable. Other ichthyosaur genera with greater morphological diversity (such as *Ichthyosaurus* and *Stenopterygius*) are not treated on the species level. It remains unclear why this special treatment is given to the genus *Cymbospondylus*, which is clearly defined by a considerable array of autapomorphies.

As a result of MOTANI's analysis, a consensus from 12 equally parsimonious trees with a length of 254 steps is found. The consistency index is 0.654. *Hupehsuchus* is – as an artifact of the choice of the outgroups – the sister-taxon of the Ichthyosauria which MOTANI calls Ichthyopterygia here and in other papers, for reasons that are rather unintelligible to me. The most basal “ichthyopterygians” sensu MOTANI are *Utatsusaurus* and *Parvinator*, followed by the grippiids (*Grippia*, *Chaohusaurus*, called Grippidia by MOTANI). Only above these basal forms MOTANI's “Ichthyosauria” begins. There is no reason for such a nomenclatorial change, and it is strongly recommended to abandon it in favour of calling all ichthyosaurs simply ichthyosaurs, as I have done previously, as well as in this study. The “Ichthyosauria” of MOTANI incidentally almost corresponds to the Hueneosauria of MAISCH & MATZKE 2000a.

The most basal “ichthyosaurs” sensu MOTANI (1999b) are the cymbospondylids, followed by the mixosaurids and the shastasaurids. *Toretocnemus*, *Californosaurus* and all more highly derived forms (which are united by MOTANI as Parvipelvia, a well-chosen name referring to one of the most striking characters of the group) are called Euichthyosauria. These and the shastasaurids together form the Merriamosauria. While the analysis of MAISCH & MATZKE (2000a) supports the monophyly of both the Parvipelvia and the Merriamosauria, this is not true for MOTANI's (1999b) Euichthyosauria, because MAISCH & MATZKE (2000a) regard the toretocnemids as more basal than MOTANI did.

Within the Parvipelvia, *Macgowania* and *Hudsonelpidia* are the most basal genera. Then follows *Suevoleviathan*, the leptonectids and *Temnodontosaurus*. All more highly derived taxa are called Thunnosauria by MOTANI (1999b), alluding to their thunniform aspect correlated with a development of the ability for faster swimming (BRAUN & REIF 1985; RIESS 1986; TAYLOR 1987; MASSARE 1988, 1995; LINGHAM-SOLIAR & REIF 1998; BUCHHOLTZ 2001). Basal thunnosaurs are *Ichthyosaurus* and *Stenopterygius*, the more highly derived are the Ophthalmosauria (better Ophthalmosauridae, MOTANI ignoring the priority of BAUR). Both the monophyly of the Thunnosauria and the Ophthalmosauridae are corroborated by the analysis of MAISCH & MATZKE (2000a).

MAISCH & MATZKE (2000a) published a second, even more exhaustive analysis of ichthyosaur ingroup relationships, in part using the results of MOTANI (1999b), but including about 40 additional characters and several additional taxa (see above). The analysis is thus based on 120 characters and 33 taxa, an all-zero ancestor is used for rooting, *Captorhinus*, *Limnoscelis*, *Petrolacosaurus* and *Youngina* were used as comparative outgroups. Six most parsimonious cladograms result from the analysis. The consensus tree has a length of 192 steps, a consistency index of 0.69 and a retention index of 0.91.

Some of MOTANI'S (1999b) characters are not used by MAISCH & MATZKE (2000a) for reasons that are each discussed in detail. This concerns only 21 of the 105 characters chosen by MOTANI. Of these, nine are excluded because they are only informative if the same outgroups are chosen. Two of his characters are obligatorily correlated and are therefore reduced to one. Another one becomes an uninformative autapomorphy for taxonomic reasons in MAISCH & MATZKE'S analysis, yet another one is uninformative already in the original analysis (as long as character states are unordered). Therefore only nine meaningful characters of MOTANI are rejected for reasons provided in detail in each case.

MAISCH & MATZKE'S (2000a) analysis corroborates some of MOTANI'S results, among these are: *Utatusaurus* is the most basal ichthyosaur (*Thaisaurus*, holding this position in MAISCH & MATZKE 2000a was not included in the analysis of MOTANI 1999b); the Grippiidae is monophyletic ("Grippidia" of MOTANI, *Grippia* and *Chaohusaurus*); the mixosaurids are monophyletic; the cymbospondylids are monophyletic; the Merriamosauria is monophyletic; there is a close relationship (although no, as MOTANI has it, monophyly) of *Besanosaurus*, *Shastasaurus* and *Shonisaurus*; *Californosaurus* is the sister-taxon of the Parvipelvia (the genus *Callawayia* holds this place in MAISCH & MATZKE 2000a, but was also erected in that paper, so MOTANI 1999b could of course not include it, as he had not recognized its generic distinctiveness from *Shastasaurus*); monophyly of the Parvipelvia and a basal position of

Macgowania and *Hudsonelpidia* within that group; monophyly of the Leptonectidae ("Eurhinosauria" of MOTANI, ignoring the priority of MAISCH); monophyly of the Thunnosauria; monophyly of the Ophthalmosauridae ("Ophthalmosauria" of MOTANI).

MAISCH & MATZKE'S (2000a) results are, however, also different in a number of important points. *Thaisaurus* from the Lower Triassic of Thailand (not included in MOTANI 1999b) is the most basal ichthyosaur. Then *Utatusaurus*, and not as MOTANI has it *Utatusaurus* and/or *Parvinator*, is the most basal taxon, *Parvinator* being even more derived than the grippiids. The Mixosauridae is the most basal member of the Hueneosauria ("Ichthyosauria" sensu MOTANI), not the Cymbospondylidae. The Shastasauridae – a monophylum in MOTANI'S view composed of *Shastasaurus*, *Besanosaurus* and *Shonisaurus*, i. e. already much reduced with respect to the pre-phylogenetic concept of the family and its usage by DAL SASSO & PINNA (1996) – is not monophyletic. Its members form successive sister-groups of the Parvipelvia. *Toretocnemus* and *Qianichthyosaurus* (not included by MOTANI as it was later described by LI 1999) from the Upper Triassic of China form a monophylum, the Toretocnemidae. These hold a basal position within the Longipinnati. This old group is resurrected by MAISCH & MATZKE (2000a) in the sense it was used by VON HUENE (1948), as it contains all the ichthyosaurs that have lost (according to MOTANI'S 1999a interpretation) the first finger of the forefin and therefore possess elongate and slender fins, at least in the grundplan.

The post-Triassic ichthyosaurs form a very stable monophylum for which the name Neoichthyosauria, proposed by SANDER (2000), is available. *Temnodontosaurus* is the most basal neoichthyosaur, whereas *Suevoleviathan* – contra MOTANI (1999b), who misinterpreted the pelvis of this genus – is the sister group of the Thunnosauria. The Leptonectidae is equally less derived than *Suevoleviathan*, but more progressive than *Temnodontosaurus*. *Ichthyosaurus* is – contra MOTANI (1999b) – less advanced than *Stenopterygius*, supporting the view of GODEFROIT (1993a, 1994). Within the Ophthalmosauridae it is not, as MOTANI (1999b) has it, *Platypterygius*, but *Ophthalmosaurus* which represents the sister-taxon of *Caypullisaurus*.

Despite these considerable differences, the comparison of the analyses of MOTANI (1999b) and MAISCH & MATZKE (2000a) demonstrates that from these two studies alone there has already emerged a remarkably stable and well-resolved concept of ichthyosaur ingroup phylogeny, and many important monophyla are equally found in both analyses and appear to be well-supported in each. It can be assumed that most remaining differences of the two phylogenies can be explained by incomplete osteological knowledge of taxa, gaps in the fossil record and simple misinterpretation of characters in certain specimens. At least the differences are still so considerable, that additional research seems to be necessary.

SANDER (2000) also published a phylogenetic analysis of the Ichthyosauria. SANDER's analysis of 120 characters (of which 16 had to be excluded from the final analysis due to various problems) and 19 taxa (one hypothetical ancestor as well as two outgroup taxa, the basal diapsids *Araeoscelis* and *Petrolacosaurus*) results in a single most parsimonious tree with a length of 375 steps and a consistency index of 0.65.

SANDER (2000) does not take the analysis of MOTANI (1999b) as much into account as MAISCH & MATZKE (2000a), although he discusses it in the text and compares the results. Otherwise he relies more on other, partially somewhat outdated and unpublished sources, (including CALLAWAY'S Ph. D. thesis which was finished in 1989). The list of characters provided by SANDER (2000) makes no mention of MOTANI (1999b), although many characters are practically identical.

SANDER'S (2000) analysis only takes 16 ingroup taxa into account, much less than the more inclusive data sets of MOTANI (1999b) and MAISCH & MATZKE (2000a). SANDER'S analysis is, however, based on a large quantity of characters (120), intermediate between the number used by MOTANI (1999b) – 105 – and those used by MAISCH & MATZKE (2000a), namely 128. It must be considered, though, that of these characters (of which, as mentioned above, 16 had to be eventually excluded) 48 only serve to distinguish ichthyosaurs from the outgroup, and are therefore uninformative for the ingroup phylogeny. MOTANI used only nine of his characters for this purpose, eight were used by MAISCH & MATZKE. If the number of characters is therefore reduced to those that are directly relevant for ichthyosaur interrelationships, there are 120 such characters used by MAISCH & MATZKE (2000a), 96 by MOTANI (1999b), but only 72 by SANDER (2000), which is therefore the least inclusive of the three data sets.

Statistical support for SANDER'S (2000) results is comparatively weak. In a bootstrap analysis only three nodes reach values higher than 70 (12 in MAISCH & MATZKE 2000a; MOTANI 1999b makes no mention of bootstrap values). A comparison of the length of the cladograms (i. e., the number of required evolutionary steps) is also instructive. While MOTANI'S (1999b) analysis considers 32 taxa and 105 characters, his tree is only 243 steps in length. MAISCH & MATZKE (2000a) even consider 128 characters and also 32 taxa, and the resulting cladogram is, with only 192 steps, even shorter. The cladogram of SANDER (2000), is based on 104 characters and only 19 taxa, but its length is remarkable 375 steps, representing a much higher number of homoplasies. This speaks in favour of the idea, that the analyses of MOTANI (1999b) and MAISCH & MATZKE (2000a) contain a more significant phylogenetic signal than that of SANDER (2000).

SANDER'S (2000) analysis therefore is a valuable – e. g. due to the recognition and formal erection of the mono-

phyletic Neoichthyosauria – contribution to ichthyosaur phylogeny, but probably should be, with respect to the analyses of MOTANI (1999b) and MAISCH & MATZKE (2000a), considered the weakest basis for further discussions on ichthyosaur phylogeny of the three. A further detailed comparison of the results of SANDER (2000) with those of MOTANI (1999b) and MAISCH & MATZKE (2000a) is therefore not provided here.

Since three exhaustive papers on ichthyosaur phylogeny have appeared within the short time period of 1999–2000, not very much has happened anymore in this particular area of research. MCGOWAN & MOTANI (2003) rely largely on the almost unaltered results of MOTANI 1999b, just complementing them by erection of some new taxa.

MAISCH & MATZKE (2001a) published an analysis concerning the ingroup relationship of the Mixosauridae on the species level. JIANG et al. (2005, 2006) and MAISCH & MATZKE (2005) further elaborated on this particular problem, particularly after some criticism of the original analysis was published by SCHMITZ et al. (2004, who did not, however, provide any alternative phylogeny).

Description of new ichthyosaur material from the Lower Triassic of Svalbard (MAISCH & MATZKE 2002a, b, 2003a, b), and additional work (NICHOLLS & MANABE 2001) and personal observations on *Qianichthyosaurus* made some changes to the original data matrix of MAISCH & MATZKE (2000a) necessary, which was therefore modified and extended two times after its original publication (MAISCH & MATZKE 2003a, b), also correcting the original analysis in places. The papers by MAISCH & MATZKE (2003a, b) are therefore necessary complements to MAISCH & MATZKE (2000a).

As mentioned above, FERNÁNDEZ (2007) has published a rather exhaustive analysis of post-Triassic ichthyosaur interrelationships, which should be tested, however, in a larger context.

2.2. System of the Ichthyosauria

Below a list of all described and currently valid ichthyosaur taxa is provided. Some are also commented upon. Two new families (Thaisauridae n. fam. and Wimaniidae n. fam.) are erected. A new genus *Barracudasauroides* n. gen. and one new species, *Omphalosaurus merriami* n. sp. are also introduced. Evidence speaks for a generic difference of *Ichthyosaurus acutirostris* OWEN, 1840 from *Temnodontosaurus*, but not having seen the type material, which was relocated rather recently, I refrain from erecting a new taxon. This short overview has become necessary, to take the recent substantial increase of knowledge into account that has taken place since the publication of the papers by MAISCH & MATZKE (2000a) and MCGOWAN & MOTANI (2003). Due to the incorporation of the Om-

phalosauridae, *Omphalosaurus*, *Tholodus* and probably *Xinminosaurus*, into the Ichthyosauria (DALLA VECCHIA 2004, pers. obs.), which has become possible due to new finds from northern Italy and probably southern China, as well as the revision of *Himalayasaurus* (MOTANI et al. 1999) and *Excalibosaurus* (MCGOWAN 2003), and the erection of the new genera *Guanlingsaurus* (YIN et al. 2000), *Guizhouichthyosaurus* (YIN et al. 2000), *Quasianosteosaurus* (MAISCH & MATZKE 2002b, 2003b), *Barracudasaurus* (JIANG et al. 2005), *Maiaspondylus* (MAXWELL & CALDWELL 2006), *Xinminosaurus* (JIANG et al. 2008), and *Hauffiopteryx* (MAISCH 2008) numerous new ichthyosauria taxa have recently emerged. In addition, several new species have been described, or old species have been resurrected based on new evidence.

The system used here follows MOTANI 1999b, MAISCH & MATZKE 2000a, and also takes suggestions by MCGOWAN & MOTANI 2003 into account. The most important references are provided for all valid genera in chronological order. It is intended that this provides a clue for the reader to find his way through the labyrinthic and widely dispersed primary literature.

Order Ichthyosauria DE BLAINVILLE, 1835

Family Thaisauridae n. fam.

Type genus: *Thaisaurus* MAZIN, SUTEETHORN, BUFFETAUT, JAEGER & HELMCKE-INGAVAT, 1991

Diagnosis. – Autapomorphies are the macroscopically smooth, conical and slender tooth crowns (convergent to the Leptonectidae), and a postfrontal that remains separated from the fenestra supratemporalis. Plesiomorphies aiding in identification are: humerus without lamina anterior, humerus, femur and zeugopodials very elongate and slender, metatarsal five long and slender, as big as metatarsal one.

Remarks. – MCGOWAN & MOTANI (2003) have the suspicion that *Thaisaurus* may be a specimen of *Chaohusaurus*. *Thaisaurus* seems, however, to be much more plesiomorphic than and morphologically widely different from *Chaohusaurus* and consequently has to remain a separate genus, unless evidence to the contrary is available. It is true, though, that a re-investigation of this taxon is badly needed.

1. Genus *Thaisaurus* MAZIN, SUTEETHORN, BUFFETAUT, JAEGER & HELMCKE-INGAVAT, 1991

Type species: *Thaisaurus chonglakmanii* MAZIN, SUTEETHORN, BUFFETAUT, JAEGER & HELMCKE-INGAVAT, 1991, Lower Triassic, Thailand.

Important references: MAZIN et al. (1991); MCGOWAN & MOTANI (2003).

Family Utatsusauridae MCGOWAN & MOTANI, 2003

2. Genus *Utatsusaurus* SHIKAMA, KAMEI & MURATA, 1978

Type species: *Utatsusaurus hataii* SHIKAMA, KAMEI & MURATA, 1978, Lower Triassic, Japan, Kanada.

Important references: SHIKAMA et al. (1978); MAZIN (1986a); CALLAWAY & MASSARE (1989a); NICHOLLS & BRINKMAN (1993); MOTANI (1996, 1997a, b, c); MOTANI et al. (1998).

Family Grippiidae WIMAN, 1929

3. Genus *Grippia* WIMAN, 1929

Type species: *Grippia longirostris* WIMAN, 1929, Lower Triassic, Svalbard, ?Canada.

Important references: WIMAN (1929, 1933); VON HUENE (1943); COX & SMITH (1973); MAZIN (1981a, 1983a, 1984); MASSARE & CALLAWAY (1990); BRINKMAN et al. (1992); MOTANI (1997a, b, 1998a, b, 2000a).

4. Genus *Chaohusaurus* YOUNG & DONG, 1972

Type species: *Chaohusaurus geishanensis* YOUNG & DONG, 1972, Lower Triassic, China.

Important references: YOUNG & DONG (1972); CHEN (1985); CALLAWAY & MASSARE (1989a); MOTANI et al. (1997); MOTANI & YOU (1998a, b); MAISCH (2001a).

Family Quasianosteosauridae MAISCH & MATZKE, 2003

5. Genus *Quasianosteosaurus* MAISCH & MATZKE, 2003

Type species: *Quasianosteosaurus vikinghoegdai* MAISCH & MATZKE, 2003, Lower Triassic, Svalbard.

Important references: MAZIN (1981b, 1982); MAISCH & MATZKE (2002b, 2003b).

Family Parvinatoridae MCGOWAN & MOTANI, 2003

6. Genus *Parvinator* NICHOLLS & BRINKMAN, 1995

Type species: *Parvinator wapitiensis* NICHOLLS & BRINKMAN, 1995, Lower Triassic, Canada.

Important references: NICHOLLS & BRINKMAN (1995).

Questionable Ichthyosauria: Family Omphalosauridae MERRIAM, 1906

7. Genus *Omphalosaurus* MERRIAM, 1906

Type species: *Omphalosaurus nevadanus* MERRIAM, 1906, Middle Triassic, USA.

Further species: *Omphalosaurus nettarhynchus* MAZIN & BUCHER, 1987, Middle Triassic, USA; *Omphalosaurus peyeri* MAISCH & LEHMANN, 2002, Middle Triassic, Germany; *Omphalosaurus wolfi* TICHY, 1995, Middle Triassic, Germany.

Remarks. — *O. wolfi* was recently re-interpreted by SANDER & FABER (2003) as *Omphalosaurus* cf. *nevadanus*. A re-investigation of the matter seems necessary, particularly as SANDER & FABER (2003) possibly misinterpreted part of the cranial material of *O. wolfi*. Until this is clarified, the species should be allowed to stand.

Omphalosaurus merriami n. sp.

Locus typicus: Middelhook, Isfjord, Svalbard.

Stratum typicum: Sticky Keep Formation, Lower Triassic.

Holotype: Neither WIMAN (1910) nor MAZIN (1983b) chose a lectotype from the original material. Therefore I hereby declare the specimen figured by WIMAN 1910, pl. 9, fig. 29, in the collections of the Palaeontological Museum of the University of Uppsala as the lectotype. Paralectotypes are the specimens WIMAN 1910, pl. 9, figs. 23–28 and 30.

Derivatio nominis: In honour of Prof. Dr. JOHN C. MERRIAM of the University of Berkeley, one of the most important ichthyosaur researchers of all time, who also was the first to recognize the omphalosaurid nature of the material in question.

Diagnosis. — Smooth enamel, three tooth rows only, lower jaw symphysis not expanded, tooth roots with plicidentine.

Remarks. — Since *Pessopteryx* (*Omphalosaurus*) *nisseri* WIMAN, 1910 should, as MCGOWAN & MOTANI 2003 have argued for, and as it is discussed below, be used for the non-omphalosaurid part of the composite hypodigm of WIMAN (1910) and therefore becomes a senior subjective synonym of *Merriamosaurus hulkei* (MAISCH & MATZKE 2000a), a new species must be erected for the undoubted omphalosaurid jaw fragments from the Sticky Keep Formation of Svalbard described by WIMAN (1910) as part of his *Pessopteryx nisseri* material.

Important references: MERRIAM (1906, 1911); MERRIAM & BRYANT (1911); WIMAN (1910, 1916); COX & SMITH (1973); MAZIN (1983b, 1986b); MAZIN & BUCHER (1987); MAZIN & SANDER (1993); TICHY (1995); SANDER & MAZIN (1993); SANDER & FABER (1998, 2003); MOTANI (2000b); MAISCH & LEHMANN (2002).

8. Genus *Tholodus* VON MEYER, 1851

Type species: *Tholodus schmidi* VON MEYER, 1851, Middle Triassic, Germany, ?China.

Remarks. — A complete skeleton is known from the Guanling Formation (Middle Triassic) of Guizhou, China. It was recently described as a new ichthyosaurian genus (JIANG et al. 2008), *Xinminosaurus* (see below), but it probably rather belongs to *Tholodus*. If this should

be corroborated, the ichthyosaurian nature of the omphalosaurids (for which DALLA VECCHIA 2004 recently provided very convincing arguments) would be definitely supported. JIANG et al. (2006) regarded *Tholodus schmidi* as species inquirenda. This can not be accepted. The genus is easily recognized and characterized by unequivocal dental autapomorphies, so that even minutest jaw and tooth fragments are diagnostic, and it is thus without question a valid taxon (see also MAISCH & LEHMANN 2002; DALLA VECCHIA 2004). It is furthermore clearly distinguishable from *Omphalosaurus* and all other known marine reptiles, except *Xinminosaurus*, which may itself turn out to be but a junior subjective synonym of *Tholodus*.

Important references: VON MEYER 1851; PEYER 1939; SANDER & MAZIN 1993; DALLA VECCHIA 2004.

9. Genus *Xinminosaurus* JIANG, MOTANI, HAO, SCHMITZ, RIEPPEL, SUN & SUN, 2008

Type species: *Xinminosaurus catactes* JIANG, MOTANI, HAO, SCHMITZ, RIEPPEL, SUN & SUN, 2008

Remarks. — This newly described taxon shows (pers. obs.) a dentition that is indistinguishable from *Tholodus schmidi*, except that all known specimens of the latter are from animals that are at average twice as large (JIANG et al. 2008). It is therefore highly plausible that these two genera are very closely related and probably even identical. Since other typical elements of the Muschelkalk fauna are known from the Guanling Formation (*Placodus*, *Nothosaurus*) this would hardly be a surprise. A detailed description of the material is desirable. Its skull is much disarticulated but the postcranial skeleton is very well preserved. Its girdles and fins show a striking resemblance to the grippiids as does, to a certain extent, the durophagous dentition. The high number of presacral vertebrae instead suggests relationships to basal merriamosaurs. At this moment, nothing more can be said about the phylogenetic placement of the taxon (and therewith of the entire Omphalosauridae).

Family not designated

10. Genus *Isfjordosaurus* MOTANI, 1999

Type species: *Isfjordosaurus minor* (WIMAN, 1910), Lower Triassic, Svalbard.

Remarks. — MAISCH & MATZKE (2000a) questioned the ichthyosaurian nature of the type specimen, an isolated humerus with a rather unlikely morphology. MCGOWAN & MOTANI (2003) could not invalidate their arguments, but raised some important points, mainly concerning the anatomy of *Hupehsuchus*. Until a new description of *Hupehsuchus* is available, which definitely clarifies the morphol-

ogy of the humerus of this enigmatic form, doubts must still remain concerning the ichthyosaurian nature of *Isfjordosaurus*.

Important references: WIMAN 1910; MOTANI 1999b.

Parvorder Hueneosauria MAISCH & MATZKE, 2000
Nanorder Mixosauria MOTANI, 1999

Family Wimaniidae n. fam.

Type genus: *Wimanius* MAISCH & MATZKE, 1998

Diagnosis. – Autapomorphy: elongation of the ramus postorbitalis of the jugal, which is as long as the ramus suborbitalis. Synapomorphy with the Mixosauridae: palate closed. Plesiomorphies helpful in identification: no sagittal crest on nasal, palatal teeth on palatine present. There is no evidence that supports the idea of MCGOWAN & MOTANI (2003) that this should be a juvenile of *Mikadocephalus*. The two genera are fundamentally different, as easily seen in their disparate phylogenetic placement (MAISCH & MATZKE 2000a). MCGOWAN & MOTANI's (2003) suggestion is not based on investigation of the type material, which they have not seen.

11. Genus *Wimanius* MAISCH & MATZKE, 1998

Type species: *Wimanius odontopalatus* MAISCH & MATZKE, 1998, Middle Triassic, Switzerland.

Important references: MAISCH & MATZKE 1998a, 1999.

Family Mixosauridae BAUR, 1887
Subfamily Mixosaurinae BAUR, 1887

12. Genus *Mixosaurus* BAUR, 1887

Type species: *Mixosaurus cornalianus* (BASSANI, 1886), Middle Triassic, Switzerland, Italy.

Further species: *Mixosaurus kuhnschnyderi* (BRINKMANN, 1998), Middle Triassic, Switzerland.

Important references: BASSANI (1886); BAUR (1887a, b); REPOSSI (1902); WIMAN (1910, 1912); VON HUENE (1916, 1925a, 1935, 1949a); BROILI (1916); PINNA (1967); MAZIN (1983c); CALLAWAY & MASSARE (1989a); CALLAWAY (1997); MAISCH & MATZKE (1997a, 1998b, c); BRINKMANN (1996, 1997, 1998a, b, 1999, 2004); RIEPPEL & DALLA VECCHIA (2001).

Subfamily Phalarodontinae MAISCH & MATZKE, 2001

13. Genus *Phalarodon* MERRIAM, 1910

Type species: *Phalarodon fraasi* MERRIAM, 1910, Middle Triassic, USA; Lower-Middle Triassic, Canada; Middle Triassic, Switzerland, Svalbard.

Further species: *Phalarodon major* (VON HUENE, 1916), Middle Triassic, Germany, Switzerland; *Phalarodon callawayi* (SCHMITZ, SANDER, STORRS & RIEPPEL, 2004), Middle Triassic, USA, Svalbard.

Important references: HULKE (1873); MERRIAM (1908, 1910); WIMAN (1910); VON HUENE (1916); COX & SMITH (1973); MAZIN (1983c, 1984); CALLAWAY & BRINKMANN (1989); CALLAWAY & MASSARE (1989a); BRINKMANN (1998a, b, 2004); NICHOLLS et al. (1999); MAISCH & MATZKE (2001a, 2005); JIANG et al. (2003); SCHMITZ et al. (2004); MOTANI (2005b); SCHMITZ (2006).

14. Genus *Contectopalatus* MAISCH & MATZKE, 1998

Type species: *Contectopalatus atavus* (QUENSTEDT, 1851–52), Middle Triassic, Germany.

Important references: QUENSTEDT (1851–52); FRAAS (1891); DAMES (1895); VON HUENE (1916); EDINGER (1935); MAZIN (1983c); CALLAWAY & MASSARE (1989a); MAISCH & MATZKE (1998b, 2000b, 2001b).

Subfamily unassigned

15. Genus *Barracudasauroides* n. gen.

Type species: *Mixosaurus panxianensis* JIANG, SCHMITZ, HAO & SUN, 2006, Middle Triassic, China.

Diagnosis. – Small mixosaurids, skull length below 250 mm, crista sagittalis low, 15 or less premaxillary teeth with elongate, conical and pointed crowns, maxillary teeth stronger than premaxillary teeth, anterior maxillary teeth robust, conical and blunt, posterior maxillary teeth slightly elongated mesiodistally, jugal with short process posteroventralis, no external contact between jugal and quadratojugal, postorbital and possibly squamosal reach incisura postjugalis, postorbital separates postfrontal and supratemporal, radius with two anterior notches (modified from JIANG et al. 2005, 2006).

Remarks. – *Mixosaurus maotaiensis* YOUNG, 1965, the type species of *Barracudasaurus* JIANG, HAO, MAISCH, MATZKE & SUN, 2005, was declared a nomen dubium by JIANG et al. (2006) because of more exhaustive comparisons than previously done. If their argumentation is accepted, the generic name *Barracudasaurus* JIANG et al. 2005 is also a nomen dubium, as noted by JIANG et al. (2006) who describe new mixosaurid material from the Guanling Formation. They amend existing descriptions, noting the presence of an accessory postaxial digit in the type of their *Mixosaurus panxianensis* which was not preserved in the material studied by JIANG et al. (2005). *M. panxianensis* is nevertheless still very different to all other mixosaurids in the arrangement of its postorbital skull bones and much more plesiomorphic than any other mixosaurid known in this respect. I therefore still consider it as the representative of a separate genus, based on arguments

provided in JIANG et al. (2005) that need not be repeated here. For this genus, I propose the name *Barracudasauroides* n. gen., with the type species *Barracudasauroides panxianensis* (JIANG et al. 2006) n. comb.

Important references: YOUNG (1965); MAZIN (1983c); CALLAWAY & MASSARE (1989a); MAISCH et al. (2003); JIANG et al. (2005, 2006).

Nanorder Longipinnati VON HUENE, 1948
Family Toretocnemidae MAISCH & MATZKE, 2000

16. Genus *Toretocnemus* MERRIAM, 1903

Type species: *Toretocnemus californicus* MERRIAM, 1903, Upper Triassic, USA.

Further species: *Toretocnemus zitteli* (MERRIAM, 1903), Upper Triassic, USA.

Important references: MERRIAM (1903, 1908); MOTANI (1999a, b); LUCAS (2002).

17. Genus *Qianichthyosaurus* LI, 1999

Type species: *Qianichthyosaurus zhoui* LI, 1999, Upper Triassic, China.

Important references: LI (1999); MAISCH & MATZKE (2000a, 2003a); MAISCH et al. (2008a); NICHOLLS et al. (2003).

Family Cymbospondylidae VON HUENE, 1948

18. Genus *Cymbospondylus* LEIDY, 1868

Type species: *Cymbospondylus piscosus* LEIDY, 1868, Middle Triassic, USA.

Further species: *Cymbospondylus petrinus* LEIDY, 1868, Middle Triassic, USA; *Cymbospondylus buchseri* SANDER, 1989, Middle Triassic, Switzerland; *Cymbospondylus nichollsi* FRÖBISCH, SANDER & RIEPPEL 2006, Middle Triassic, USA.

Remarks. – Whether the type material of *Cymbospondylus piscosus* and *C. petrinus* is really diagnostic is questionable (but see FRÖBISCH et al. 2006). MCGOWAN & MOTANI (2003) indicate that they are aware of this problem and want to try to stabilize the genus, an action which I can only support, as it would be highly desirable in the interest of nomenclatorial stability. FRÖBISCH et al. (2006) recently described what they regard as a new species of *Cymbospondylus*, identifying a large posterolaterally positioned postparietal in their *Cymbospondylus nichollsi*. It has practically the identical shape, morphology and position as the supratemporal in just any other known ichthyosaur. In turn, they did not find the unpaired postparietal of *C. petrinus* (MAISCH & MATZKE 2004), the position of which makes its homology obvious, and which agrees better in position with the rudimentary postparietals of *Phan-*

tomosaurus (MAISCH & MATZKE 2006). A definite clarification of this, as well as other major problems in the interpretation of the cranial osteology of *C. nichollsi*, must await a re-investigation. Until this is done, the species is – provisionally – accepted as valid.

Important references: LEIDY (1868); MERRIAM (1908); VON HUENE (1916); CORROY (1928); CAMP (1980); BROILI (1931); SANDER (1989, 1992); MASSARE & CALLAWAY (1990); MAISCH & MATZKE (2000a, 2004), FRÖBISCH et al. (2006).

19. Genus *Phantomosaurus* MAISCH & MATZKE, 2000

Type species: *Phantomosaurus neubigi* (SANDER, 1997), Middle Triassic, Germany.

Important references: SANDER (1997); MAISCH & MATZKE (2000a, 2006).

Hyporder Merriamosauria MOTANI, 1999
Family Merriamosauridae MAISCH & MATZKE, 2003

20. Genus *Pessopteryx* WIMAN, 1910 (= *Merriamosaurus* MAISCH & MATZKE, 2002)

Type species: *Pessopteryx nisseri* WIMAN, 1910 (= *Merriamosaurus hulkei* (MAISCH & MATZKE, 2000)), Lower Triassic, Svalbard.

Remarks. – MCGOWAN & MOTANI (2003) have made a convincing case for the interpretation that WIMAN (1910, 1916) erected his genus *Pessopteryx* mainly with regard to the undoubtedly ichthyosaurian postcranial material he described, and not with respect to the associated omphalosaurid jaw fragments which form part of his original hypodigm. It seems therefore correct not to regard the name *Pessopteryx* WIMAN, 1910 as a junior subjective synonym of *Omphalosaurus* MERRIAM, 1906, as done by MAISCH & MATZKE (2000a), but to accept it as the valid generic designation for the large basal merriamosaur from the Sticky Keep Formation of Svalbard which was re-described in detail by MAISCH & MATZKE (2000a, 2002a, 2003a) and named *Merriamosaurus (Rotundopteryx)* nom. praeocc., see MAISCH & MATZKE 2002a). MCGOWAN & MOTANI (2003) did not designate a lectotype for *Pessopteryx*, as they regarded it as a nomen dubium and suggested referral of the material to *Besanosaurus*, a very distantly related form from the alpine Middle Triassic, or MOTANI's doubtfully ichthyosaurian *Isfjordosaurus*. The papers that have appeared since (MAISCH & MATZKE 2002a, 2003a) have clearly demonstrated that *Pessopteryx* is quite different from *Besanosaurus* and represents a valid genus, as phylogenetic analysis (MAISCH & MATZKE 2003a) has demonstrated. The question of the association of the isolated bones described by WIMAN (1910) has also been satisfactorily solved by the discovery of a partial articulated

skeleton (MAISCH & MATZKE 2002a). MAISCH & MATZKE (2000a) proposed the humerus at the Palaeontological Museum Uppsala figured by WIMAN (1910, pl. 8, fig. 1) as the lectotype of *Rotundopteryx hulkei*. To avoid nomenclatorial complications this specimen should therefore not be chosen as the lectotype of *Pessopteryx nisseri*. I therefore declare the humerus figured by WIMAN (1910, pl. 8, fig. 2) as the lectotype of *Pessopteryx nisseri* WIMAN, 1910. The humerus pair of WIMAN (1910, pl. 8, figs. 3–4) constitutes the paralectotypes. Thus *Pessopteryx nisseri* WIMAN, 1910 and *Merriamosaurus hulkei* (MAISCH & MATZKE 2000a) remain two taxa based on different material. *Merriamosaurus hulkei* is thus not an objective but a subjective junior synonym of *Pessopteryx nisseri*. With the removal of *Pessopteryx nisseri* from the genus *Omphalosaurus* it was necessary to designate a new species for the Svalbard omphalosaurid (see above). Despite the “resurrection” of *Pessopteryx*, the valid name for the family remains Merriamosauridae MAISCH & MATZKE, 2003.

Important references: WIMAN (1910); COX & SMITH (1973); MAZIN (1983b, 1984); MAISCH & MATZKE (2000a, 2002a, 2003a).

Family Besanosauridae MCGOWAN & MOTANI, 2003

21. Genus *Besanosaurus* DAL SASSO & PINNA, 1996

Type species: *Besanosaurus leptorhynchus* DAL SASSO & PINNA, 1996, Middle Triassic, Italy, Switzerland.

Important references: DAL SASSO (1993); DAL SASSO & PINNA (1996); MAISCH & MATZKE (2000a).

Family Shastasauridae MERRIAM, 1895

22. Genus *Shastasaurus* MERRIAM, 1895

Type species: *Shastasaurus pacificus* MERRIAM, 1895, Upper Triassic, USA.

Further species: *Shastasaurus alexandrae* MERRIAM, 1902, Upper Triassic, USA.

Important references: MERRIAM (1895, 1902, 1908); VON HUENE (1916, 1925b); CALLAWAY & MASSARE (1989a, b); MAISCH (2000).

Family Shonisauridae CAMP, 1980

23. Genus *Shonisaurus* CAMP, 1976

Type species: *Shonisaurus popularis* CAMP, 1976, Upper Triassic, USA.

Further species: *Shonisaurus sikkaniensis* NICHOLLS & MANABE, 2004, Upper Triassic, USA.

Important references: CAMP (1976, 1980); MAZIN (1985); KOSCH (1990); MOTANI & MCGOWAN (1999); MOTANI et al. (1999); NICHOLLS & MANABE (2004).

24. Genus *Himalayasaurus* YOUNG & DONG, 1972

Type species: *Himalayasaurus tibetensis* YOUNG & DONG, 1972, Upper Triassic, Tibet.

Important references: YOUNG & DONG (1972); MOTANI et al. (1999).

25. Genus *Guizhouichthysaurus* CAO & LUO, 2000 in YIN, ZHOU, CAO, YU & LUO, 2000

Type species: *Guizhouichthysaurus tangae* CAO & LUO in YIN, ZHOU, CAO, YU & LUO, 2000, Obertrias, China.

Further species: *Guizhouichthysaurus wolonggangensis* (CHENG, CHEN & SANDER, 2007) n. comb. (see *Callawayia* for discussion).

Remarks. – SHANG & LI (2009) have recently described additional well-preserved material of this taxon, focussing mainly on the postcranial skeleton. They ascribe the species *G. tangae* (and therewith the genus *Guizhouichthysaurus*) to the genus *Shastasaurus*, based on similarities in the postcranium, which are indeed striking. Nevertheless most of these similarities are plesiomorphic with respect to other derived Triassic ichthyosaurs, and a more rigorous phylogenetic assessment is needed, before a synonymy of the two genera can be formally established. Therefore the genus *Guizhouichthysaurus* is here still accepted as provisionally valid.

Important references: YIN et al. (2000); LI & YOU (2001); CHEN & CHENG (2003); JIANG et al. (2005); MAISCH et al. (2006a); SHANG & LI (2009).

Family Guanlingsauridae YIN in YIN, ZHOU, CAO, YU & LUO, 2000

26. Genus *Guanlingsaurus* YIN in YIN, ZHOU, CAO, YU & LUO, 2000

Type species: *Guanlingsaurus liangae* YIN in YIN, ZHOU, CAO, YU & LUO, 2000, Upper Triassic, China.

Important references: YIN et al. (2000); MAISCH et al. (2006a); SHANG & LI (2009).

27. Genus *Mikadocephalus* MAISCH & MATZKE, 1997

Type species: *Mikadocephalus gracilirostris* MAISCH & MATZKE, 1997, Middle Triassic, Switzerland, Svalbard.

Important references: WIMAN (1910); MAISCH & MATZKE (1997b, 1999, 2000a).

Family Californosauridae VON HUENE, 1948

28. Genus *Californosaurus* KUHN, 1934

Type species: *Californosaurus perrini* (MERRIAM, 1902), Upper Triassic, USA.

Important references: MERRIAM (1902, 1908); KUHN (1934).

?29. Genus *Callawayia* MAISCH & MATZKE, 2000

Type species: *Callawayia neoscapularis* (McGOWAN, 1994), Upper Triassic, Canada (non *Callawayia wolonggangense* CHEN, CHENG & SANDER, 2007), Upper Triassic, China.

Remarks. – The genus *Callawayia* was erected by MAISCH & MATZKE (2000a). This was criticized as NICHOLLS & MANABE (2001) erected *Metashastasaurus* for the same taxon. MAISCH (2000) pointed out differences between *Callawayia* and *Shastasaurus*, but did not erect a new taxon, referring to planned work by NICHOLLS. This paper by MAISCH was submitted in July 1999. There was no exhaustive phylogenetic framework available at that time, and enough time should be given to NICHOLLS (& MANABE) to publish their observations, if they wanted to do so. More than a year later, nothing was published still. MOTANI (in McGOWAN & MOTANI 2003: 72) made some remarks that I can not leave without comment. That *Shastasaurus neoscapularis* represents a genus different from *Shastasaurus* was clear to me before my visit to Berkeley in 1999, Dr. MOTANI knows this. I developed this idea independent from NICHOLLS, not even knowing about any relevant new material. At Berkeley I tried to convince both NICHOLLS and MOTANI from my view, but whereas NICHOLLS remained somewhat indecisive at first, tending to accept it, MOTANI has not accepted it until now (see McGOWAN & MOTANI 2003). The paper by NICHOLLS & MANABE was submitted July 23rd 2000, more than a year after I submitted my paper on *Shastasaurus*. I visited Berkeley in April 1999. I therefore let more than a year pass until I erected a new genus together with A. T. MATZKE, just as the ICZN (Appendix A, 2: “a reasonable period, no less than a year”) that we were accused of having violated by NICHOLLS, MANABE and MOTANI, suggests. (The paper by MAISCH & MATZKE 2000a was finished and submitted in its final form in September 2000, it appeared in December 2000, more than one and a half years later). I therefore have to declare that the erection of the genus *Callawayia* was in no way a breach of the “Code of Ethics” of the ICZN, as MAISCH & MATZKE 2000a were accused of. Instead we have completely fulfilled the requirements of the ICZN, Appendix A, 2. The entire case may be considered as unlucky, caused mainly by lack of necessary communication, but there was never any breach of the “Code of Ethics” and I completely reject any unfounded accusations of myself or my co-author Dr. ANDREAS T. MATZKE in this matter. It should be said on a personal behalf, that there was never an intention on my or Dr. MATZKE’s side to upset any of our colleagues, particularly not Dr. NICHOLLS, for whom we held and hold the greatest respect. We chose the name *Callawayia* with the best intentions in honour of

the late JACK M. CALLAWAY, particularly because we were aware that he and Dr. NICHOLLS were good friends.

The species *C. wolonggangense* (CHENG et al. 2007) is most probably just another junior subjective synonym of *Guizhouichthyosaurus tangae* (see MAISCH et al. 2006a and SHANG & LI 2009 for critical discussions of this taxon and its synonyms). The single more or less remarkable difference concerns the sutural pattern of some skull roof bones, which, as was pointed out elsewhere, is particularly unreliable as a taxonomic criterion in these forms for preservational and preparational reasons (MAISCH et al. 2006a). Without reinvestigation the species may be allowed to stand, but it is certainly not a *Callawayia*. It is here referred to *Guizhouichthyosaurus* as a provisionally valid species.

Important references: McGOWAN (1994c, 1997a); MAISCH & MATZKE (2000a); NICHOLLS & MANABE (2001).

Minorder Parvipelvia MOTANI, 1999 Family Hudsonelpidiidae McGOWAN & MOTANI, 2003

30. Genus *Hudsonelpidia* McGOWAN, 1995

Type species: *Hudsonelpidia brevirostris* McGOWAN, 1995, Upper Triassic, Canada.

Important references: McGOWAN (1995, 1997a).

Family Macgowaniidae McGOWAN & MOTANI, 2003

31. Genus *Macgowania* MOTANI, 1999

Type species: *Macgowania janiceps* (McGOWAN, 1996), Upper Triassic, Canada.

Important references: McGOWAN (1991, 1996a, 1997a); MOTANI (1999a, b).

Suborder Neoichthyosauria SANDER, 2000 Family Temnodontosauridae McGOWAN, 1994

32. Genus *Temnodontosaurus* LYDEKKER, 1889

Type species: *Temnodontosaurus platyodon* (CONYBEARE, 1822), Lower Jurassic, England, Germany, Belgium.

Further species: *Temnodontosaurus trigonodon* (VON THEODORI, 1843), Lower Jurassic, Germany, France; *Temnodontosaurus crassimanus* (BLAKE, 1876), Lower Jurassic, England; *Temnodontosaurus nuertingensis* (VON HUENE, 1931), Lower Jurassic, Germany; *Temnodontosaurus eurycephalus* (McGOWAN, 1974), Lower Jurassic, England.

Important references: HOME (1814, 1819); CONYBEARE (1822); HAWKINS (1834, 1840); OWEN (1840, 1881); VON THEODORI (1843, 1844, 1854); BLAKE (1876); LYDEKKER (1889a, b); FRAAS (1891, 1913); GAUDRY (1892); VON HUENE (1922a, 1930, 1931a, b, 1949c, 1952); BERCKHEMER (1938); McGOWAN (1972a, b,

1974a, 1979, 1994b, 1996c); BÖTTCHER (1989); GODEFROIT (1993b); MAISCH (1998b, 1999, 2002, 2004); MAISCH & HUNGERBÜHLER (1997a, b, 2001).

33. Genus unnamed

Ichthyosaurus acutirostris OWEN, 1840

Stratum typicum: Alum Shale Formation; Lower Toarcian.

Locus typicus: Saltwick Alum Pit, close to Whitby, Yorkshire, England.

Holotype: BM (NH) 14553, skull – the snout is now missing and is only documented photographically and by a drawing published by OWEN (1881), see CHAPMAN & DOYLE (2002) – entire right and part of the left fore fin, part of the shoulder girdle and the cervical and dorsal axial skeleton.

Referred specimens: SMC J351576, holotype of *Ichthyosaurus zetlandicus* SEELEY, 1880, a three-dimensional skull from Whitby, BM(NH) 1500a, a complete skull in dorsal view; other specimens, particularly those at the Whitby Museum, need re-investigation, as it seems that they represent a variety of taxa.

Diagnosis. – Large ichthyosaur with more than 60 cm adult skull length, snout very elongate, more than $\frac{2}{3}$ skull length, orbits large, postorbital skull segment short (less than half orbital diameter), jugal contacts premaxilla, forefins extremely long and slender, much longer than the skull and more than 10% longer than the mandible, with more than 25 phalanges in the longest digit (unique among ichthyosaurs), radius, radial and distal carpal 2 can be notched.

Remarks. – It remains unclear whether this form is really a temnodontosaurid. A detailed re-investigation of the entire material is necessary to assess its status. Cranial characters speak in favour of it, but a closer relationship to the leptonectids can likewise not be excluded. MCGOWAN (1974a) referred several additional specimens to this species, which are all kept at the Whitby Museum in Whitby, Yorkshire. At this time the holotype was considered lost. Meanwhile it was re-located in a damaged state in the Natural History Museum, London (CHAPMAN & DOYLE 2002). The forefin of the specimen, which was never described in detail, is actually so highly autapomorphic (if authentic), that at the present state of knowledge previous suggestions regarding the classification of this elusive species all seem to be inadequate. MCGOWAN (1974a), MCGOWAN & MOTANI (2003), HUNGERBÜHLER & SACHS (1996), MAISCH (1997a) and MAISCH & MATZKE (2000a) referred the species to either *Stenopterygius*, *Leptonectes* or *Temnodontosaurus*. The uncertainty is clearly a reflection of the incomplete description and subsequent loss of the holotype. In fact it appears very plausible that the species represents a genus of its own which so far has not been recorded outside of Great Britain. As I have had no opportunity to study the type material myself, and as Liassic ichthyosaurs are

known to have regularly fallen victim to preparatorial alterations, the question of authenticity of the specimen remains unresolved. I therefore refrain from erecting a new genus, but I remove the species *Ichthyosaurus acutirostris* from *Temnodontosaurus*, to which I had previously referred it in 1997.

Important references: OWEN (1840, 1881); SEELEY (1880a); LYDEKKER (1889b, c); VON HUENE (1922a, 1939); MCGOWAN (1974a); BENTON & TAYLOR (1984); HUNGERBÜHLER & SACHS (1996); MAISCH (1997a); CHAPMAN & DOYLE (2002); MCGOWAN & MOTANI (2003).

Family Leptonectidae MAISCH, 1998

34. Genus *Leptonectes* MCGOWAN, 1996

Type species: *Leptonectes tenuirostris* (CONYBEARE, 1822), Lower Jurassic, England, Germany, Switzerland, Belgium.

Further species: *Leptonectes solei* (MCGOWAN, 1993), Lower Jurassic, England; *Leptonectes moorei* MCGOWAN & A. C. MILNER, 1999, Lower Jurassic, England.

Important references: CONYBEARE (1822); HAWKINS (1834, 1840); OWEN (1840, 1881); LYDEKKER (1889b); FRAAS (1892); VON HUENE (1922a); MCGOWAN (1974a, 1989b, 1993; 1996b); GODEFROIT (1992); MAISCH (1999); MAISCH & MATZKE (2003c); MAISCH & REISDORF (2006).

35. Genus *Excalibosaurus* MCGOWAN, 1986

Type species: *Excalibosaurus costini* MCGOWAN, 1986, Lower Jurassic, England.

Remarks. – The genus *Excalibosaurus* was synonymized by MAISCH & MATZKE (2000a) with *Eurhinosaurus*. MCGOWAN (2003) has since then described new and more complete material (a complete skeleton) of the taxon which was only known from a skull and some postcrania before. This new find provides evidence, that a generic separation of the species from both *Leptonectes* and *Eurhinosaurus* can be justified. The genus is therefore, as done by MCGOWAN & MOTANI (2003), regarded as valid.

Important references: MCGOWAN 1986, 1989a, 2003; MAISCH & MATZKE 2000a.

36. Genus *Eurhinosaurus* ABEL, 1909

Type species: *Eurhinosaurus longirostris* OWEN & VON JAEGER in VON JAEGER, 1856, Lower Jurassic, Germany, England, France, Luxemburg.

Important references: MANTELL (1851); VON THEODORI (1854); VON JAEGER (1856); LYDEKKER (1889b); FRAAS (1891); ABEL (1909); VON HUENE (1922a, 1928, 1931a, b, 1949c, 1951, 1952); SWINTON (1930); MCGOWAN (1979, 1990, 1994a); MAISCH & MATZKE (2000a).

Family Suevoleviathanidae MAISCH, 2001

37. Genus *Suevoleviathan* MAISCH, 1998

Type species: *Suevoleviathan disinteger* (VON HUENE, 1926), Lower Jurassic, Germany.

Further species: *Suevoleviathan integer* (BRONN, 1844), Lower Jurassic, Germany.

Important references: BRONN (1844a, b); FRAAS (1891); VON HUENE (1926a, 1952); MAISCH (1998a, 2001b).

Infraorder Thunnosauria MOTANI, 1999

Family Ichthyosauridae BONAPARTE, 1841

38. Genus *Ichthyosaurus* DE LA BECHE & CONYBEARE, 1821

Type species: *Ichthyosaurus communis* CONYBEARE, 1822, Lower Jurassic, England, Belgium, Switzerland.

Further species: *Ichthyosaurus intermedius* CONYBEARE, 1822, Lower Jurassic, England; *Ichthyosaurus breviceps* OWEN, 1881, Lower Jurassic, England; *Ichthyosaurus conybeari* LYDEKKER, 1888, Lower Jurassic, England.

Important references: DE LA BECHE & CONYBEARE (1821); CONYBEARE (1822); HAWKINS (1834, 1840); EGERTON (1837); OWEN (1840, 1881); PEARCE (1846a, b); COLES (1853); LYDEKKER (1889a, b); SOLLAS (1916); VON HUENE (1922a); ANDREWS (1924); ROMER (1968); MCGOWAN (1973a, b, 1974b); BENTON & TAYLOR (1984); GODEFROIT (1996); MAISCH (1997c); MAISCH & MATZKE (2000c); MAISCH et al. (2008b); MOTANI (2005a).

Family Stenopterygiidae WOODWARD in VON ZITTEL, 1932

39. Genus *Stenopterygius* JAEKEL, 1904

Type species: *Stenopterygius quadriscissus* (QUENSTEDT, 1856), Lower Jurassic, Germany, Luxemburg, France.

Further species: *Stenopterygius triscissus* (QUENSTEDT, 1856), Lower Jurassic, England, France, Germany, Luxemburg, Belgium, ?Switzerland; *Stenopterygius uniter* VON HUENE, 1931, Lower Jurassic, Germany.

Important references: VON JAEGER (1824, 1828, 1852); OWEN (1881); BRONN (1844a); WAGNER (1852); QUENSTEDT (1851–52, 1856–58); VON THEODORI (1844, 1854); EÜDES-DESLONGCHAMPS (1875); VON WURSTEMBERGER (1876); SEELEY (1880b); LYDEKKER (1889b, c); FRAAS (1891, 1911); BAUR (1895); BAUER (1900, 1901); JAEKEL (1904); VON BRANCA (1908a, b); WIMAN (1921); VON HUENE (1922a, b, 1926a, 1931a, b, 1939, 1949b, c, 1952); HAUFF (1953); JOHNSON (1979); MCGOWAN (1979, 1992b); HAUFF & HAUFF (1981); BENTON & TAYLOR (1984); MAZIN (1988); BÖTTCHER (1990); GODEFROIT (1993a, 1994); HUNGER-BÜHLER (1994, 1995); CALDWELL (1997a, b); MAISCH 1997a, 1998b, 2008); MAISCH & ANSORGE (2004); MOTANI (2005a).

40. Genus *Chacaicosaurus* FERNÁNDEZ, 1994

Type species: *Chacaicosaurus cayi* FERNÁNDEZ, 1994, Middle Jurassic, Argentina.

Important references: FERNÁNDEZ (1994).

41. Genus *Hauffiopteryx* MAISCH, 2008

Type species: *Hauffiopteryx typicus* (VON HUENE, 1931), Lower Jurassic, Germany, England, Luxemburg.

Important references: VON HUENE (1922a, b, 1926a, 1931a, b, 1939, 1949b, c, 1952); HAUFF (1953); MCGOWAN (1979, 1992b); HAUFF & HAUFF (1981); GODEFROIT (1993a, 1994); MAISCH (1997a, 1998b, 2008).

Family Ophthalmosauridae BAUR, 1887

42. Genus *Ophthalmosaurus* SEELEY, 1874

Type species: *Ophthalmosaurus icenicus* SEELEY, 1874, Middle-Upper Jurassic, England, France.

Further species: *Ophthalmosaurus natans* (MARSH, 1879), Upper Jurassic, USA; *Ophthalmosaurus saveljeviensis* (ARKHANGELSKY, 1997), Upper Jurassic, Russia; *Ophthalmosaurus yasikovi* (EFIMOV, 1999), Upper Jurassic, Russia; *Ophthalmosaurus periallus* (FERNÁNDEZ, 1999), Middle Jurassic, Argentina.

Important references: SEELEY (1874); MARSH (1879, 1880); BAUR (1887a, b); LYDEKKER (1889b); BAUER (1900); GILMORE (1905, 1906); ANDREWS (1907, 1910, 1915); VON HUENE (1922a); MEHL (1927); RUSCONI (1938, 1940, 1942, 1948); APPLEBY (1956, 1958, 1961); GODEFROIT (1993a); ARKHANGELSKY (1997, 1998a, 1999); MCGOWAN (1997b); MAISCH (1997b, 1998c); MASSARE et al. (2006); EFIMOV (1998, 1999a, b); FERNÁNDEZ (1999).

43. Genus *Undorosaurus* EFIMOV, 1999

Type species: *Undorosaurus gorodischensis* EFIMOV, 1999, Upper Jurassic, Russia.

Remarks. – MAISCH & MATZKE (2000a) synonymized this genus with *Ophthalmosaurus*. MCGOWAN & MOTANI (2003), however, pointed out two noteworthy differences to *Ophthalmosaurus*, an incompletely fused ischiopubis (reminiscent of *Hauffiopteryx*) and a remarkably strong dentition. Although incomplete fusion of the pelvic bones occurs as a rare individual variation in *Ophthalmosaurus*, the strong, unreduced dentition probably overstretches the boundaries of the genus. Pending a thorough re-investigation I therefore follow MCGOWAN & MOTANI (2003) inasmuch as I regard the genus as provisionally valid.

Important references: EFIMOV (1999b); MAISCH & MATZKE (2000a); MCGOWAN & MOTANI (2003).

44. Genus *Brachypterygius* VON HUENE, 1922

Type species: *Brachypterygius extremus* (BOULENGER, 1904), Upper Jurassic, England.

Further species: *Brachypterygius mordax* (MCGOWAN, 1979), Upper Jurassic, England; *Brachypterygius pseudoscythius*

(EFIMOV, 1998), Upper Jurassic, Russia; *Brachypterygius alekseevi* (ARKHANGELSKY, 2001) n. comb. (= *Ochevia alekseevi* ARKHANGELSKY, 2001), Upper Jurassic, Russia; *Brachypterygius cantabrigiensis* (LYDEKKER, 1888), Lower Cretaceous, England.

Important references: LYDEKKER (1888, 1889b); BOULENGER (1904); VON HUENE (1922a); MCGOWAN (1976, 1997b); FERNÁNDEZ (1997b); ARKHANGELSKY (1998b, 2001); EFIMOV (1998).

45. Genus *Nannopterygius* VON HUENE, 1922

Type species: *Nannopterygius enthekiodon* (HULKE, 1871), Upper Jurassic, England, Germany.

Important references: HULKE (1871); LYDEKKER (1889b); VON HUENE (1922a).

46. Genus *Aegirosaurus* BARDET & FERNÁNDEZ, 2000

Type species: *Aegirosaurus leptospondylus* (WAGNER, 1853), Upper Jurassic, Germany, Argentina.

Important references: WAGNER (1853); BAUER (1898); VON HUENE (1922a); GASPARINI (1988); BARDET & FERNÁNDEZ (2000).

47. Genus *Caypullisaurus* FERNÁNDEZ, 1997

Type species: *Caypullisaurus bonapartei* FERNÁNDEZ, 1997, Upper Jurassic, Argentina.

Important references: FERNÁNDEZ (1997a, 1998, 2001, 2007); MOTANI (1999a, b); FERNÁNDEZ et al. (2005).

48. Genus *Platypterygius* VON HUENE, 1922

Type species: *Platypterygius platyductylus* (BROILI, 1907), Lower Cretaceous, Germany.

Further species: *Platypterygius australis* (M'COY, 1867), Lower Cretaceous, Australia; *Platypterygius hauthali* (VON HUENE, 1927), Lower Cretaceous, Argentina; *Platypterygius americanus* (NACE, 1939), Lower Cretaceous, USA; *Platypterygius hercynicus* KUHN, 1946, Lower Cretaceous, Germany; *Platypterygius kiprijanoffi* ROMER, 1968, Lower Cretaceous, Russia; *Platypterygius birjukovi* OTSCHEV & EFIMOV, 1985, Lower Cretaceous, Russia; *Platypterygius bedengensis* (EFIMOV, 1997), Lower Cretaceous, Russia; *Platypterygius sachicarum* PÁRAMO, 1997, Lower Cretaceous, Colombia; *Platypterygius bannovkensis* ARKHANGELSKY, 1998, Upper Cretaceous, Russia; *Platypterygius ochevi* ARKHANGELSKY in ARKHANGELSKY, AVERIANOV, PERVUSHOV, RATNIKOV & ZOZYREV, 2008, Lower (?Upper) Cretaceous, Russia.

Important references: CARTER (1846a, b); OWEN (1851); M'COY (1867, 1869); KIPRIJANOFF (1881); ETHERIDGE (1888); LYDEKKER (1889b); BROILI (1907, 1908, 1909); VON HUENE (1922a, 1925c, 1926b); LONGMAN (1922); NACE (1939, 1941); KEAR (2003, 2005); KUHN (1946, 1957); ROMER (1968); MCGOWAN (1972c); WADE (1984, 1990); OCHEV & EFIMOV (1985); BARDET (1989, 1990); EFIMOV (1997); PÁRAMO (1997); ARKHANGELSKY (1998b);

SIROTTI & PAPPAZONI (2002); FERNÁNDEZ & AGUIRRE-URRETA (2005); ARKHANGELSKY et al. (2008); KOLB & SANDER (2009).

49. Genus *Maiaspondylus* MAXWELL & CALDWELL, 2006

Type species: *Maiaspondylus lindoei* MAXWELL & CALDWELL, 2006, Lower Cretaceous, Canada.

Remarks. – Whether this really is a genus distinct from *Platypterygius* remains questionable, regarding the rather fragmentary type material. Nevertheless, a revision of *Platypterygius* is long overdue, and it is quite probable that it has become a waste-basket taxon including species that in fact belong to several closely related genera. With respect to these uncertainties, it makes little sense to sink *Maiaspondylus* and it is therefore provisionally accepted as a valid taxon.

Important references: MAXWELL & CALDWELL 2006.

3. The origin of the Ichthyosauria

3.1. Previous research

The question of the origin of ichthyosaurs has been discussed for more than a century. The highly autapomorphic skeletal morphology of these animals, representing the nightmare of any phylogeneticist, has made it difficult from the beginning to place them into existing tetrapod classifications. The anatomy of these animals is just so unusual, that their relationships to any terrestrial amniotes are almost impossible to evaluate. An analogous example is found in the mammalian Cetacea, the origin of which could only very recently be elucidated based on both molecular and morphological studies. The latter were made possible by a suite of spectacular new fossil finds of basal representatives of the group (GINGERICH et al. 2001; THEWISSEN et al. 2001, 2007).

Neither are molecular data available for ichthyosaurs, nor do we have fossil finds comparable in quality and importance to *Indohyus*, the pakicetids and their relatives that helped so much to clarify the origin of whales. The problem of elucidating ichthyosaur ancestry, working only with morphological data from rather derived and usually very fragmentary representatives of the group, appears therefore one of the most difficult that remains in the systematics of lower tetrapods in general. It will be shown below, that previous claims that the ichthyosaurs can safely be assumed to form part of the Diapsida were premature, and that morphological data are not yet sufficient to even place them in one of the large reptilian subgroups with any degree of confidence.

In the past, there were few tetrapod groups that have not, at least at one occasion, been discussed as probable ichthyosaur ancestors or at least their close relatives. The

most detailed and exhaustive studies on the subject in the first half of the last century were carried out by FRIEDRICH VON HUENE, who was the best connoisseur of the group at this time, but even he came to totally different results in the progress of his studies.

In his great monograph “Die Ichthyosaurier des Lias und ihre Zusammenhänge” VON HUENE (1922a) considered the mesosaurs, anapsid amniotes of still uncertain (but probably parareptilian, see, e. g. MODESTO et al. 2009; MÜLLER & TSUJI 2007; TSUJI & MÜLLER 2009) systematic position found in the uppermost Carboniferous and lowermost Permian of South Africa and South America, as the closest relatives and potential ancestors of ichthyosaurs. This view was shared at this time by several other well-renowned vertebrate palaeontologists, such as MACGREGOR (1908), ABEL (1919) and VON NOPCSA (1923).

Later VON HUENE undertook a detailed study on the skeletal morphology of mesosaurs, based on rich material from the Lower Permian of Brazil (VON HUENE 1941). He recognized a suite of important differences between ichthyosaurs and mesosaurs which prompted him to regard the mesosaurs as basal synapsids afterwards (VON HUENE 1940, 1941). Ironically, the feature that VON HUENE considered most important in this context, the presence of a lower (synapsid) temporal fenestra in mesosaurs, has since been demonstrated to be based on misinterpretation (MODESTO 1999; ROSSMANN & MAISCH 1999). Mesosaurs were in fact anapsids, and his original interpretation (VON HUENE 1922a) was the correct one. Therefore the main argument that prompted VON HUENE to categorically exclude a closer relationship between mesosaurs and ichthyosaurs (VON HUENE 1940, 1941) is no longer valid.

Concerning the origin of ichthyosaurs, VON HUENE changed his mind completely and in 1937 he published a very influential and rather original alternative hypothesis, in which he attempted to demonstrate a close similarity between ichthyosaurs and embolomeres “amphibians”. He tried to establish the idea, that ichthyosaurs should not be classified as “reptiles” (i. e. amniotes in this context) at all, but that they developed independently from the “labyrinthodont amphibians” of the Palaeozoic. A large number of characters that VON HUENE (1937, also 1956) cited to support this view have since been demonstrated to be invalid, as we now know that they in fact only occur in the later, more derived ichthyosaurs but are not present in the Lower Triassic forms (which, at that time, were very poorly known). One of these characters would be, for example, the large interpterygoid vacuities, separated by a very long and slender processus cultriformis of the parasphenoid. Other apparent similarities turned out to be homoplasies, as later studies demonstrated. A good example is the labyrinthodont dentition of ichthyosaurs, which, as SCHULTZE (1969) has demonstrated convincingly, is quite different from that found in the rhipidistians and true

“labyrinthodonts”. Some truly very plesiomorphic characters of ichthyosaurs that VON HUENE pointed out and which are also known to occur in basal members of the group remain unexplained, however, to the present day. These include the size and arrangement of the supratemporal in the skull roof, the deeply concave condylus occipitalis and the very plesiomorphic atlas-axis complex, and these features should not be ignored.

The interpretation that ichthyosaurs were derived from embolomeres was favoured for a long time by VON HUENE and it gained rather wide acceptance. Later still, he regarded the temnospondyls (the stem-group of the lissamphibians) as most closely related to ichthyosaurs instead. He was mainly prompted to this by the discovery and description of the partial skull and vertebral column of the Lower Triassic temnospondyl *Tupilakosaurus heilmanni* from Eastern Greenland (NIELSEN 1954), which seemed to show striking similarities to early ichthyosaurs. Among the temnospondyls, VON HUENE regarded the equally longirostrine, piscivorous and partially marine trematosaur as the closest relatives of ichthyosaurs. This interpretation is also found in his monumental “Paläontologie und Phylogenie der niederen Tetrapoden” (1956). When VON HUENE visited the collections in Moscow, however, in 1957 he had the opportunity to study better and more complete material of *Tupilakosaurus* from the Lower Triassic of Russia, which was later described by SHISHKIN (1958). He clearly recognized that he had been on the wrong trail, “auf einer falschen Fährte”, and rejected the idea of a temnospondyl, and in fact generally “labyrinthodont” ancestry of ichthyosaurs entirely. He showed remarkable self-criticism for a scientist more than 80 years old at this time who was forced to give up an idea that he had wholeheartedly believed in for more than 30 years (see VON HUENE 1959).

Despite VON HUENE’s own statements, the idea of the “amphibian origin” of ichthyosaurs remained popular, and the notion that they were a very “basal” and “primitive” group that were not truly “reptiles” was discussed for a long time afterwards and even vehemently supported by a few authors (e. g. RIESS 1986).

In his last paper on the origin of ichthyosaurs (1960) VON HUENE declared that they were true reptiles (amniotes), but possibly derived from rather basal ancestors that were not clearly identifiable. In reading the paper one gets the impression of a certain resignation, as he recognized that he faced a problem that was probably entirely unsolvable with the data and material that were available in 1960.

The authority of VON HUENE on the field of fossil reptile systematics in general, and the ichthyosaurs in particular, was so great that only few authors expressed themselves clearly on the question of ichthyosaur origins during his lifetime. Just after he ceased to publish on the question, the first alternative interpretations were offered. APPLEBY (1961) was the first author to address the problem

of ichthyosaur origins on a broad basis of comparative anatomical data, focussing in particular on the structure of the neurocranium. He found anatomical evidence that suggested that ichthyosaurs were derived from anapsid reptiles (“cotylosaurs”) and he also noted an amazing similarity to turtles (ironically, one of the few groups the origin of which is almost as uncertain and debated as that of the ichthyosaurs).

Unfortunately APPLEBY’S scholarly and in parts brilliant argumentation (which was widely ignored in the later literature) was largely based, again, on material of highly derived ichthyosaurs from the Jurassic, particularly unusually well preserved specimens of the Middle Jurassic *Ophthalmosaurus icenicus* from the English Oxford Clay (APPLEBY 1956, 1961), but also, e. g., the Lower Jurassic *Ichthyosaurus*. The reason for this is not ignorance on the part of APPLEBY, but simply the fact that practically all Triassic ichthyosaur finds up to the present day are so incompletely and inadequately preserved, that they are near to worthless for such an investigation. The neurocranium is still not completely known in a single Triassic ichthyosaur taxon, and only a few taxa have preserved at least some parts of it in a satisfactory manner.

At the time of APPLEBY’S studies, the general notion was still that the temporal region of ichthyosaurs was fundamentally different from that of all other reptiles, living or fossil. As was – and after unnecessary complications again is – known, ichthyosaurs possess a single temporal opening situated high up on the skull roof, which is mainly surrounded by the postfrontal, parietal and supratemporal in derived forms. The postorbital and the frontal may enter the margin of the fenestra in earlier forms, whereas the squamosal is always excluded from it. There is thus no proof, and actually little indication for, homology of this fenestra to the supratemporal fenestra of diapsids. WILLISTON (1917) had termed this skull construction – as well as several other apparently similar ones, which can, however, be clearly derived from a diapsid pattern – as parapsid. VON HUENE (1943) instead called the ichthyosaurian condition metapsid, to clearly distinguish it from all other types of temporal architecture, a term that should be used in connection to the ichthyosaur temporal region as long as unequivocal proof is lacking that it is derived from a diapsid condition.

Because of the unique temporal skull roof of ichthyosaurs, virtually none of the earlier authors ever considered any close relationship of ichthyosaurs and diapsids as a viable alternative. Even the “euryapsids”, an assemblage including protorosaurs, placodonts and sauropterygians with only the fenestra supratemporalis preserved, which is, however, usually surrounded by postorbital, parietal, postfrontal and squamosal, were hardly thought comparable. After long and cumbersome discussions it is nowadays generally accepted that all the “euryapsid” forms are indeed derived diapsids that have lost or reduced the fenestra infratempo-

ralis, partially in a slightly different manner, but retained the fenestra supratemporalis which is homologous to the same opening in archosaurs and lepidosaurs. In the case of the sauropterygians, JAEKEL (1902) was the first author to provide good arguments why at least the sauropterygians should be interpreted as derived diapsids.

In 1968 and 1973 two very influential studies appeared, based on very well preserved Jurassic and Cretaceous ichthyosaur skull material, published by A. S. ROMER (1968) and C. MCGOWAN (1973a). They did not in fact shed any new light on the discussion of the origin of ichthyosaurs, but unfortunately muddied the waters for decades to come. In both papers, the presence of a third (middle) element in the temporal region of ichthyosaurs could not be corroborated, and it was convincingly demonstrated in the material at hand that only two elements were present. In congruence with the skull anatomy of other reptiles, and ignoring the data published on numerous other ichthyosaur specimens for more than 100 years, the upper element was interpreted as the squamosal, the ventral one as quadratojugal. In this way, ichthyosaurs became suddenly very similar to other “euryapsid” reptiles in this important region of the skull. They were classified accordingly by ROMER and put in the subclass Euryapsida, together with protorosaurs, placodonts and sauropterygians. After this idea was established, it was only a small step to declare ichthyosaurs diapsids. As EMIL KUHN-SCHNYDER (1967) and other authors had convincingly shown that the “Euryapsida” was nothing but an unnatural polyphyletic grouping of diapsids with a modified skull architecture, it became even more plausible to assume a similar course of cranial evolution for ichthyosaurs as well.

MAZIN (1982) followed by PINNA (1989), TARSITANO (1982, 1983) and MASSARE & CALLAWAY (1990) were probably the most influential authors that postulated a diapsid origin of ichthyosaurs, but none of them supported their views with a phylogenetic analysis to test this hypothesis. The possibility that a third element in the temporal region could indeed be present (called by ROMER (1968) VON HUENE’S “figment of imagination”) was excluded by all these authors, although some remained uncertain, yet its absence had been so convincingly demonstrated.

GODEFROIT (1993a, 1994) suggested that the third element was a neomorphous ossification, present in only a few taxa, when he was confronted with its undoubted presence in well-preserved material of the Jurassic genus *Stenopterygius*. As an ossification in similar position had been mentioned (but never figured, this was done by MAISCH (1998c) for the first time) in the Middle Jurassic *Ophthalmosaurus* by ANDREWS (1910) and APPLEBY (1956), GODEFROIT declared its presence a potential autapomorphy of the Stenopterygiidae.

MAISCH (1997a) therefore was the first author not only to challenge the by that time well-established interpreta-

tion of ichthyosaurs as sharing the same skull architecture with other “modified” diapsids, but also to clarify the homology of the temporal elements. The traditional interpretation was supported, and the correct observations of FRIEDRICH VON HUENE and his predecessors were confirmed. The dorsalmost element, being in the same position and assuming the same shape and relationships as the squamosal in the diapsid skull, was identified as the supratemporal. The middle element, displaced laterally, always excluded from the temporal fenestra and with no close resemblance to its homologue in any diapsid, was identified as the squamosal. The identification of the ventral element as quadratojugal was never in question (only NICHOLLS & BRINKMAN (1995) declared it as the squamosal in *Parvinator*, for reasons unknown). This interpretation gained wide acceptance rapidly, particularly because MAISCH & HUNGERBÜHLER (1997b, 2001), MAISCH (1998c) und MAISCH & MATZKE (1997b, 1998b, 2000a, c) published additional detailed descriptions of well-preserved material from the Jurassic as well as the Triassic which supported the interpretation of MAISCH (1997c) which, originally, only relied on material of the Jurassic species *Stenopterygius triscissus* (as it was also described before by GODEFROIT (1993a, 1994)).

MOTANI et al. (1998) also followed MAISCH’s interpretation in the description of the Lower Triassic *Utatusaurus*, as well as MOTANI (2000a) did when he redescribed the equally Lower Triassic *Grippia longirostris*. In both these cases the reconstruction of the temporal region is not unproblematic, however, due to the fragmentary nature of the material. The same is true for the interpretation of the presumably Lower Triassic *Parvinator* by NICHOLLS & BRINKMAN (1995) and also for MAISCH’s (2001a) description of the Lower Triassic *Chaohusaurus geishanensis* (see MAISCH 1997a, 1998c; MAISCH & MATZKE 2002b for a more detailed discussion on the problems posed by these basal ichthyosaurs).

The definite end of the idea of ichthyosaurian “euyapsid” came with the publication by MAISCH & MATZKE (2000c) which demonstrated that a centrally placed squamosal was also present in the Lower Jurassic *Ichthyosaurus*. It was this genus in which MCGOWAN (1973a) was unable to detect a squamosal, although he had excellent, acid-prepared, three-dimensional material at his disposal. This was not MCGOWAN’s fault, however, since, as MAISCH (1998c) and MOTANI (1999c) demonstrated, the squamosal is often not well integrated into the skull of derived Jurassic ichthyosaurs and shows a tendency to get disarticulated very early. MCGOWAN probably had just bad luck with his material. He himself was always very reluctant regarding the question of ichthyosaur origins, and never expressed a strong opinion on this difficult question. Nevertheless his detailed investigation, and even more the very influential paper by A. S. ROMER (1968), brought about the

change in paradigm regarding the interpretation of the ichthyosaur temporal fenestration.

MOTANI et al. (1998) were the first authors who tried to elucidate ichthyosaur relationships with the aid of a large-scale phylogenetic analysis. CALDWELL (1996) also made an earlier attempt, but he had only a very limited data set at his disposal. They introduced the Ichthyosauria into the great amniote data matrix of RIEPPEL & DE BRAGA (1996) respectively DE BRAGA & RIEPPEL (1997). It was not surprising that this resulted in ichthyosaurs being placed firmly among the basal diapsids, despite their aberrant skull construction. A re-analysis of CALDWELL’S (1996) data, which a priori only had diapsid taxa in the ingroup and was therefore rather biased from the beginning, also showed a similar result. Ichthyosaurs were interpreted as the sister-group of the Sauria (Archosauromorpha and Lepidosauromorpha). A closer look on the coding of the characters (which is debatable in many instances) as well as the selection of characters shows that the placement of the ichthyosaurs is highly likely to be the result of numerous convergences shared with the aquatic eosuchians, *Claudiosaurus* and the sauropterygians. Evidence for this is found by the unsuspected placement of the mesosaurs in the analysis carried out below. Of course such characters can not be ignored a priori, but they should be viewed with caution.

The matrix of DE BRAGA & RIEPPEL (1997) was modified several times after its first publication. At first LEE (1997b) proposed some changes of character codings. MOTANI et al. (1998) suggested to delete two characters of the original matrix, (162 and 163) entirely. RIEPPEL & REISZ (1999) accepted some, but not all, of LEE’S suggestions and did not take the proposal of MOTANI et al. (1998) into account, only adding the new terminal taxon *Cyamodus*, an armoured placodont superficially similar to turtles.

For my own analysis I have taken this latter version of the data matrix, but I have, unlike RIEPPEL & REISZ (1999), accepted the proposal of MOTANI et al. (1998) and ignored the original characters 162 and 163, as I consider the arguments for doing so convincing. Into this matrix I have entered two new terminal taxa, namely the Mesosauria (as has not been done before) and the Ichthyosauria. The Mesosauria were entered as a test of the hypothesis formulated above, i. e., that the matrix overemphasizes convergences due to aquatic adaptations. Should the mesosaurs – which have never been considered as diapsids before – occupy a similar place in the resulting cladogram as the ichthyosaurs, something must be doubtful about the entire data matrix, at least with respect to secondarily aquatic taxa. Of course I have not taken the codings for ichthyosaurs by MOTANI et al. (1998) at face value, but have completely recoded the group according to the results of more than ten years of intensive personal study, as well as the accumulation of new data due to the work of other authors since 1998. Skull characters for mesosaurs were coded accord-

ing to the excellent and detailed studies of MODESTO (1999, 2006) on the skulls of *Stereosternum tumidum* and *Mesosaurus tenuidens*. The postcranial skeleton was coded with the aid of the monograph of VON HUENE (1941). In addition, I have personally observed material of all three mesosaur genera (*Stereosternum*, *Mesosaurus* and *Brazilosaurus*) in several collections, including Tübingen (MAISCH 1995, original specimens of VON HUENE 1941 as well as numerous additional ones), Frankfurt, Stuttgart and Munich (see ROSSMANN & MAISCH 1999). Over the years, more than one hundred mesosaur specimens were closely investigated.

The result of the analysis does not differ very much from that of MOTANI et al. (1998). The ichthyosaurs are of course nested within the diapsids. But, and this is the important result, the same is true for the undoubtedly anapsid and very basal mesosaurs that are universally regarded as either parareptiles or even more basal amniotes (MODESTO et al. 2009; MÜLLER & TSUJI 2007; TSUJI & MÜLLER 2009). In fact, ichthyosaurs and mesosaurs turn out to be sister-groups in the resulting cladogram. Both groups together are the sister-group of the Neodiapsida, so that the ichthyosaurs plus mesosaurs hold a much more basal position than suggested by MOTANI et al. (1998). In my opinion the resulting cladogram can only be interpreted in one way: there is a high number of characters in the data matrix that are related to or strongly affected by secondarily aquatic adaptations, which are very suspect of being due to convergences rather than to common ancestry. Most of these characters are reductional, too. Due to this, totally unrelated secondarily aquatic groups, as exemplified by the Mesosauria, and possibly also the Ichthyosauria, are forced into a position within basal diapsids, close to the aquatic eosuchians (taken here as a grade or possibly clade, of stem-group diapsids including *Youngina*, *Acerosodontosaurus* and the tangasaurids) and *Claudiosaurus* and not too far from the sauropterygians and placodonts. The phylogenetic relevance of the resulting cladogram, at least concerning aquatic forms, is therefore in my opinion highly doubtful.

As I was so unsatisfied by the results of this analysis, I chose to undertake a second one that uses a different set of taxa and characters, to test if in such a case a different result may be obtained, or whether additional independent evidence for diapsid relations of ichthyosaurs could be found. For this test, I chose the matrix of LAURIN & REISZ (1995) in the emended version that was provided by MODESTO (1999). There is one – in my opinion – major advantage of this matrix compared to that of DE BRAGA & RIEPPEL (1997), because it – at least partially and implicitly – works with reconstructed grundplans of the terminal taxa. The ambiguity of polymorphous characters and the multiple character states allegedly of equal value that characterize the matrices of DE BRAGA & RIEPPEL (1997) respectively RIEPPEL & REISZ (1999) are therefore much rarer (my codings of Mesosauria and Ichthyosauria

are completely based, as will be easily recognized, on reconstructed grundplans in the HENNIGIAN sense).

Surprisingly, phylogenetic analysis shows a completely different result when ichthyosaurs are entered into the data matrix of LAURIN & REISZ (1995). Ichthyosaurs are well nested within the primarily anapsid Parareptilia, forming the sister-group of a monophylum that contains Procolophonia, Pareiasauria and Testudines. There is, however, no closer relation to the Mesosauria or the eosuchians (i. e., younginiforms, the monophyly of which has been recently doubted by BICKELMANN et al. 2009, I therefore chose to use the more neutral term eosuchians for these taxa, which does not necessarily imply monophyly). An attraction of unrelated secondarily aquatic forms is therefore not apparent in this data matrix. The phylogenetic signal, at least for secondarily aquatic forms, therefore seems to be more trustworthy, and the results support the notion that the matrix of RIEPPEL & REISZ (1999) contains an overemphasis on convergences and reductions due to secondarily aquatic adaptations.

The most interesting effect of the inclusion of ichthyosaurs is, however, that the most stable monophylum of the original analysis of LAURIN & REISZ (1995), the sister-group relationship between turtles and procolophonians, is not reproduced. Instead turtles become the sister-group of pareiasaurs, as was suggested by LEE (1997a).

It is even more interesting, that, as MOTANI et al. (1998), when including ichthyosaurs into the original matrix of DE BRAGA & RIEPPEL (1997) already recognized, the same effect is found in the analysis of RIEPPEL & REISZ' (1999) matrix. MOTANI et al. (1998) already noted that an inclusion of ichthyosaurs destroys the sister-group relationship of turtles and sauropterygians, and makes turtles the sister-group of pareiasaurs. RIEPPEL & REISZ (1999) noted this strange threat to the “diapsid turtle scenario” and wrote: “The addition of ichthyosaurs, a group of dolphin-like Mesozoic aquatic reptiles, to the data matrix of DE BRAGA & RIEPPEL again appears to switch turtles back into parareptiles”. However, they assumed that with their new and improved data matrix, this should not happen again. Maybe they trusted that the inclusion of the armoured and superficially turtle-like placodont *Cyamodus* may have some positive effect: “Although we do not anticipate the same result if ichthyosaurs were added to the data matrix in its current corrected form, it certainly is a hypothesis that has to be tested”. The test has been done, and the results are obvious: turtles are, even after analysis of the modified matrix of RIEPPEL & REISZ (1999), the sister-group of pareiasaurs when ichthyosaurs and mesosaurs are included. I assume this would also have happened if I had used the ichthyosaur codings of MOTANI et al. (1998), because these are generally quite similar to my own.

In this whole context I have to indicate, that two changes of character codings proposed by RIEPPEL & REISZ (1999)

do not make sense. The coding of character 78 shall be, as they propose, changed from “2” to “0”, but it is already “0” in the original matrix. The same is true for the suggested change of character 68 in the Rhynchocephalia, which should be changed from “0” to “0 & 1”, as the latter coding is also already found in the original matrix. RIEPPEL & REISZ (1999) also suggest to change the coding of character 30 in kuehneosaurids from “?” to “0”. Again the coding is already “0” in the original matrix, whereas character 29 is in fact coded with a “?”. I have therefore interpreted this statement as referring to character 29, not character 30, probably because the authors missed the right column of their matrix. If one omits this change completely, the results are not different anyway, as a test has shown.

The modified data matrices of RIEPPEL & REISZ (1999) and LAURIN & REISZ (1995) are provided below (Tabs. 1 and 2), in a hopefully more readable form than in previous publications (which should lessen the chance of missing the right line or column in the future). I have also provided a discussion for my codings of the ichthyosaurs below, in order to make my reasons for each coding completely transparent and allow easier criticism and/or modification, if future researchers should consider these or future finds make them necessary.

It should be noted, that since the publication of the large-scale analyses that I have used here, several others have appeared, including those of MÜLLER (2003, 2004). These analyses, although relying heavily on the earlier work (particularly of DE BRAGA & RIEPPEL 1997, but also DILKES 1998), added new important observations and included additional taxa, such as the Thalattosauriforms, which were found to be the sister group of Ichthyosaurs at the base of saurian diapsids by MÜLLER (2003, 2004). The analysis of HILL (2005) also needs to be mentioned. HILL (2005) followed a total-evidence approach, including morphological and molecular data (which are, as pointed out above, unavailable for ichthyosaurs, rendering their inclusion in such an analysis problematic). That I have stuck to the traditional analyses instead of the later ones has been done for several reasons. The analyses of DE BRAGA & RIEPPEL (1997) and LAURIN & REISZ (1995) in their original and expanded forms have been in the centre of discussion on amniote interrelationships for a long time. They have formed the basis of numerous studies and have been largely expanded upon by later researchers (e. g. MÜLLER 2003, 2004; MÜLLER & TSUJI 2007), but no fundamentally new morphology-bases analysis of amniote interrelationships on a large scale has since become available. The original analyses are widely known among specialists and non-specialists, and are still frequently cited in support or refusal of hypotheses of amniote interrelationships. The purpose of the present paper is not, to “clarify” ichthyosaur interrelationships, but instead to investigate potential shortcomings of the original analyses on which – im-

plicitly or explicitly – the overwhelming majority of work on large-scale amniote interrelationships has been based ever since. To carry this out, it is relevant to go “back to the roots”, not to pick out the most recent additions to the original work. It should be noted, that these later analyses can also not be considered as being uninfluenced or unbiased with respect to the original shortcomings and problems of the original analyses, although it is admitted that much work has been put into improving this situation.

3.2. Discussion of the data matrix of RIEPPEL & REISZ (1999)

Discussion of the character codings for the Ichthyosauria in the data matrix of RIEPPEL & REISZ (1999). I have used the original formulations, only correcting some orthographic mistakes. The original characters 162 and 163 were excluded, following the suggestion of MOTANI et al. (1998).

- 1 Premaxilla exposure: exposure anterolateral to external nares small restricted to low posterolateral process forming less than one-half the height of the premaxilla (0); posterolateral process tall reaching dorsal process (1). Modified from RIEPPEL (1994) #1.
Coding for Ichthyosauria: 0
Discussion. – An anterolateral process of the premaxilla (i. e. a processus subnarialis) is only developed as a very small structure in basal ichthyosaurs, such as *Utatsusaurus*. In mixosaurids, *Cymbospondylus* and *Besanosaurus*, it is even completely absent. The most basal taxon in which it has a considerable size is *Mikadocephalus*, it is also quite large in the Neoichthyosauria. There is never any contact with the dorsal premaxillary process (processus supranarialis) in any ichthyosaur.
- 2 Premaxilla/prefrontal contact: absent (0); present (1).
Coding for Ichthyosauria: 0
Discussion. – No known ichthyosaur shows a sutural contact between premaxilla and prefrontal. They are always separated clearly by the intervening maxilla, nasal and lacrimal.
- 3 Premaxilla dentition: present (0); absent (1).
Coding for Ichthyosauria: 0
Discussion. – With the exception of the fully adult representatives of some highly derived species of the Stenopterygiidae and Ophthalmosauridae which reduce the entire dentition, the premaxilla is fully toothed in all ichthyosaurs.
- 4 Premaxilla/external nares relationship: excluded from posterior border of nares (0); contributes to posterior border (1). From RIEPPEL (1994) #2.
Coding for Ichthyosauria: 0
Discussion. – The premaxilla usually forms the anterior and also part of the dorsal and ventral narial margin, but never contacts the posterior narial margin in ichthyosaurs.
- 5 Septomaxilla facial process: absent (0); present (1). From REISZ et al. (1992) #6.

Coding for Ichthyosauria: 0

Discussion. – A septomaxilla has been found only in a few ichthyosaur taxa so far (SOLLAS 1916; ROMER 1968; MAISCH & MATZKE 1997a, 2000c). In all these cases it is always deeply recessed within the narial aperture and never forms a processus facialis.

- 6 External nares exposure: dorsal process of premaxilla broad restricting nares to a lateral exposure (0); dorsal process narrow resulting in dorsal exposure of nares (1).

Coding for Ichthyosauria: 1

Discussion. – Although the external naris is situated in a lateral position in the well-known Jurassic ichthyosaurs this is different in the basal forms. In *Utatusaurus* and *Grippia*, the internarial bar is narrow and the external nares point largely dorsally. This was also found by SCHMITZ et al. (2004) in the basal phalarodontine mixosaur *Phalarodon callawayi*, where it may be an autapomorphic reversion, however. Nevertheless, available evidence suggests that a dorsally placed naris is the ancestral state in ichthyosaurs, whereas a laterally facing naris is derived within the group (see MAISCH & MATZKE 2000a, character 13).

- 7 External nares: separated by intranarial bar of premaxilla (0); confluent (1).

Coding for Ichthyosauria: 0

Discussion. – In all known ichthyosaurs there is a complete internarial bar formed by the premaxillaries and/or the nasals.

- 8 Choana palatal exposure: parallel medial border of maxilla (0); deflected posteromedially (1); hidden in palatal view (2).

Coding for Ichthyosauria: 0

Discussion. – The palate of the most basal ichthyosaurs is very incompletely known. The most plesiomorphic taxon in which sufficient data are present is the phalarodontine mixosaur *Contectopalatus atavus* from the Middle Triassic. It clearly shows choanae the long axes of which parallel the medial margins of the maxillaries. This state is also found in all more derived ichthyosaurs where the palate is known, so this is assumed to represent the ancestral state in ichthyosaurs.

- 9 Nasals: paired (0); fused (1); lost (2).

Coding for Ichthyosauria: 0

Discussion. – The nasals are paired in all ichthyosaurs.

- 10 Nasal/frontal ratio: nasal equal to or shorter than frontal (0); nasal at least one-third longer, or better (1). From RIEPPEL (1994) #4.

Coding for Ichthyosauria: 0

Discussion. – Most ichthyosaurs have nasals that are much longer than the frontals, due to the elongation of the snout and entire preorbital skull region. This is not true, however, for the most basal taxa. In both *Utatusaurus hatai* and *Grippia longirostris*, and even in the mixosaurids like *Contectopalatus atavus*, the nasal is either shorter or at maximum as long as the frontal. This is therefore considered as the grundplan state of ichthyosaurs. An elongation of the nasals on expense of the frontals is apomorphic within the group (see MAISCH & MATZKE 2000a, character 14).

- 11 Maxilla ascending process: absent (0); present between orbit and external nares (1). From LAURIN & REISZ (1995) #19.

Coding for Ichthyosauria: 1

Discussion. – The neoichthyosaurs of the Jurassic and Cretaceous have lost the ascending process (processus ascendens or processus postnarialis) of the maxilla. It is, however, usually present in the Triassic forms, including the most basal taxa, as exemplified, e. g., by *Utatusaurus*, *Grippia*, or the mixosaurids. They all have a well-developed, although narrow processus postnarialis which also excludes the lacrimal from the external naris. The reduction of this process is apomorphic within the group (see MAISCH & MATZKE 2000a, character 11).

- 12 Maxillary horn: absent (0); present directly behind external nares (1). From LEE (1994) #25.

Coding for Ichthyosauria: 0

Discussion. – A maxillary horn, as in *Macroleter* and *Scutosaurus*, has never been recorded in ichthyosaurs.

- 13 Anterolateral maxillary foramen: absent or if present equal in size to all other foramina (0); present at least twice the diameter of all other foramina (1). From LAURIN & REISZ (1995) #20.

Coding for Ichthyosauria: 0

Discussion. – Foramina within the maxilla are known in a variety of ichthyosaurs, although they are usually not mentioned or explicitly described in the literature. They have, e. g., been described in detail by MAISCH & MATZKE (1998b, 2001b) in *Contectopalatus atavus* from the Middle Triassic, where both character states can occur. In other Triassic ichthyosaurs the maxillary foramina are usually smaller and less conspicuous. It is therefore assumed that the enlarged anterolateral maxillary foramen found in many parareptiles is lacking in the grundplan of ichthyosaurs.

- 14 Maxilla length: extends to posterior orbital margin (0); does not reach posterior margin of orbit (1).

Coding for Ichthyosauria: 1

Discussion. – In ichthyosaurs the maxilla never reaches the posterior border of the orbit. This is not correlated to the enlargement of the orbit within the group, as this character state is equally found in taxa which possess rather small orbits, such as *Cymbospondylus*.

- 15 Maxilla orbital exposure: absent (0); present (1). From LEE (1994) #28.

Coding for Ichthyosauria: 0

Discussion. – An orbital exposure of the maxilla is unknown in ichthyosaurs, with exception of the highly derived *Suevoleviathan disinteger* from the Lower Jurassic, where it is clearly autapomorphic (MAISCH 1998a).

- 16 Maxilla/quadratojugal relationship: not in contact (0); in contact (1). From LAURIN & REISZ (1995) #22.

Coding for Ichthyosauria: 0

Discussion. – Maxilla and quadratojugal are separated in all ichthyosaurs by the intervening jugal.

- 17 Lacrimal morphology: present and contributing to external nares (0); present at least as long as tall, but excluded from external nares (1); if present small, restricted to orbital margin, or absent entirely (2). From RIEPPEL (1994) #7.

Coding for Ichthyosauria: 1

Discussion. – Although the lacrimal of basal ichthyosaurs such as *Utatusaurus*, *Grippia* or *Parvinator* is well-developed, it is always separated from the external naris by the processus postnarialis of the maxilla. Within the group, the processus postnarialis is reduced, resulting in a lacrimal-naris contact (see MAISCH & MATZKE 2000a, character 11).

- 18** Lacrimal duct: enclosed by lacrimal only (0); lateral border formed by maxilla (1). Modified from LAURIN & REISZ (1995) #10.
Coding for Ichthyosauria: ?
Discussion. – There is no identifiable ductus nasolacrimalis or foramen lacrimale in known ichthyosaurs, so that this character can not be coded. It appears likely that these structures were reduced as a result of the aquatic adaptation of the group.
- 19** Skull proportions: preorbital skull length equal to postorbital length (0); preorbital length exceeds postorbital skull length (1); postorbital length exceeds preorbital skull length (2). From RIEPPEL (1994) #9.
Coding for Ichthyosauria: 1
Discussion. – Due to the enormous autapomorphic development of the rostrum, the preorbital skull segment is always longer than the postorbital skull segment in ichthyosaurs. This tendency increases during evolution of the group, and can result in extreme values, such as in the Lower Jurassic *Eurhinosaurus longirostris* where the preorbital skull segment is about 20 times as long as the postorbital segment(!). In basal forms like *Thaisaurus*, *Utatusaurus* or *Chaohusaurus* the preorbital skull segment is at least twice as long as the postorbital one.
- 20** Prefrontal/palatine antorbital contact: narrow forming less than one-third the transverse distance between the orbits (0); contact broad forming at least one-half the distance between the orbits (1). Modified from LAURIN & REISZ (1995) #6 and #7.
Coding for Ichthyosauria: 0
Discussion. – There is no definite prefrontal-palatine contact in ichthyosaurs, but particularly with regard to the basal forms our morphological data are very restricted. In *Contectopalatus atavus* such a contact could have occurred, as the lamina descendens orbitalis of the prefrontal extends extremely far ventrally on the internal surface of the skull in this taxon (MAISCH & MATZKE 2001b). If such a contact was present in this rather basal form, it was nevertheless certainly quite narrow. In the well-known neoichthyosaurs such as *Ichthyosaurus*, *Stenopterygius* or *Ophthalmosaurus* there was certainly no such contact, not even a narrow one.
- 21** Bulbous medial process of prefrontal: absent (0); present (1). From LEE (1995) #22.
Coding for Ichthyosauria: 0
Discussion. – A bulbous medial process of the prefrontal has never been observed in ichthyosaurs. It is definitely not present in the few Triassic taxa where the medial surface of the prefrontal is known, such as *Contectopalatus* and *Mikadocephalus*.
- 22** Frontal orbital contribution: present (0); absent (1). From LAURIN & REISZ (1995) #2.
Coding for Ichthyosauria: 0
Discussion. – In most ichthyosaurs prefrontal and postfrontal are in contact and exclude the frontal from the orbital margin. This is not true, however, for the basal taxa *Utatusaurus*, *Grippia* and *Chaohusaurus*. In *Parvinator* and *Thaisaurus* a prefrontal-postfrontal contact has been described (MAZIN et al. 1991; NICHOLLS & BRINKMAN 1995). A re-investigation seems necessary in these cases, particularly in *Thaisaurus* which – as it is probably the most basal ichthyosaur known – is of particular importance in this context (see also MAISCH & MATZKE 2000a, character 21).
- 23** Frontal anterior margins: frontal suture with nasal transverse (0); oblique forming an angle of at least 30° with long axis of the skull (1).
Coding for Ichthyosauria: 1
Discussion. – The suture between frontal and nasal can show a variety of shapes in different ichthyosaurs. In the best known basal taxa, *Utatusaurus* and *Grippia*, it is oriented at an angle of approximately 45° to the long axis of the skull. In *Thaisaurus* and *Chaohusaurus* (MAZIN et al. 1991; MAISCH 2001a) it seems to run rather transversely, but these taxa are less well known and described. A rather transversal course is also present in *Shastasaurus alexandrae* (MERRIAM 1902; MAISCH 2000), whereas a strongly angulated course is found in *Cymbospondylus petrinus* (MERRIAM 1908; MAISCH & MATZKE 2000a, 2004). The data presently available suggest that a suture forming an oblique angle with the long axis of the skull is probably the ancestral state in ichthyosaurs.
- 24** Frontal lateral lappet: absent (0); present (1). From MODESTO (1995) #9.
Coding for Ichthyosauria: 0
Discussion. – This character is in part correlated to the presence or absence of a frontal-orbital contact, and therefore problematic. It is to some extent present in *Utatusaurus* and particularly *Grippia*, but apparently absent in *Thaisaurus*, *Chaohusaurus*, *Parvinator* and all other Triassic taxa. Available evidence therefore suggests that it was possibly absent in the ichthyosaurian grundplan, but this character remains one of the most difficult to evaluate.
- 25** Frontal posterolateral processes: absent (0); present (1). From RIEPPEL (1994) #12.
Coding for Ichthyosauria: 1
Discussion. – A posterolateral process of the frontal was certainly present in the ichthyosaurian grundplan, as it is seen in *Utatusaurus*, *Grippia* (MOTANI 2000a contra MAISCH & MATZKE 2000a) and many other Triassic forms, although rarely well developed.
- 26** Frontal proportions: length exceeds width by at least four times (0); length no greater than twice the width (1). From LEE (1995) #24.
Coding for Ichthyosauria: 1
Discussion. – A very elongate frontal, as usually found at least in the grundplan of most amniote groups, is absent in ichthyosaurs. All basal forms, such as *Utatusaurus*, *Grippia* and *Thaisaurus*, have frontals that are about twice as long as they are wide, and this is here considered as the ancestral state.
- 27** Frontal morphology: parallelogram shaped (0); hour-glass shaped (1).
Coding for Ichthyosauria: 0
Discussion. – The classical hourglass-shape of the frontals, as characteristic for the majority of diapsids, does not occur in ichthyosaurs, with exception of the Upper Triassic *Shastasaurus alexandrae* (MAISCH 2000), where it is clearly autapomorphic.
- 28** Orbit shape: generally circular (0); anteroposteriorly elongate so that the length exceeds the height by at least 30% (1). Modified from LEE (1995) #23.
Coding for Ichthyosauria: 1
Discussion. – Although most of the “typical” post-Triassic ichthyosaurs have subcircular orbits, this is a derived state within the group. Basal forms, including

Utatusaurus, *Grippia*, *Mixosaurus*, *Phalarodon* and *Cymbospondylus* possess rather elliptical orbits which are clearly longer than high, and this most likely represents the ancestral state.

- 29 Postfrontal contribution to upper temporal fenestra: postfrontal excluded (0); postfrontal included (1). Modified from RIEPPEL (1994) #10.
Coding for Ichthyosauria: 1
Discussion. – In all known ichthyosaurs the postfrontal forms part of the margin of the fenestra supratemporalis, with one particularly noteworthy exception, *Thaisaurus chonglakmanii* (MAZIN et al. 1991). This is important because *Thaisaurus* is the sister-taxon of all remaining ichthyosaurs (MAISCH & MATZKE 2000a). As the skull of *Thaisaurus* is not very well preserved and the original description is relatively meager, a re-investigation appears to be necessary. With regard to the clear expression of the derived state of this character in all other adequately known ichthyosaurs, this is considered as the ancestral state of the group here, despite the anomalous condition in *Thaisaurus*, which is here interpreted as an autapomorphy.
- 30 Postorbital/supratemporal relationship: in contact (0); not in contact (1); supratemporal absent (1). Modified from LAURIN & REISZ (1995) #12.
Coding for Ichthyosauria: 0
Discussion. – In basal ichthyosaurs there is always a usually extensive external sutural contact between supratemporal and postorbital, which is, however, not easily seen in later and more derived forms, due to the “tel-escoping” of the skull roof elements. If the squamosal is removed, an extensive postorbital-supratemporal contact is nevertheless also found in highly derived ichthyosaurs, such as MAISCH 1998c has shown it in *Ophthalmosaurus icenicus*.
- 31 Postorbital/parietal relationship: in contact (0); contact absent (1).
Coding for Ichthyosauria: 1
Discussion. – In ichthyosaurs, the parietal and postorbital are always widely separated.
- 32 Postorbital posterior extent: terminates prior to reaching posterior limit of parietal (0); extends to at least the posterior limit of the parietal (1).
Coding for Ichthyosauria: 0
Discussion. – The postorbital of ichthyosaurs never reaches the posterior margin of the skull, in contrast to the parietal. The plesiomorphic state of this character is found throughout the group.
- 33 Jugal posterior process: extends posteriorly only to the middle of the cheek (0); reaches nearly the posterior limit of the skull (1).
Coding for Ichthyosauria: 0
Discussion. – In those basal ichthyosaurs where the cheek region is best known, *Utatusaurus*, *Grippia*, *Parvinator* and *Quasianosteosaurus*, the jugal reaches to the middle of the cheek region at maximum before it contacts the extensive quadratojugal. The apomorphic state is reached late in the history of the group in some highly derived taxa, in connection with the increasing enlargement of the orbit and the shortening of the postorbital skull segment.
- 34 Zygomatic arch configuration: squamosal excluded (0); squamosal included (1).
Coding for Ichthyosauria: 0

Discussion. – No ichthyosaur shows the synapsid skull construction where the squamosal enters the zygomatic arch.

- 35 Squamosal lateral exposure: ventral process long descends to level limit of orbital margin (0); ventral process short terminates prior to reaching ventral orbital margin (1); ventral process absent or restricted to region above dorsal limit of orbit (2).
Coding for Ichthyosauria: 1
Discussion. – As far as basal ichthyosaurs are known in this respect, they show a moderately elongate ventral process of the squamosal that ends above the level of the ventral orbital margin. In *Utatusaurus* and *Grippia* the ventral extent of the squamosal is particularly large, but gets reduced rapidly within the group (as already seen in *Parvinator* and *Quasianosteosaurus*).
- 36 Squamosal contribution to posttemporal fenestra: absent (0); present (1). From LAURIN & REISZ (1995) #26.
Coding for Ichthyosauria: 0
Discussion. – The occiput of the most basal ichthyosaurs is practically unknown. Reliable data are first available for the basal longipinnate *Cymbospondylus petrinus* (MERRIAM 1908; MAISCH & MATZKE 2000a, 2004) from the early Middle Triassic. In this taxon, the squamosal is clearly excluded from the fenestra posttemporalis. In later ichthyosaurs, the following elements can contribute to the fenestra: opisthotic, exoccipital, supraoccipital, parietal and supratemporal. The squamosal, however, always remains widely excluded and is restricted to the lateral skull surface. Without data on more basal forms at hand that show otherwise, this is also assumed to be the ancestral ichthyosaurian state.
- 37 Squamosal occipital flange: absent or poorly developed forming only a thin ridge (0); flange well developed forming a broadly exposed lappet (1). Modified from LAURIN & REISZ (1995) #27.
Coding for Ichthyosauria: 0
Discussion. – As indicated above, the squamosal is restricted to the lateral skull surface in all adequately known ichthyosaurs. An occipital flange of the bone is completely absent, as it is already well seen in the basal mixosaurids. This is therefore taken as the ancestral state of ichthyosaurs.
- 38 Quadrate excavation: absent along posterior edge (0); posterior edge deeply excavated forming a concave region (1); quadrate greatly reduced (2). Modified from RIEPPEL (1994) #29.
Coding for Ichthyosauria: 0
Discussion. – In contrast to some claims in the literature, there is no evidence for any posterior quadrate emargination in ichthyosaurs. The quadrates of the most basal forms are not well known. In mixosaurs and all more highly derived ichthyosaurs, the posterior margin of the quadrate is in contrast always slightly convex, as it is shown, e. g., in *Contectopalatus atavus* (MAISCH & MATZKE 2001b) or *Cymbospondylus petrinus* (MERRIAM 1908; CAMP 1980; MAISCH & MATZKE 2004).
- 39 Quadrate exposure laterally: absent (0); present (1). From RIEPPEL (1994) #30.
Coding for Ichthyosauria: 0
Discussion. – In all ichthyosaurs where articulated skulls are known, the quadrate is covered laterally – except for the condylar area – by the squamosal and/or quad-

ratojugal. This is well shown already in basal forms such as the mixosaurs, *Cymbospondylus* and also the presumably Lower Triassic *Parvinator wapitiensis* (NICHOLLS & BRINKMAN 1995).

- 40 Quadrate lateral conch: absent (0); present (1). From RIEPPEL (1994) #31.

Coding for Ichthyosauria: 0

Discussion. – A lateral conch of the quadrate for the insertion of the tympanum is absent in ichthyosaurs. There is also no other evidence that these animals possessed an impedance-matching ear.

- 41 Quadrate anterior process: long, extending forward along its sutural contact with the quadrate process of the pterygoid to nearly reach the level of the transverse flange (0); short, not extending anteriorly beyond 55% the length of the quadrate process of the pterygoid (1).

Coding for Ichthyosauria: 1

Discussion. – The quadrate of ichthyosaurs is ill-known in the most basal forms, so that few statements about its orientation and length relative to the palatal elements are possible. However, mixosaurids and cymbospondylids are rather well-known in this respect and demonstrate that the anterior extension of the quadrate along the ramus quadrati of their pterygoid was quite short. In more highly derived ichthyosaurs, this is usually not the case, because of a massive shortening of the ramus quadrati in these forms. This was, however, with great certainty not the ancestral condition. A short extension of the quadrate is therefore assumed for the ichthyosaurian grundplan.

- 42 Quadratojugal morphology: present and horizontal dimension exceeds vertical dimension by a factor of at least three (0); present but vertical dimension exceeds horizontal by a factor of at least two (1); present, but greatly reduced and restricted to condylar region (2); absent (3).

Coding for Ichthyosauria: 1

Discussion. – As shown by the investigations of MAISCH & MATZKE (2002b), a high and narrow quadratojugal, bordering a deep incisura postjugalis posteriorly, must be postulated for the grundplan of ichthyosaurs. Such a “styliiform” quadratojugal is definitely present in *Parvinator wapitiensis* and *Quasianosteosaurus vikinghoegdai*. In the other Lower Triassic taxa the conditions are either unknown or not yet satisfactorily clarified. In later ichthyosaurs, the quadratojugal is in the articulated state mostly covered by the squamosal. This creates the impression that the bone was rather low and elongate in these forms, which is untrue, as is shown by disarticulated material of even highly derived taxa such as *Ichthyosaurus* (McGOWAN 1973a) or *Ophthalmosaurus* (MAISCH 1998c). Here, the quadratojugal is also an anteroposteriorly narrow and very high element.

- 43 Quadratojugal ornamentation: absent (0); present (1).

Coding for Ichthyosauria: 0

Discussion. – There is no quadratojugal ornamentation in any ichthyosaur.

- 44 Stapedial shaft: rod-like in cross section (0); blade-like in cross section (1). From REISZ et al. (1992) #41.

Coding for Ichthyosauria: 0

Discussion. – Basal ichthyosaur stapes are largely unknown, except for *Thaisaurus chonglakmanii* (MAZIN et al. 1991) where it was not described in detail. Stapes are rather well-known in *Mixosaurus* and *Cymbospondylus*. As

far as it can be ascertained, the stapedial shaft has a rounded cross-section in all three taxa, and this is universally the case in more highly derived ichthyosaurs.

- 45 Stapes morphology: robust with its greatest depth exceeding one-third of its total length (0); slender with the length at least four times the depth (1).

Coding for Ichthyosauria: 0

Discussion. – Although the stapes of *Thaisaurus* and *Mixosaurus* is rather slender, the width of its proximal end nevertheless exceeds one third of its entire length. This is universally the case in more derived ichthyosaurs with the notable exception of *Cymbospondylus petrinus* (MERRIAM 1908; MAISCH & MATZKE 2004), which shows a very long and slender stapes. This, however, seems to be an autapomorphy of this taxon. A robust stapes is therefore the ancestral state in ichthyosaurs.

- 46 Stapedial dorsal process: present as ossified process (0); absent (1). From LAURIN & REISZ (1995) #67.

Coding for Ichthyosauria: 1

Discussion. – There is no ossified processus dorsalis of the stapes in any known ichthyosaur.

- 47 Parietal skull table: broad with the mid-line, transverse, width not less than half of the length measured along the element's midline (0); constricted with the length exceeding the width by at least three times (1); forming sagittal crest (2). Modified from RIEPPEL (1994) #16.

Coding for Ichthyosauria: 0

Discussion. – A rather short and wide intertemporal skull roof formed by the parietals is characteristic for all ichthyosaurs. This is also well seen in *Thaisaurus*, *Grippia*, *Utatusaurus* and *Chaohusaurus* among the most basal taxa. A strong median constriction of the parietals does never occur. A sagittal crest is developed in some taxa, particularly the mixosaurids, but this is apomorphic within ichthyosaurs (see MAISCH & MATZKE 2000a, character 15).

- 48 Parietal shelf for adductor musculature: absent (0); present as shallow excavations on the lateral margins of the parietal (1). From DE BRAGA & REISZ (1995) #6.

Coding for Ichthyosauria: 1

Discussion. – A lateral shelf of the parietal for attachment of the external jaw adductors is, as far as known, characteristic for all ichthyosaurs including the basal taxa *Utatusaurus* and *Grippia*. Even the mixosaurids retain this feature, notwithstanding their otherwise highly aberrant skull roof morphology.

- 49 Pineal foramen position: located in the middle of the body of the parietal (0); displaced posteriorly (1); displaced anteriorly (2); absent (3). From RIEPPEL (1994) #15.

Coding for Ichthyosauria: 2

Discussion. – The foramen parietale (not pineale, which is not found in amniotes) is displaced anteriorly already in the oldest and most basal ichthyosaurs. In *Thaisaurus* it is already situated between frontal and parietal. In *Utatusaurus* it lies very close to the anterior parietal margin. A position in the anterior portion of the parietal, and mostly even along the frontoparietal suture is characteristic for all other ichthyosaurs, with the notable exception of the Grippiidae. In these (*Grippia* and *Chaohusaurus*) the foramen parietale occupies a “normal” position at half the length of the parietals. At the present state of knowledge, this must be regarded as an autapomorphic reversion of the grippiids.

- 50** Upper temporal fenestra: absent (0); present (1).
Coding for Ichthyosauria: 1
Discussion. – The possession of a fenestra supratemporalis is characteristic for all ichthyosaurs. In the grundplan, it appears to have been bordered by the frontal, postfrontal, postorbital, supratemporal and parietal, whereas in the derived forms only postfrontal, parietal and supratemporal contribute to its margins. Despite claims to the contrary in the literature there is no evidence for a contribution of the squamosal in any known ichthyosaur (MAISCH & MATZKE 2002b).
- 51** Lower temporal fenestra: absent (0); present quadratojugal included (1); present quadratojugal excluded (2); open ventrally (3).
Coding for Ichthyosauria: 0
Discussion. – Although some basal ichthyosaurs, especially *Quasianosteosaurus*, *Parvinator*, *Barracudasauroides* and *Cymbospondylus* show a deep ventral emargination of the cheek, positioned between jugal and quadratojugal (incisura postjugal), which may be in part bordered (such as in *Barracudasauroides*) by squamosal and postorbital, there is no complete lower temporal fenestra or lower zygomatic arch known in any ichthyosaur. The grundplan state of ichthyosaurs may either result from reduction of a lower temporal fenestra, or from an embayment of the ventral margin of the cheek. With the data presently at hand, it is impossible to decide between these two alternatives.
- 52** Postparietal: present and paired (0); present but fused (1); absent (2). From LAURIN & REISZ (1995) #4.
Coding for Ichthyosauria: 0
Discussion. – A postparietal is at the moment only recorded in two genera of ichthyosaurs, *Cymbospondylus* (MAISCH & MATZKE 2000a, 2004) and *Phantomosaurus* (MAISCH & MATZKE 2000a, 2006). In the case of *Cymbospondylus* it is a large, unpaired, occipital element (contra FRÖBISCH et al. 2006). In *Phantomosaurus* there are paired, rudimentary postparietals that are situated dorsal to the supraoccipital. As the occiput of more basal forms is virtually unknown, the presence or absence of a postparietal can not be determined. In the more highly derived ichthyosaurs, it seems to be completely reduced, though. Nevertheless, the data provided by the cymbospondylids unequivocally demonstrate that a paired postparietal was present in the grundplan of ichthyosaurs.
- 53** Supratemporal: present and large with its transverse dimension nearly equal to its parasagittal dimension (0); present but reduced so that its transverse dimension is less than half of its parasagittal dimension (1); absent (2).
Coding for Ichthyosauria: 0
Discussion. – All ichthyosaurs have a large supratemporal of comparable length and width. Within the group the supratemporal gets even enlarged and increases in complexity.
- 54** Intertemporal: present (0); absent (1).
Coding for Ichthyosauria: 1
Discussion. – As in all amniotes, an intertemporal is lacking in ichthyosaurs.
- 55** Tabular: present but restricted to dorsal region of occiput (0); present but ventrally elongate descending to level of occipital condyle (1); absent (2).
Coding for Ichthyosauria: 2
- Discussion.** – In all adequately known ichthyosaurs the tabular is absent.
- 56** Supraoccipital: plate-like with no sagittal crest (0); body of supraoccipital constricted at midline forming sagittal crest (1). Modified from LAURIN & REISZ (1995) #55.
Coding for Ichthyosauria: 0
Discussion. – The supraoccipital is little known or not known at all in most basal forms. Most data are available for *Mixosaurus*, *Wimanius* and *Cymbospondylus*. In all these, it is – disregarding its lateral process for contact with the exoccipitals – a laterally broadened bony plate with a convex posterior surface, but without a sagittal crest. Such a crest is also always absent in more highly derived forms.
- 57** Occiput configuration: broad and plate-like forming broad sutural contact with the tabular dorsolaterally (0); open with only slight contact, if any, with tabular (1).
Coding for Ichthyosauria: 1
Discussion. – In all ichthyosaurs where the occiput is adequately known, it shows an open construction. All elements of the occiput and braincase are – probably as a result of aquatic adaptation and progressive chondrification – incompletely ossified and well separated from each other. There is considerable fenestration of the occiput, as well. This condition is definitely recorded in the mixosaurids and cymbospondylids. The few data available on Lower Triassic forms suggest that their occiputs were of similar build. The lack of articulated occipital elements and their general rarity of preservation in these taxa is in itself compelling evidence for this hypothesis.
- 58** Angle of occiput: oriented primarily vertically (0); tilted or sloping anteriorly at an angle of about 45° (1). From ROMER & PRICE (1940).
Coding for Ichthyosauria: ?
Discussion. – As the basal ichthyosaurian occiput is very little known, and as there is no articulated three-dimensional material available to assess this character with any degree of confidence in any Triassic ichthyosaur, it is left as uncoded.
- 59** Posttemporal fenestra: absent (0); present but diameter less than half of the diameter of the foramen magnum (1); large posttemporal fenestra with a diameter at least equal to that of the foramen magnum (2).
Coding for Ichthyosauria: 2
Discussion. – As indicated above (character 57) all ichthyosaurs have an open occiput. This includes a very large, although only vaguely defined, fenestra posttemporalis that is usually at least as large as the foramen occipitale magnum.
- 60** Orientation of paroccipital process: extends laterally forming 90° with parasagittal plane (0); paroccipital process deflected posterolaterally at an angle of about 20° from the transverse width of the skull (1); paroccipital process deflected dorsolaterally at an angle of nearly 45° (2).
Coding for Ichthyosauria: ?
Discussion. – The orientation of the processus paroccipitalis in basal ichthyosaurs is, again, not definitely known due to the lack of three-dimensional and articulated material. All derived neoichthyosaurs in which the orientation is known show a paroccipital process that is strongly posterolaterally oriented (for about 45°), but also of a very robust and rather rudimentary build. As it is now known,

this does not correspond to the grundplan of ichthyosaurs. There, the processus paroccipitalis was much more elongate and slender, and probably anteroposteriorly flattened as well (see MAISCH & MATZKE 2006; MAISCH et al. 2006b). Its orientation is, however, unknown and the character must be left uncoded.

- 61** Paroccipital process morphology: slender with anteroposterior dimension not exceeding dorsoventral dimension (0); heavy with anteroposterior dimension at least one-third greater than dorsoventral dimension (1).
Coding for Ichthyosauria: 0
Discussion. – In the most basal ichthyosaurs with a well-known opisthotic, the mixosaurid *Mixosaurus cornalianus* and the cymbospondylid *Phantomosaurus neubigi*, both from the Middle Triassic (see MAISCH & MATZKE 2006, MAISCH et al. 2006b) the processus paroccipitalis is elongate and slender, whereas it is rudimentary in the derived ichthyosaurs of the Jurassic and Cretaceous. The Middle Triassic *Mikadocephalus gracilirostris* (pers. obs.) and *Shonisaurus popularis* (CAMP 1980) from the Upper Triassic show a somewhat intermediate state with a well-developed, but already shortened processus paroccipitalis. In the grundplan, there was certainly a long and slender processus paroccipitalis, the dorsoventral height of which was certainly no less than the anteroposterior length. To the contrary, the processus paroccipitalis is even strongly flattened anteroposteriorly in both *Mixosaurus* and *Phantomosaurus*.
- 62** Exoccipital bones: meet below foramen magnum (0); do not meet (1). From RIEPPEL (1994) #28.
Coding for Ichthyosauria: 1
Discussion. – Data are available for mixosaurids and cymbospondylids, but not for more basal ichthyosaurs. In these, as well as in all more derived taxa, the exoccipitals never meet below the foramen occipitale magnum, and this is considered as the ancestral ichthyosaurian state.
- 63** Basioccipital/basisphenoid relationship: floor of braincase with gap between both elements (0); elements fused to floor brain cavity (1). From LEE (1993) #A5.
Coding for Ichthyosauria: 0
Discussion. – Basioccipital and basisphenoid never fuse in ichthyosaurs. In Triassic forms where the basis cranii is known, such as *Chaohusaurus* (MAISCH 2001a), *Mixosaurus* (MAISCH & MATZKE 1997a) and *Mikadocephalus* (MAISCH & MATZKE 1997b) the basisphenoid is even, in comparison to the parasphenoid, an ossification of minor extent. Not before the neoichthyosaurs does the basisphenoid become larger on expense of the parasphenoid. But in these forms as well, there always remains a wide gap between basioccipital and basisphenoid. Even in fully adult animals there is not even a suture.
- 64** Basi/parasphenoid ratio: narrowest transverse width no more than 60% of the maximum length measured from basiptyergoid process to posterior most limit (0); narrowest part (waist) exceeds 80% of the length (1). Modified from LEE (1994) #12.
Coding for Ichthyosauria: 0
Discussion. – The basis cranii of the most basal ichthyosaurs is incompletely known. At least the parasphenoid of *Chaohusaurus* (MAISCH 2001a) and *Mixosaurus* (MAISCH & MATZKE 1997a) is well-known. In *Chaohusaurus* the ratio is ca. 63%, in *Mixosaurus* approximately 66%. Basal ichthyosaurs therefore are somewhat intermediate between the character states as originally defined, but closer to the plesiomorphic condition.
- 65** Ventral braincase tubera: absent (0); present and restricted to basioccipital (1); present, very large, and restricted to basisphenoid (2). Modified from LEE (1994) #13.
Coding for Ichthyosauria: 1
Discussion. – Tubera basioccipitalia are typical for ichthyosaurs. Although the basioccipital is practically unknown in the Lower Triassic taxa, well-developed tubera are recorded in *Cymbospondylus*, *Phantomosaurus* and *Mixosaurus* from the Middle Triassic. Tubera basisphenoidalia have, in contrast, not been found so far in any known ichthyosaur.
- 66** Opisthotic/cheek contact: not in contact (0); in contact and tightly sutured (1). From LEE (1993) #A3.
Coding for Ichthyosauria: 0
Discussion. – Again there are no data for the most basal ichthyosaurs. Triassic forms are largely unknown in this respect, but at least the cymbospondylids *Cymbospondylus* and *Phantomosaurus* provide some data. These are not unequivocal, however. The very long processus paroccipitalis of *Phantomosaurus* could have reached the cheek region of the skull. As recorded by MERRIAM (1908) and MAISCH & MATZKE (2004) in the single known specimen of *Cymbospondylus petrinus* which shows the occiput, the left opisthotic is ill-preserved and somewhat dislocated, the right one is apparently completely absent. There is, nevertheless, some contact with the supratemporal. Such a contact is also always present in the neoichthyosaurs, but it is never close and there is no suture formed, not even in old adults. Available data in summa suggest that the plesiomorphic state of this character is characteristic for ichthyosaurs.
- 67** Prootic/parietal contact: absent (0); present (1).
Coding for Ichthyosauria: 0
Discussion. – Within Triassic ichthyosaurs, the prootic is only well-known in *Mixosaurus* (MAISCH et al. 2006b). In the neoichthyosaurs it is so much reduced, that it neither has a contact with the parietal nor with any other cranial element. In *Mixosaurus* there was definitely a contact with supraoccipital, basisphenoid and opisthotic, but there is no evidence for contact with the parietal. It is therefore assumed that such a contact was never present in ichthyosaurs.
- 68** Medial wall of inner ear: unossified (0); ossified (1). From LEE (1993) #A6.
Coding for Ichthyosauria: 0
Discussion. – There is no evidence for ossification of the medial wall of the inner ear in ichthyosaurs. However, there are also no reliable data on any Triassic form. In the neoichthyosaurs, the middle ear cavity is even open laterally due to the incomplete ossification of the otic capsule. It is therefore assumed that in the grundplan at least the medial wall of the middle ear was probably also unossified.
- 69** Occipital flange: absent (0); present (1). From LEE (1995) #30.
Coding for Ichthyosauria: 1
Discussion. – An occipital flange of the parietal is present in all well-known ichthyosaurs.
- 70** Sphenethmoid: present (0); absent (1).
Coding for Ichthyosauria: 1
Discussion. – A sphenethmoid has never been recorded in ichthyosaurs.

- 71 Pleurospenoid: absent (0); present (1). See node description for Sauria for details.
Coding for Ichthyosauria: 0
Discussion. – A pleurospenoid is not known in any ichthyosaur.
- 72 Palate: kinetic (0); akinetic (1). From RIEPPEL (1994) #32.
Coding for Ichthyosauria: 0
Discussion. – The most basal ichthyosaurs of which we know the palate, *Utatusaurus* and *Chaohusaurus*, have a completely functional basiptyergoid articulation. It is therefore considered that the palate of ichthyosaurs was kinetic in the grundplan. During evolution of the group, palatal kinesis is, however, reduced. This happens both in the mixosaurs, which completely close the interptyergoid vacuities, and in the neoichthyosaurs, where the basiptyergoid joint has become dysfunctional because of the strong ventral overlap of the pterygoid onto the basioccipital. In most Middle and Upper Triassic forms, the palate is still too incompletely known to assess this character. Nevertheless it appears plausible that the loss of palatal kinesis might turn out to be an autapomorphy of the Hueneosauria.
- 73 Interptyergoid vacuity: anterior end tapers sharply (0); anterior border crescentic (1); absent (2). From LEE (1994) #18.
Coding for Ichthyosauria: 0
Discussion. – All ichthyosaurs, except the mixosaurs, have well-developed interptyergoid vacuities, the size of which even increases during evolution of the group. Basal forms such as *Chaohusaurus* have small, slit-like openings. At any rate, they have a sharply pointed anterior end in all ichthyosaurs in which they occur.
- 74 Suborbital fenestra: absent (0); present but with contribution from either maxilla or jugal along lateral border (1); present, but with both maxilla and jugal excluded from lateral border (2). Modified from RIEPPEL (1994) #34.
Coding for Ichthyosauria: ?
Discussion. – Because there is no ectopterygoid in ichthyosaurs it can not be said whether there was a fenestra suborbitalis in their stem-line or not. The character is therefore left uncoded.
- 75 Cultriform process: long exceeding length of parasphenoid body and reaching forward to the level of the posterior limit of the internal nares (0); short not reaching the level of the internal nares (1). Modified from LAURIN & REISZ (1995) #52.
Coding for Ichthyosauria: 0
Discussion. – The Processus cultriformis of the parasphenoid is very long in all adequately known ichthyosaurs. Among basal forms this morphology is well-documented in *Chaohusaurus* (MAISCH 2001a) and *Mixosaurus* (MAISCH & MATZKE 1997b). The posterior margin of the choanae is reached by the processus cultriformis in these, as well as in all more highly derived forms.
- 76 Palatal process of pterygoid: extends anterior to the anterior limit of the palatine (0); forms oblique suture with palatine but process ends before reaching anterior limit of palatine (1); forms transverse suture with palatine (2).
Coding for Ichthyosauria: 1
Discussion. – The conditions in basal ichthyosaurs are not clear. In the more derived forms, the plesiomorphic state is universally found, where the palatine processes of the pterygoid usually extend even further anteriorly than the palatines. In *Mixosaurus*, *Contectopalatus* and *Cymbospondylus*, however, the apomorphic state occurs and an oblique palatine-ptyergoid suture is formed. As these are the most basal forms for which data are available, this condition is here assumed to be closest to the grundplan of ichthyosaurs.
- 77 Orientation of transverse flange of pterygoid: directed predominantly laterally (0); oriented in an anterolateral direction (1). From LAURIN & REISZ (1995) #45.
Coding for Ichthyosauria: 0
Discussion. – The processus transversus of the pterygoid is completely reduced in most ichthyosaurs. It is retained, however, in *Utatusaurus hataii* (MOTANI et al. 1998; pers. obs.) and in *Cymbospondylus petrinus* (MERRIAM 1908), where it shows a lateral orientation.
- 78 Dentition on transverse flange: present as a shagreen of teeth (0); present but with one large distinct row of teeth along the posterior edge of the transverse flange (1); edentulous (2). Modified from LAURIN & REISZ (1995) #46.
Coding for Ichthyosauria: 1
Discussion. – The single ichthyosaur in which this character can be assessed is *Utatusaurus hataii* (MOTANI et al. 1998; pers. obs.), where some teeth that were most probably originally arranged in a single row are present on the processus transversus ptyergoidei.
- 79 Ventral extent of transverse flange: extends below maxillary tooth row (0); terminates at level of or above maxillary tooth row (1). From LEE (1995) #14.
Coding for Ichthyosauria: 1
Discussion. – In the two genera which retain a processus transversus, *Utatusaurus* and *Cymbospondylus*, it does not reach far ventrally but ends somewhat dorsal to the maxillary tooth row.
- 80 Transverse flange lateral margin: posterolateral margin forms sharp edge with anteromedial margin (0); posterolateral margin merges smoothly into anteromedial margin forming a smoothly convex lateral outline (1).
Coding for Ichthyosauria: 0
Discussion. – This character again is only observable in *Utatusaurus* and *Cymbospondylus*. Both show the plesiomorphic state.
- 81 Ectopterygoid: present and edentulous (0); present and dentigerous (1); absent replaced by medial process of jugal (2); absent replaced by lateral process of pterygoid (3).
Coding for Ichthyosauria: 3
Discussion. – All ichthyosaurs have lost the ectopterygoid.
- 82 Mandibular joint: even with occiput (0); behind occiput (1); anterior to occiput (2). From RIEPPEL (1994a) #27.
Coding for Ichthyosauria: 0
Discussion. – In all ichthyosaurs that are adequately known, the articulatio cranio-mandibularis is – more or less – on the same level as the occiput. Apparently there is much variation in the group, but this should not be overestimated, particularly with regard to the fact that these regions of the skull are particularly easily affected by dislocations, due to their incomplete ossification.
- 83 Coronoid process: absent (0); present formed by coronoid (1); present formed by dentary (2). Modified from LAURIN & REISZ (1995) #79.
Coding for Ichthyosauria: ?
Discussion. – MOTANI et al. (1998) have correctly pointed out, that this character, as its states are defined, is not applicable to ichthyosaurs. These have a processus

coronoideus which is formed by the supraangular. It was therefore most probably developed convergently to other groups of tetrapods. MOTANI et al. (1998) therefore propose a new character state, but this is, in fact, only an uninformative autapomorphy at present. I therefore left the character uncoded.

- 84** Coronoid number: more than one (0); only one coronoid (1). From LAURIN & REISZ (1995) #74.
Coding for Ichthyosauria: 1
Discussion. – The coronoid has only been identified in a very limited number of ichthyosaurs. These include, however, the basal taxa *Utatusaurus* and *Mixosaurus* (personal observations). In both genera, as well as in the more highly derived ones where the mandible is adequately known, there is only a single coronoid ossification.
- 85** Meckelian fossa: faces mediodorsally (0); faces dorsally due to greatly expanded prearticular (1). From LAURIN & REISZ (1995) #70.
Coding for Ichthyosauria: 0
Discussion. – The medial mandibular surface is only known in few Triassic ichthyosaurs. These include *Utatusaurus*, *Mixosaurus* and *Cymbospondylus*. In all these, the prearticular (particularly in its posterior portion) is rather low, and the fossa meckelii therefore has a mediodorsal orientation.
- 86** Surangular length: extends anterior to coronoid eminence (0); terminates prior to reaching level of coronoid eminence (1). From LAURIN & REISZ (1995) #72.
Coding for Ichthyosauria: ?
Discussion. – As the processus coronoideus of ichthyosaurs, as indicated above (character 83) always belongs to the supraangular, the latter of course extends far anterior to the processus. As the processus coronoideus of ichthyosaurs is not considered homologous to that of other tetrapods here, it is nevertheless not possible to code this character.
- 87** Surangular lateral shelf: absent (0); present (1). Modified from LAURIN & REISZ (1995) #78.
Coding for Ichthyosauria: 0
Discussion. – A lateral shelf of the articular and/or supraangular (see the original definition of this character by LAURIN & REISZ 1995, who consider the derived states in turtles and pareiasaurs as non-homologous) is not known in ichthyosaurs, at least not – what is meant here – in the glenoid region of the lower jaw.
- 88** Splenial: enters mandibular symphysis (0); present but excluded from mandibular symphysis (1); entirely absent (2). Modified from REISZ & LAURIN (1991) #7.
Coding for Ichthyosauria: 0
Discussion. – In all adequately known ichthyosaurs, the splenial enters the very long mandibular symphysis.
- 89** Angular lateral exposure: exposed along one-third the lateral face of the mandible (0); exposed only as a small sliver along the lateral face (1); absent from lateral aspect (2).
Coding for Ichthyosauria: 0
Discussion. – The angular is a large element in ichthyosaurs, but little of it is exposed in most basal forms. In the course of ichthyosaur evolution, the lateral angular exposure becomes larger (see MAISCH & MATZKE 2000a, character 46). Nevertheless it contributes to at least one third of the lateral mandibular surface already in basal taxa.
- 90** Ventral edge of angular: smooth no ventral projection (0); keeled (reflected lamina) (1). From ROMER & PRICE (1940).
Coding for Ichthyosauria: 0

Discussion. – A lamina reflecta angularis, as found in sphenacodontians and therapsids, is absent in all ichthyosaurs.

- 91** Prearticular: extends anterior to coronoid eminence (0); terminates prior to reaching coronoid eminence (1). From LAURIN & REISZ (1995) #75.
Coding for Ichthyosauria: ?
Discussion. – In all well known ichthyosaurs the prearticular extends far anterior to the processus coronoideus of the supraangular. Nevertheless what has been said concerning character 86 also applies here: as the processus coronoideus of ichthyosaurs is not homologous to that of other tetrapods, this character can not be coded.
- 92** Retroarticular process: absent (0); present (1). From RIEPPEL (1994) #38.
Coding for Ichthyosauria: 1
Discussion. – A processus retroarticularis is found in all ichthyosaurs, although in different shape and size. It is clearly present in the basal taxa *Utatusaurus*, *Grippia* and *Chaohusaurus*. In the equally quite basal *Parvinatator wapitiensis* it is (probably autapomorphously) very strongly developed (NICHOLLS & BRINKMAN 1995).
- 93** Labyrinthine infolding: present (0); absent (1). From LAURIN & REISZ (1995) #68.
Coding for Ichthyosauria: 0
Discussion. – A plicidentine infolding of the dentine is characteristic for most ichthyosaurs. However, ichthyosaurian labyrinthodonty is much less complex than that seen in the majority of early amphibians. In some taxa, the labyrinthodonty is secondarily reduced, such as in *Mixosaurus* (MAISCH & MATZKE 1997a), but this is a derived state within the Mixosauridae (see JIANG et al. 2005; MAISCH & MATZKE 2005)
- 94** Tooth implantation: set in deep sockets (0); loosely attached to medial surface of jaw (1); ankylosed to jaw (2). Modified from RIEPPEL (1994) #42.
Coding for Ichthyosauria: 0
Discussion. – In the grundplan, ichthyosaurs most probably had a subthecodont mode of tooth implantation (MOTANI 1996, 1997a, b; MAISCH & MATZKE 1997a). A few Triassic taxa show a special mode of true thecodonty (MOTANI 1997a). The neoichthyosaurs display a unique kind of tooth implantation, where all teeth are set in deep continuous grooves, called aulacodonty by MAZIN (1983a). This is a derived state within the group, though (see MAISCH & MATZKE 2000a, character 1).
- 95** Caniniform teeth: present (0); absent (1). From LAURIN & REISZ (1995) #24.
Coding for Ichthyosauria: 1
Discussion. – Caniniform teeth are unknown in ichthyosaurs.
- 96** Single canine tooth: absent (0); present (1). From LAURIN & REISZ (1995) #25.
Coding for Ichthyosauria: 0
Discussion. – There are no single canine teeth in ichthyosaurs.
- 97** Presacral vertebral number: more than twenty (0); twenty or less (1). From LEE (1995) #35.
Coding for Ichthyosauria: 0
Discussion. – All ichthyosaurs have an elongated presacral vertebral column. This is an adaptation to their initially anguilliform mode of locomotion (MOTANI et al.

- 1997). In *Utatusaurus* (MOTANI et al. 1998) and *Chaohusaurus* (MOTANI et al. 1997) there are already more than 40 presacral vertebrae. This, or a slightly higher number, is typical for most ichthyosaurs, although much higher numbers have been recorded in some Triassic taxa (60 in *Besanosaurus*, 65 in *Mikadocephalus* and *Cymbospondylus* and more than 80 in *Guanlingsaurus*) (see MAISCH & MATZKE 2000a, character 55).
- 98** Number of caudal vertebrae: twenty or more usually twenty-five (0); less than twenty (1). From LEE (1994) #70.
Coding for Ichthyosauria: 0
Discussion. – All ichthyosaurs have a very long caudal vertebral column with much more than 25 segments.
- 99** Vertebral centra: notochordal (0); non-notochordal (1). From RIEPPEL (1994) #48.
Coding for Ichthyosauria: 0
Discussion. – All ichthyosaurs possess notochordal vertebral centra.
- 100** Vertebral central articulations: amphicoelous (0); platycoelous (1); other (2). From RIEPPEL (1994) #49.
Coding for Ichthyosauria: 0
Discussion. – All ichthyosaurs have deeply amphicoelous vertebral centra.
- 101** Accessory vertebral articulations: absent (0); present (1). From RIEPPEL (1994) #53.
Coding for Ichthyosauria: 0
Discussion. – Vertebral articulations apart of the central and zygapophyseal ones are unknown in ichthyosaurs.
- 102** Atlantal ribs: ossified (0); not ossified (1).
Coding for Ichthyosauria: 0
Discussion. – Ossified atlantal ribs are known in most ichthyosaurs. Atlantal rib facets are also shown in *Utatusaurus* (pers. obs.) the most basal ichthyosaur in which the atlantal pleurocentrum is well preserved, the same is true for the Middle Triassic *Pessopteryx* (MAISCH & MATZKE 2003a). In *Cymbospondylus* (MERRIAM 1908) there is, however, no indication of atlantal ribs. With the data at hand, this appears as an autapomorphy of this genus.
- 103** Cervical centra: ventrally smooth or rounded (0); ventrally keeled (1). From LAURIN & REISZ (1995) #87.
Coding for Ichthyosauria: 0
Discussion. – There are no sharpened ventral keels of the cervical vertebrae in ichthyosaurs. Ventrolateral keels are known, though, in *Phantomosaurus neubigi* from the Middle Triassic (SANDER 1997; MAISCH & MATZKE 2000a) as an autapomorphy.
- 104** Cervical intercentra: present (0); absent (1). From RIEPPEL (1994) #51.
Coding for Ichthyosauria: 0
Discussion. – Cervical intercentra are known in most ichthyosaurs. Particularly the Triassic genera, as shown for *Shastasaurus* and *Cymbospondylus* by MERRIAM (1908) have them well developed. They are therefore a grundplan feature of ichthyosaurs.
- 105** Cervical ribs: without anterior process (0); anterior process present (1). From RIEPPEL (1994) #56.
Coding for Ichthyosauria: 0
Discussion. – There are no anterior processes of the cervical ribs in any known ichthyosaur.
- 106** Trunk neural arches: swollen with heavy zygapophyseal buttress (0); narrow, strongly excavated neural arch with no heavy buttress (1); swollen, but with narrow tall zygapophyseal buttress (2). From LAURIN & REISZ (1995) #86.
Coding for Ichthyosauria: 1
Discussion. – The neural arches of all known ichthyosaurs are slender or very slender and do not have swollen zygapophyses. In some cases, such as in *Shastasaurus* (MERRIAM 1908) the processus spinosus can be somewhat more robust, but is still remains comparatively elongate and slender.
- 107** Dorsal intercentra: present (0); absent (1). From RIEPPEL (1994) #50.
Coding for Ichthyosauria: 1
Discussion. – Intercentra of the dorsal vertebral column are – in contrast to the cervical vertebrae – not known in any ichthyosaur.
- 108** Dorsal transverse processes: short no more than the total transverse width of the neural arch (0); long exceeding the transverse width of the neural arch (1). Modified from RIEPPEL (1994) #55.
Coding for Ichthyosauria: ?
Discussion. – The ichthyosaurs have – autapomorphously – completely reduced the dorsal processus transversi, so that the ribs articulate exclusively with the centra (see MAISCH & MATZKE 2000a, character 126). This state – unique among amniotes – does not allow coding of the character.
- 109** Number of sacral vertebrae: two (0); three or more (1). Modified from RIEPPEL (1994) #58.
Coding for Ichthyosauria: 0
Discussion. – In most ichthyosaurs there is no differentiation of a sacrum. The only form in which a sacrum is retained that is known so far is *Utatusaurus hataii* (MOTANI et al. 1998; see MAISCH & MATZKE 2000a, characters 57 und 58). *Utatusaurus* clearly possesses two sacral vertebrae.
- 110** Caudal lateral projections (transverse processes): absent beyond fifth caudal (0); present beyond fifth caudal (1). From LEE (1993) #A10.
Coding for Ichthyosauria: 1
Discussion. – At least small lateral processes for articulation with the caudal ribs are universally developed in ichthyosaurs far beyond the fifth caudal vertebra.
- 111** Caudal rib shape: L-shaped, curved (0); straight (1). From LEE (1994) #72.
Coding for Ichthyosauria: 1
Discussion. – In all ichthyosaurs where caudal ribs are known these show a slender and straight shape. L-shaped caudal ribs have never been found.
- 112** Chevron position: intercentral (0); located on anterior pedicel (1). From LEE (1993) #A11.
Coding for Ichthyosauria: 0
Discussion. – In Triassic ichthyosaurs, which retain ossified haemapophyses, these are always in an intercentral position. The neoichthyosaurs reduce the haemapophyses entirely, they are only found as cartilaginous rudiments at maximum (see MAISCH & MATZKE 2000a, character 63).
- 113** Cleithrum: present (0); absent (1).
Coding for Ichthyosauria: 1
Discussion. – There is no ossified cleithrum in any known ichthyosaur.
- 114** Clavicle: interclavicular process of clavicle broad and blade-like with the maximum anteroposterior length at

- least one-third of its transverse dimension (0); slender with its anteroposterior length less than one-fifth of the transverse dimension (1).
Coding for Ichthyosauria: 0
Discussion. – Ichthyosaurian clavicles are usually very slender. Exceptions are found among basal forms, such as *Chaohusaurus* (MAISCH 2001), *Utatusaurus* (pers. obs.), *Cymbospondylus* (MERRIAM 1908; SANDER 1989) and the mixosaurids. The widening of the medial portion of the clavicle is thus reduced within the group (MAISCH & MATZKE 2000a, character 68), whereas in the grundplan a medially broad clavicle (i. e. with a wide processus interclavicularis) must have been present.
- 115** Interclavicle: anterior end rhomboidal (0); T-shaped but with broad transverse bar with its anteroposterior dimension at least one-fourth the transverse width of the bar (1); T-shaped but transverse bar slender with its anteroposterior dimension much less than one-fourth the transverse width (2).
Coding for Ichthyosauria: 0
Discussion. – The interclavicle is little or not at all known in most Triassic ichthyosaurs. The only exceptions among basal forms are *Utatusaurus* (pers. obs.) and the mixosaurids. In *Utatusaurus* the interclavicle is very different from all other ichthyosaurs. It has a heart-shaped to rhombic anterior end and is very elongate. In the mixosaurids it is broadly triradiate. In the neoichthyosaurs it becomes slender and triradiate. In the grundplan, a rhomboidal anterior end was therefore most probably present (see MOTANI 1999b; MAISCH & MATZKE 2000a, character 67).
- 116** Mineralized sternum: absent (0); present (1). From LAURIN & REISZ (1995) #100.
Coding for Ichthyosauria: 0
Discussion. – There is no mineralized sternum known in ichthyosaurs.
- 117** Scapula: short and broad with its height not exceeding its width (measured at the level of the glenoid) by more than three times (0); tall and blade-like with its height exceeding the width by at least a factor of four (1); tall and slender nearly cylindrical in cross-section (2). Modified from LEE (1993) #B2.
Coding for Ichthyosauria: 0
Discussion. – In basal ichthyosaurs the scapula is a low and wide element, in which the width is usually even more considerable than the height, as is seen in *Utatusaurus*, *Grippia*, *Chaohusaurus* and the mixosaurids. During the evolution of the ichthyosaurian shoulder girdle, the scapula becomes a high and elongate element the height of which exceeds its width (see MAISCH & MATZKE 2000a, characters 69–71), but this is certainly a secondary condition.
- 118** Acromion process: absent (0); present, blade-like, parallel-ogram in lateral aspect, and arising from the lateral edge of the scapula (1); present, triangular in lateral aspect, and arising from ventromedial border of scapula (2). Modified from LEE (1993) #A12.
Coding for Ichthyosauria: 0
Discussion. – In no ichthyosaur is there an acromion of the scapula.
- 119** Supraglenoid buttress: present (0); absent (1). From RIEPPEL (1994) #69.
Coding for Ichthyosauria: 1
Discussion. – There is no processus supraglenoideus of the scapula in any known ichthyosaur.
- 120** Coracoid ossifications: one (0); two (1). From RIEPPEL (1994) #70.
Coding for Ichthyosauria: 0
Discussion. – All known ichthyosaurs have a single coracoid ossification.
- 121** Coracoid foramen: enclosed by coracoid only (0); enclosed by coracoid and scapula (1). From RIEPPEL (1994) #71.
Coding for Ichthyosauria: 0
Discussion. – A foramen coracoideum is unknown in ichthyosaurs, probably due to incomplete ossification, with the noteworthy exception of the Middle Triassic *Cymbospondylus buchseri* (SANDER 1989), where it is exclusive to the coracoid. As no other evidence is available, it has to be assumed that this may have also been the ancestral state in ichthyosaurs.
- 122** Humeral epicondyles: large, forming distinct processes (0); reduced so that distal end of humerus appears only marginally broader than shaft (1). From RIEPPEL (1994) #75.
Coding for Ichthyosauria: 1
Discussion. – Of course the ectepicondyles are – as a result of aquatic adaptation – reduced in all known ichthyosaurs, and the distal end of the humerus is therefore only slightly wider (or, due to a general widening of the humerus, even narrower) than the shaft.
- 123** Humeral torsion: proximal and distal ends of humerus set off at 45° angles from one another (0); angle between opposing ends reduced to no more than 20° (1). Modified from LEE (1996b) #F3.
Coding for Ichthyosauria: 1
Discussion. – There is no noteworthy torsion in the broadened and flattened humerus of known ichthyosaurs. This may be related to aquatic adaptation, as well.
- 124** Humeral shaft/distal end ratio: shaft length less than one-third the maximum width of the distal end of the humerus (0); shaft long at least four times the width of the distal end (1).
Coding for Ichthyosauria: 0
Discussion. – All ichthyosaurs show the plesiomorphic state. Even *Thaisaurus chonglakmanii* (MAZIN et al. 1991), who has the most primitive limbs of all ichthyosaurs known so far, has a humerus the distal end of which is almost half as wide as the shaft is long. In other ichthyosaurs the humerus is always even shorter and wider. The shortening of the humerus may be related to aquatic adaptation.
- 125** Humeral distal articulations: distinct trochlea and capitellum (0); low double condyle (1).
Coding for Ichthyosauria: 1
Discussion. – There is no clear differentiation of capitellum and trochlea in any known ichthyosaur. This, again, is certainly due to aquatic adaptations and a character that has to be viewed with caution.
- 126** Supinator process: large angled away from humeral shaft (0); large confluent with shaft (1); small or absent (2). Modified from LAURIN & REISZ (1995) #101.
Coding for Ichthyosauria: 2
Discussion. – There is no differentiated processus supinatorius in known ichthyosaurs. Once again this is a feature liable to reduction due to aquatic adaptation, and its value is highly doubtful for assessing phylogenetic relationships of aquatic amniotes.
- 127** Ectepicondylar groove/foramen: foramen absent, but deep groove present along anterior edge of humerus (0); foramen and groove absent, but a small notch present anterodistally

- (1); completely enclosed foramen present, no deep groove (2). Modified from LAURIN & REISZ (1995) #102.
Coding for Ichthyosauria: 0
Discussion. – It is difficult to evaluate this character in the most basal ichthyosaurs. In *Grippia* and *Mixosaurus* there is a clear anterodistal groove of the humerus, which may be interpreted as a remnant of the ectepicondylar groove. In later ichthyosaurs even this is absent. Nevertheless available data suggests, that in the ichthyosaurian grundplan the plesiomorphic state of this character was present.
- 128** Entepicondylar foramen: present (0); absent (1). From REISZ & LAURIN (1991) #10.
Coding for Ichthyosauria: 1
Discussion. – A foramen entepicondylare is absent in all ichthyosaurs. In connection to the distal foramina of the humerus again the question arises, whether their absence is not – analogous to what is seen in sauropterygians and placodonts – a simple result of reductions due to aquatic adaptations. It is well conceivable that many features of the girdles and limbs looked completely different in the unknown terrestrial ancestors of ichthyosaurs than they do in the fully marine forms that we exclusively know.
- 129** Radius/ulna ratio: radius shorter than ulna (0); radius longer than ulna (1); radius and ulna sub-equal (2). From RIEPPEL (1994) #78.
Coding for Ichthyosauria: 2
Discussion. – In almost all known ichthyosaurs radius and ulna are of subequal length. If at all, it is the ulna which is somewhat reduced in length and width, such as in *Parvinator*, *Shonisaurus*, *Callawayia* and *Guizhouichthyosaurus*.
- 130** Olecranon: large and set off from proximal end of ulna (0); small or entirely absent (1). Modified from LAURIN & REISZ (1995) #105.
Coding for Ichthyosauria: 1
Discussion. – A differentiated olecranon is absent in all ichthyosaurs. This may well be a reduction due to aquatic adaptation.
- 131** Perforating foramen of manus: present (0); absent (1).
Coding for Ichthyosauria: 1
Discussion. – A foramen perforans of the manus is usually absent in ichthyosaurs. A deep notch in the intermedium is, however, present in *Mixosaurus*, *Utatusaurus* and particularly in *Parvinator wapitiensis*. At least an open foramen perforans was therefore probably present in the grundplan of ichthyosaurs, but it is unlikely that a complete foramen was present.
- 132** Metacarpal IV/III ratio: fourth longer than third (0); fourth equal to or shorter than third (1).
Coding for Ichthyosauria: 1
Discussion. – Metacarpalia III and IV are already of almost equal length in basal ichthyosaurs such as *Utatusaurus*, *Grippia* and *Chaohusaurus*, usually metacarpal IV is already somewhat shorter usually. This condition is therefore assumed for the ichthyosaurian grundplan.
- 133** Thyroid fenestra: absent (0); present (1).
Coding for Ichthyosauria: 0
Discussion. – A fenestra thyroidea is not known in ichthyosaurs.
- 134** Posterior process of iliac blade: long, extending posteriorly well past level of acetabulum (0); posterior process reduced, distal end of ilium fan-shaped (1). From LAURIN & REISZ (1995) #108.
Coding for Ichthyosauria: 1
Discussion. – In almost all ichthyosaurs the ilium is so much reduced that it is hardly comparable to that of other amniotes. In *Utatusaurus* (MOTANI et al. 1998) this is not yet the case, apparently. *Utatusaurus* shows the apomorphic state of this character, and this is assumed to represent the primitive ichthyosaurian condition.
- 135** Anterior process of iliac blade: blade not expanded anteriorly with at most only a very small anterior process (0); anterior process large often exceeding dimension of posterior process (1). From LEE (1994) #97.
Coding for Ichthyosauria: 0
Discussion. – The ilium is largely much reduced in ichthyosaurs. In *Utatusaurus* (MOTANI et al. 1998) the plesiomorphic state of this character is, however, clearly displayed.
- 136** Pubic tubercle: if present small and directed anteroventrally (0); large and strongly turned ventrally (1). From DE BRAGA & REISZ (1995) #36.
Coding for Ichthyosauria: 0
Discussion. – A tuberculum pubis is not known to occur in ichthyosaurs.
- 137** Acetabulum: oval (0); circular (1). From RIEPPEL (1994) #82.
Coding for Ichthyosauria: 0
Discussion. – A true acetabulum is not formed by ichthyosaurian pelvis anymore, i.e. it was largely cartilaginous. In *Utatusaurus* it had, following MOTANI et al. (1998), a rather oval shape and this is regarded as the primitive ichthyosaurian condition.
- 138** Acetabular process: weakly developed (0); large, overhangs femoral head, appears as triangular lateral extension when viewed from below (1). From LEE (1993) #A16.
Coding for Ichthyosauria: 0
Discussion. – A true acetabular process is – probably as a result of aquatic adaptations – not found in any ichthyosaur.
- 139** Femoral shaft: short and stout (0); sigmoidally curved and slender (1). From RIEPPEL (1994) #83.
Coding for Ichthyosauria: 0
Discussion. – All ichthyosaurs have a rather short and stout femur. This is already true – although much less than for the more highly derived forms – for *Thaisaurus* (MAZIN et al. 1991).
- 140** Femoral fourth trochanter: present (0); absent (1).
Coding for Ichthyosauria: 1
Discussion. – The trochanter quartus of the femur is absent in adequately known ichthyosaurs. This is another character suspect of being related to aquatic adaptation and reduction.
- 141** Femoral trochanter major: absent (0); present and deflected distally from the proximal head of the femur (0); pyramidal in shape and nearly in line with the head of the femur (2); similar in shape to state (1) but positioned at mid-shaft length (3). Modified from LEE (1995) #50.
Coding for Ichthyosauria: 0
Discussion. – A trochanter major can not be found in ichthyosaurs. This is again a reductional character related to aquatic adaptation.
- 142** Intertrochanteric fossa: well defined (0); reduced (1); absent (2). From RIEPPEL (1994) #84.

- Coding for Ichthyosauria: ?
 Discussion. – As the femur of ichthyosaurs has no differentiated trochanters, this character can not be coded.
- 143** Distal femoral condyles: large, projecting from distal end of shaft (0); reduced, not projecting beyond distal end of femur (1). From RIEPPEL (1994) #85.
 Coding for Ichthyosauria: 1
 Discussion. – This is another reductional character found in all ichthyosaurs which is certainly related to their secondary aquatic adaptation.
- 144** Anterior femoral condyle: larger, extends distal to posterior condyle (0); anterior condyle reduced and sub-equal or smaller than posterior condyle (1). From RIEPPEL (1994) #86.
 Coding for Ichthyosauria: 0
 Discussion. – At least basal forms such as *Chaohusaurus* and *Mixosaurus* show the plesiomorphic condition. Although one can not really say that the anterior (tibial) condyle extends further distally than the fibular condyle, it is nevertheless always considerably larger. In later ichthyosaurs this difference is usually no longer obvious, but this is a secondary state within the group (see also MAISCH & MATZKE 2000a, character 112).
- 145** Fibula: bowed away from tibia (0); straight not bowed away (1).
 Coding for Ichthyosauria: 0
 Discussion. – Ichthyosaurs show the plesiomorphic state in the grundplan, as seen in many Triassic forms such as *Chaohusaurus*, *Mixosaurus*, *Phalarodon* and *Cymbospondylus*. It is rapidly changed, however, within the group (see MOTANI 1999b; MAISCH & MATZKE 2000a, character 116). Generally there is a trend in ichthyosaurs, in which the hind fin always drags behind the fore fin in its degree of aquatic adaptation, so that plesiomorphic characters are retained longer in the hind fins.
- 146** Perforating artery of pes: located between astragalus and calcaneum (0); located between distal ends of tibia and fibula (1). From RIEPPEL (1994) #87.
 Coding for Ichthyosauria: ?
 Discussion. – Due to a lack of adequately preserved hind fin material of basal ichthyosaurs, it is probably best to code this character as unknown at present.
- 147** Tibia/astragalus articulation: loose fitting (0); tightly fitting with well developed articulation (1). Modified from LAURIN & REISZ (1995) #116.
 Coding for Ichthyosauria: 0
 Discussion. – There is always only a loose joint between astragalus and tibia in ichthyosaurs. This is very likely caused by aquatic adaptation.
- 148** Discrete astragalus: absent (0); present (1).
 Coding for Ichthyosauria: 1
 Discussion. – An astragalus is present in ichthyosaurs, as in amniotes generally.
- 149** Astragalus/calcaneum relationship in adult: never fused (0); fused (1); hinge present (2). Modified from LAURIN (1991) #F8.
 Coding for Ichthyosauria: 0
 Discussion. – There is no fusion between the proximal tarsals in any ichthyosaur, and there is also no well defined joint. This may well be brought about due to aquatic adaptation.
- 150** Astragalus/distal tarsal IV articulation: articulation poorly defined (0); articulation well defined (1); articulation absent (2).
 Coding for Ichthyosauria: 1
 Discussion. – There is no well defined joint between astragalus and distal tarsal IV in ichthyosaurs. It can not be excluded that this is a reduction due to aquatic adaptations.
- 151** Calcaneal tuber: absent (0); present (1). Modified from LAURIN (1991) #F9.
 Coding for Ichthyosauria: 0
 Discussion. – A tuber calcanei is not known in any ichthyosaur.
- 152** Distal tarsal I: present (0); absent (1).
 Coding for Ichthyosauria: 0
 Discussion. – The distal tarsal I is still present in the ichthyosaurian grundplan. Within the group the number of toes is reduced to four to three (see MAISCH & MATZKE 2000a, character 120). Homologies are, in contrast to the fore fin (MOTANI 1999a), unclear, but it can be assumed that, analogous to the fore fin, it is probably digits I and V that have been reduced.
- 153** Distal tarsal V: present (0); absent (1).
 Coding for Ichthyosauria: 1
 Discussion. – The distal tarsal V appears to be lost in the mixosaurids. To assess this character in more basal forms is at present impossible, due to the lack of material.
- 154** Metatarsal V: long and slender with length exceeding the width of the base by at least three times (0); short and broad with base width equivalent to at least two times the length of the of the element measured along its midline (1). Modified from RIEPPEL (1995) #69.
 Coding for Ichthyosauria: 0
 Discussion. – Metatarsal V is a long and slender element, just as the other metatarsals in the Lower Triassic *Thaisaurus* (MAZIN et al. 1991), but already in the Lower Triassic grippiid *Chaohusaurus* (MAISCH 2001a) metatarsal V is strongly shortened, as in all other more derived ichthyosaurs.
- 155** Metatarsal V shape: straight (0); hooked (1).
 Coding for Ichthyosauria: 0
 Discussion. – No known ichthyosaur shows a hooked metatarsal V, but this is also found in other secondarily aquatic groups and therefore may easily represent a simple reduction.
- 156** Metatarsal V plantar tubercle: absent (0); present (1).
 Coding for Ichthyosauria: 0
 Discussion. – A plantar tubercle of metatarsal V is not known in any ichthyosaur.
- 157** Metatarsal I / IV ratio: metatarsal I greater than 50 % the length of metatarsal IV (0); metatarsal I less than 50 % the length of metatarsal IV (1). From DE BRAGA & REISZ (1995) #41.
 Coding for Ichthyosauria: 0
 Discussion. – In the ichthyosaurian grundplan metatarsal I is almost as large as metatarsal V. This condition is shown e. g. in *Thaisaurus* (MAZIN et al. 1991) and the mixosaurids. In *Chaohusaurus* metatarsal I seems to be smaller (MAISCH 2001a). Available data are thus not unequivocal, but the majority of basal ichthyosaurs appears to show the plesiomorphic state.
- 158** Number of pedal centralia: both lateral and medial centralia present (0); medial pedal centralia lost (1); both centralia lost (2).
 Coding for Ichthyosauria: 2

D i s c u s s i o n . – No known ichthyosaur retains ossified centralia in the tarsus.

- 159** Fifth pedal digit: longer than first digit (0); shorter and more lightly built than first (1). From LEE (1993) #A15.
C o d i n g f o r I c h t h y o s a u r i a : 1
D i s c u s s i o n . – The fifth toe of ichthyosaurs is significantly weaker than the first already in *Chaohusaurus*, even more so in the mixosaurids. In more highly derived ichthyosaurs reduction of toes and unclear homologies make an evaluation difficult.
- 160** Metapodials: not overlapping proximally (0); overlapping (1). From LAURIN & REISZ (1995) #121.
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – No known ichthyosaur shows a proximal overlap of the metapodials. This may be a result of aquatic adaptation.
- 161** Pedal phalangeal formula: 2,3,4,5(4),4 (0); 2,3,4,4,3 (1); 2,3,3,4,3 or less (2). From LAURIN & REISZ (1995) #122.
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – At the moment the pedal phalangeal formula of basal ichthyosaurs is unknown, as well ossified and articulated hind fins have not been found. The mixosaurs, however, already show strong hyperphalangy. This suggests that in the grundplan at least the normal reptilian phalangeal formula was present, and ichthyosaurs are coded accordingly.
- 162** Ungual size: unguals shorter than phalanges (0); unguals at least 50 % longer than penultimate phalanges (1).
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – The terminal phalanges are always the smallest in all known ichthyosaurs, enlarged unguual phalanges never occur in either the hand or foot skeleton. This may be a result of aquatic adaptation.
- 163** Body osteoderms: absent (0); present but few restricted to mid-line (1); present but spread all over back (2). From LEE (1994) #123.
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – No ichthyosaurs have any kind of osteoderms.
- 164** Osteodermal ridges: absent (0); fine regular spaced ridges (2); heavy irregularly spaced ridges (3). From LEE (1994) #125.
C o d i n g f o r I c h t h y o s a u r i a : ?
D i s c u s s i o n . – As ichthyosaurs do not possess osteoderms, this character can not be coded.
- 165** Osteodermal limb studs: absent (0); present as conical studs (1). From LEE (1994) #128.
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – Osteodermal ossifications on the limbs are unknown in ichthyosaurs.
- 166** Gastralia: present (0); lost (1). From LEE (1994) #129.
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – All known ichthyosaurs, with the possible exception of the highly derived Jurassic genus *Suevoleviathan* (MAISCH 1998a), have well-developed gastralia, the number of which is, however, reduced during the evolution of the group (see MOTANI 1999b and MAISCH & MATZKE 2000a, character 64)

3.3. Discussion of the data matrix of LAURIN & REISZ (1995)

Discussion of character codings for Ichthyosaurs in the data matrix of LAURIN & REISZ (1995) as modified by MODESTO (1999). Original formulations of characters, except for slight orthographic corrections, have been used. Where the same characters and codings have been employed as in the matrix of RIEPPEL & REISZ (1999), reference is made to the discussion provided above.

- 1** Narial shelf absent (0) present (1)
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – A lateral shelf of the nasal above the naris, as it is found in the procolophonians and some synapsids, is absent in ichthyosaurs.
- 2** Frontal-orbital contact absent (0) present (1)
C o d i n g f o r I c h t h y o s a u r i a : 1
D i s c u s s i o n . – See above, character 22.
- 3** Pineal foramen position: in center of parietal or farther posteriorly (0) close to frontoparietal suture (1)
C o d i n g f o r I c h t h y o s a u r i a : 1
D i s c u s s i o n . – See above, character 49.
- 4** Postparietal: paired (0) median (1) absent (2)
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – See above, character 52.
- 5** Postparietal position: dorsally exposed (0) occipital (1)
C o d i n g f o r I c h t h y o s a u r i a : 1
D i s c u s s i o n . – In the only known ichthyosaurs were a postparietal is demonstrably present, namely *Cymbospondylus petrinus* (MAISCH & MATZKE 2000a, 2004) and *Phantomosaurus neubigi* (MAISCH & MATZKE 2000a, 2006), it does not reach onto the skull roof but is restricted to the occipital surface.
- 6** Prefrontal-palatal contact: absent (0) weak (1) strong (2)
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – See above, character 20.
- 7** Prefrontal medial flange: narrow (0) wide (1)
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – See above, character 20.
- 8** Bulbous medial process of prefrontal: absent (0) present (1)
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – See above, character 21.
- 9** Lacrimal narial contact: present (0) absent (1)
C o d i n g f o r I c h t h y o s a u r i a : 1
D i s c u s s i o n . – See above, character 17.
- 10** Foramen orbitonasale: absent (0) represented by a medial indentation on the Lacrimal and a dorsal indentation on the palatine (1) enclosed between prefrontal, lacrimal and palatine (2)
C o d i n g f o r I c h t h y o s a u r i a : 0
D i s c u s s i o n . – There is no Foramen orbitonasale in any known ichthyosaur.
- 11** Jugal anterior process: does not extend to anterior orbital rim (0) extends at least to level of anterior orbital rim (1)
C o d i n g f o r I c h t h y o s a u r i a : 1
D i s c u s s i o n . – In all ichthyosaurs, including the most basal forms, as far as their skulls are adequately known, the jugal is an elongate element which forms most of the ventral orbital margin and extends far anteriorly, usually up to and some times even beyond the anterior margin of the orbit.

- 12 Postorbital-supratemporal contact: present (0) absent (1) (modified)
Coding for Ichthyosauria: 0
Discussion. – See above, character 30.
- 13 Postorbital far from occiput (0) close to occiput (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 32.
- 14 Intertemporal: present (0) absent (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 54.
- 15 Posterolateral corner of skull roof: formed by tabular (0) formed mostly by supratemporal (1) formed by parietal and small supratemporal (2)
Coding for Ichthyosauria: 1
Discussion. – See above, character 53.
- 16 Tabular and opisthotic: in contact (0) separated (1)
Coding for Ichthyosauria: ?
Discussion. – Since the tabular is lost in all known ichthyosaurs, this character can not be coded.
- 17 Tabular size: large (0) small (1) absent (2)
Coding for Ichthyosauria: 2
Discussion. – See above, character 55.
- 18 Supratemporal size: large (0) small (1) absent (2)
Coding for Ichthyosauria: 0
Discussion. – See above, character 53.
- 19 Anterodorsal process of maxilla: absent (0) low, does not reach nasal or mid-height of external naris (1) high, reaches nasal and mid-height of external naris (2)
Coding for Ichthyosauria: 0
Discussion. – There is no anterodorsal process of the maxilla in ichthyosaurs, even in the most basal forms the maxilla is always low anteriorly.
- 20 Anterior lateral maxillary foramen: equal in size to other maxillary foramina (0) larger than other foramina (1) the lateral surface of the maxilla lacks large foramina (2)
Coding for Ichthyosauria: 0
Discussion. – See above, character 30.
- 21 Maxillary anterior narial foramen: absent (0) present in maxilla only or between maxilla and premaxilla (1)
Coding for Ichthyosauria: 0
Discussion. – An anterior narial foramen of the maxilla, as in pareiasaurs, procolophonians and turtles is never found in ichthyosaurs.
- 22 Maxilla and quadratojugal: in contact (0) separated (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 16.
- 23 Quadratojugal: reaches orbit (0) does not reach orbit (1)
Coding for Ichthyosauria: 1
Discussion. – There is no contact between orbit and quadratojugal in any known ichthyosaur. The skull reconstruction of *Phalarodon* by NICHOLLS et al. (1999), in which such a contact is found, is incorrect (see MAISCH & MATZKE 2000a for a corrected version).
- 24 Caniniform region: present (0) absent (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 95.
- 25 Caniniform maxillary tooth: absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 96.
- 26 Squamosal and post-temporal fenestra: separated (0) in contact (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 36.
- 27 Occipital flange of squamosal: in otic notch and overlaps pterygoid (0) gently convex all along the posterior edge of the skull (1) convex above quadrate emargination and concave medial to tympanic ridge (2) absent (3) medial to tympanic ridge, facing posteromedially (4) medial to tympanic ridge, concave, facing posterolaterally or ventrolaterally (5)
Coding for Ichthyosauria: 3
Discussion. – See above, character 37.
- 28 Quadratojugal shape: narrow (0) dorsally expanded (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 42.
- 29 Upper temporal fenestra: absent (0) present (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 50.
- 30 Lower temporal fenestra: absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 51.
- 31 Temporal emargination: absent (0) with squamosal and supratemporal (1) with quadratojugal and squamosal (2) facing posteriorly and exposed on occiput with squamosal, quadratojugal and quadrate (3)
Coding for Ichthyosauria: 0
Discussion. – A posterior emargination of the temporal region is universally absent in ichthyosaurs.
- 32 Postorbital region of skull: long, more than 15% skull length (0) short (15% skull length or shorter) (1)
Coding for Ichthyosauria: 1
Discussion. – Already in the most basal ichthyosaurs the enlargement of the orbits and the elongation of the rostrum results in a strong relative shortening of the postorbital skull segment, which reaches less than 15% of the entire skull length. In the more highly derived members of the group, this is usually even more extreme.
- 33 Ventral margin of postorbital region of skull: expanded ventrally (0) rectilinear (1) emarginated (2)
Coding for Ichthyosauria: 2
Discussion. – See above, character 51.
- 34 Quadrate lateral exposure: absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 39.
- 35 Quadrate anterior process: long (0) short (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 41.
- 36 Jaw articulation position: posterior to occiput (0) even with occiput (1) anterior to occiput (2)
Coding for Ichthyosauria: 1
Discussion. – See above, character 82.
- 37 Posterior extension of orbit: absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – A posterior elongation of the orbit, as found in derived procolophonians, is not known in ichthyosaurs. Instead the entire orbit (as is also seen if one compares the size and position of the sclerotic rings in both groups) is regularly enlarged.
- 38 Dermal sculpturing: absent (0) tuberosities (1) tuberosities and pits (2) honeycomb pattern of ridges and pits (3)
Coding for Ichthyosauria: 0

- Discussion.* – There is no dermal sculpturing of the skull bones known in any ichthyosaur. See also above, character 43.
- 39** Interpterygoid vacuity: short, less than 15% skull length (0) absent (1) long, longer than 15% skull length (2)
Coding for Ichthyosauria: 0
Discussion. – Although derived ichthyosaurs show a large and elongate fenestra interpterygoidea, this is definitely lacking in more basal members of the group. In the only basal ichthyosaurs the palate of which is completely known, the mixosaurids, the fenestra is even (autapomorphously) completely closed. Data available for other basal taxa suggest small fenestrae at maximum. The most basal taxon with large fenestrae is the Middle Triassic *Mikadocephalus* (MAISCH & MATZKE 1997b).
- 40** Choana: parallel to maxilla, palatine forms posterior edge only (0) curved posteromedially, palatine forms its posterior and part of the lateral edge (1) parallel to maxilla and palatine forming posterior and part of the lateral edge (2)
Coding for Ichthyosauria: 2
Discussion. – It is necessary to establish a new character state for ichthyosaurs in this case, because in them (see above, character 8) the choanae do parallel the maxillary margins, but are still posteriorly and in part laterally bordered by the palatines.
- 41** Suborbital foramen: bordered by maxilla or jugal laterally (0) bordered by palatine, pterygoid and in some cases ectopterygoid laterally (1)
Coding for Ichthyosauria: ?
Discussion. – See above, character 74.
- 42** Arcuate flange of pterygoid present (0) absent (1)
Coding for Ichthyosauria: 1
Discussion. – Such a structure does not occur in any known ichthyosaur.
- 43** Cranio-quadrate space: small, quadrate ramus of pterygoid and paroccipital process converge posteriorly (0) large, quadrate ramus of pterygoid and paroccipital process are parallel (1)
Coding for Ichthyosauria: ?
Discussion. – Our knowledge on the structure of the basal ichthyosaurian palate and occiput is still so limited, that a reliable coding for this character is impossible.
- 44** Pterygoid anterior extent: reaches level of posterior end of choana (0) posterior to choana (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 76 (differently defined, but equal in meaning).
- 45** Transverse flange of pterygoid orientation: directed posterolaterally or transversely (0) directed anterolaterally (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 77.
- 46** Transverse flange of pterygoid dentition: shagreen of denticles no ventral ridge (0) row of large teeth, no ventral ridge (1) edentulous with ventral ridge (2)
Coding for Ichthyosauria: 1
Discussion. – See above, character 78.
- 47** Ectopterygoid: large (0) small (1) absent (2)
Coding for Ichthyosauria: 2
Discussion. – See above, character 81.
- 48** Ectopterygoid dentition: present (0) absent (1)
Coding for Ichthyosauria: ?
- Discussion.* – This character can not be coded, as all ichthyosaurs have lost the ectopterygoid.
- 49** Suborbital foramen absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – A well-defined foramen suborbitale has not been observed in ichthyosaurs so far.
- 50** Parasphenoid pocket for cervical musculature present (0) absent (1)
Coding for Ichthyosauria: 1
Discussion. – Pocket-shaped attachment zones for the cervical musculature are not found on the parasphenoid of any known ichthyosaur.
- 51** Parasphenoid wings: present, psph broad posteriorly (0) absent, psph narrow posteriorly (1)
Coding for Ichthyosauria: 1
Discussion. – As in most amniotes, the parasphenoid of ichthyosaurs is only slightly expanded posteriorly, without extensive lateral processes.
- 52** Cultriform process: long (0) short (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 75.
- 53** Psph teeth: absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – There is never any dentition on the parasphenoid of ichthyosaurs.
- 54** Soc plate: absent (0) broad, plate-like (1) narrow (2) very narrow, reduced to sagittal pillar (3)
Coding for Ichthyosauria: 2
Discussion. – See above, character 56.
- 55** Paroccipital process: vertically broad (0) antero-posteriorly expanded (1) narrow (2) tabular, composed of opisthotic (3)
Coding for Ichthyosauria: 0
Discussion. – See above, character 61.
- 56** Contact between paroccipital process and dermatocranium: to tabular (0) to supratemporal and tabular (1) to tabular and squamosal (2) to squamosal and supratemporal (3) to supratemporal (4) to squamosal and quadrate (5) ends freely (6)
Coding for Ichthyosauria: 4
Discussion. – In all ichthyosaurs where this feature can be assessed, the processus paroccipitalis exclusively contacts the supratemporal distally, as already seen in *Cymbospondylus* (MERRIAM 1908). Reliable data are, however, not available for any more basal ichthyosaurs.
- 57** Otic trough in ventral flange of opisthotic absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – A trough on the ventral surface of the opisthotic is absent in all adequately known ichthyosaurs.
- 58** Medial wall of prootic unossified (0) ossified with acoustic nerve foramina (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 68.
- 59** Post-temporal fenestra: small (0) large (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 59.
- 60** Osseous contact between basisphenoid and basioccipital absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 63.
- 61** Occipital condyle transversely broad (0) reniform to circular (1)
Coding for Ichthyosauria: 1

- Discussion*. – All known ichthyosaurs have an almost circular condylus occipitalis in occipital view. This is equally true for the taxa with a concave condylus, such as *Cymbospondylus* (MERRIAM 1908).
- 62 Basioccipital tubera absent (0) paired (1) median (2)
Coding for Ichthyosauria: 1
Discussion. – See above, character 65.
- 63 Lateral flange of exoccipital absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – In all ichthyosaurs the exoccipitals are just bony pillars lateral to the foramen occipitale magnum, there is never any lateral enlargement of these elements.
- 64 Quadrate condyle articular surface: strongly convex, anteroposteriorly long (0) nearly flat, anteroposteriorly short (1)
Coding for Ichthyosauria: 1
Discussion. – Even in rather basal taxa the quadrate is relatively well known, such as *Contectopalatus* and *Pes-sopteryx* (MAISCH & MATZKE 2001b, 2003a). Its condyle is shortened anteroposteriorly and only slightly convex, being rather saddle-shaped, as in all later ichthyosaurs.
- 65 Stapes: massive, perforate (0) slender, imperforate (1)
Coding for Ichthyosauria: 1
Discussion. – See above, characters 44, 45.
- 66 Stapedial dorsal process ossified (0) unossified (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 46.
- 67 Labyrinthodont infolding present (0) absent (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 93.
- 68 Foramen intermandibularis: anterior symphyseal foramen (0) two foramina, a symphyseal and a posterior foramen located anterior to coronoid process (1) two foramina, a symphyseal and a posterior foramen located posterior to or at level of coronoid process (2)
Coding for Ichthyosauria: ?
Discussion. – The internal surface of the mandible is not well enough known in any basal ichthyosaur to assess this character beyond doubt.
- 69 Meckelian fossa orientation: faces mediodorsally, prearticular narrow (0) faces dorsally, prearticular wide (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 85.
- 70 Fossa meckelii long, occupies at least 20% of lower jaw length (0) short, occupies less than 20% of lower jaw length (1)
Coding for Ichthyosauria: 1
Discussion. – The relative shortening of the fossa meckelii is a direct result of the elongated rostral region of the skull in ichthyosaurs. Nevertheless it is already reduced to less than 20% skull length in Triassic forms such as *Cymbospondylus* or the mixosaurids, and this is considered as the primitive state in the group.
- 71 Surangular length: extends beyond coronoid eminence (0) does not extend beyond coronoid eminence (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 86.
- 72 Accessory lateral shelf of surangular anterior to articular region: absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 87.
- 73 Coronoid number: two or three (0) one (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 84.
- 74 Prearticular extends beyond coronoid eminence (0) no farther than the coronoid eminence (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 91.
- 75 Retroarticular process: absent or small and narrow (0) transversely broad, dorsally concave (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 92.
- 76 Retroarticular process composition: articular only (0) three or more elements (1)
Coding for Ichthyosauria: 1
Discussion. – The processus retroarticularis is formed in all adequately known ichthyosaurs at least by the articular, supraangular and angular. This can already be excellently seen in the presumably Lower Triassic *Parvinator* (NICHOLLS & BRINKMAN 1995).
- 77 Lateral shelf on articular region: absent (0) on articular (1) on surangular (2)
Coding for Ichthyosauria: 0
Discussion. – Such a lateral shelf is not found in any ichthyosaur.
- 78 Coronoid process: small eminence composed of several elements (0) high process composed of coronoid only (1) formed by supraangular (2)
Coding for Ichthyosauria: 2
Discussion. – None of the original codings fits for ichthyosaurs whose processus coronoideus is exclusively formed by the supraangular. For this morphology a new character state (2) has therefore been introduced.
- 79 Splenial contributes to symphysis (0) excluded from symphysis (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 88.
- 80 Presacral vertebral count: more than 20 (0) twenty or less (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 97.
- 81 Axial centrum orientation: in plane of axial skeleton (0) sloping anterodorsally (1)
Coding for Ichthyosauria: 0
Discussion. – In this character, ichthyosaurs are extremely primitive, as the centrum of the epistropheus is always completely in line with those of the following cervical vertebrae and never tilted anterodorsally. This is already evident in Triassic taxa like *Shastasaurus* and *Cymbospondylus* (MERRIAM 1908). If this truly is a plesiomorphy (which would push ichthyosaurs towards the base of all amniotes) or a reversion can not be decided at present, but the latter alternative appears more plausible at the moment.
- 82 Atlantal neural spine: nearly as tall as axial spine (0) reduced to a small spinous process (1)
Coding for Ichthyosauria: 1
Discussion. – In this character ichthyosaurs resemble other amniotes and always show a strongly shortened processus spinosus of the atlantal neural arch. This is assumed to be the primitive state in the group, although this character is insufficiently known in basal ichthyosaurs.
- 83 Axial intercentrum with rounded anteroventral edge (0) with strong anterior process (1)

- Coding for Ichthyosauria: 0
Discussion. – As far as it is known the intercentrum of the epistropheus never shows a long anteroventral process in ichthyosaurs.
- 84** Atlantal pleurocentrum and axial intercentrum: separate elements (0) attached or fused (1)
Coding for Ichthyosauria: 0
Discussion. – In this character ichthyosaurs are also very plesiomorphic. It could be assumed that this is a result of a reversion – possibly due to incomplete ossification or paedomorphosis – which may be connected to their secondarily marine adaptations.
- 85** Trunk neural arches: swollen with wide zygapophyseal buttresses (0) narrow (1) swollen with narrow zygapophyseal buttresses (2)
Coding for Ichthyosauria: 1
Discussion. – See above, character 106.
- 86** Ventral surface of anterior pleurocentra: rounded (0) keeled (1) with double ridge (2)
Coding for Ichthyosauria: 0
Discussion. – See above, character 103.
- 87** Number of sacral vertebrae: one (0) two (1) three or four (2)
Coding for Ichthyosauria: 1
Discussion. – See above, character 109.
- 88** Sacral ribs distal overlap. Broad with narrow gap between ribs (0) small or absent with wide gap between ribs (1)
Coding for Ichthyosauria: 1
Discussion. – Because of the highly derived state of the sacrum, already in the most basal ichthyosaurs, as exemplified by *Utatusaurus* (MOTANI et al. 1998), this character can only be cautiously evaluated. Nevertheless, *Utatusaurus* clearly shows the derived condition. This is of course also the case in later ichthyosaurs, where the sacral ribs do not overlap at all, but remain widely separated.
- 89** Transverse processes or ribs: present only on a few anterior caudals (0) present on at least 13 caudals (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 110.
- 90** Caudal haemal arches: wedged between centra (0) attached to anterior centrum (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 112.
- 91** Interclavicle: diamond shaped (0) T-shaped with long and slender lateral process (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 115.
- 92** Interclavicle attachment for clavicle: ventral sutural area (0) anteriorly directed groove (1) tightly sutured into plastron (2)
Coding for Ichthyosauria: 0
Discussion. – As in most amniotes, the ichthyosaurian clavicles are invariably attached to the ventral side of the interclavicle.
- 93** Cleithrum: caps scapula anterodorsally (0) does not cap scapula at all (1) absent (2)
Coding for Ichthyosauria: 2
Discussion. – See above, character 113.
- 94** Scapulocoracoid ossifications: two (0) three (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 120.
- 95** Scapula: broad (0) narrow, thin (1) narrow, cylindrical (2)
Coding for Ichthyosauria: 0
Discussion. – See above, character 117.
- 96** Supraglenoid foramen: present (0) absent (1)
Coding for Ichthyosauria: 1
Discussion. – There is no foramen supraglenoideum in any known ichthyosaur.
- 97** Glenoid: anteroposteriorly long, helicate (0) short, bipartite (1)
Coding for Ichthyosauria: 0
Discussion. – As most amniotes, ichthyosaurs possess a helicate, anteroposteriorly elongated glenoid. In Triassic forms it is particularly well seen and described in *Pesopteryx* (MAISCH & MATZKE 2003a).
- 98** Acromion: absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 118.
- 99** Sternum: not mineralised (0) mineralised (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 116.
- 100** Supinator process: strongly angled relative to shaft, separated from it by a groove (0) parallel to shaft, separated from shaft by a groove (1) parallel to shaft, not separated from shaft (2)
Coding for Ichthyosauria: ?
Discussion. – As there is no differentiated processus supinatorius in ichthyosaurs (see above, character 126), this character can not be coded.
- 101** Ectepicondylar foramen and groove: only groove present (0) groove and foramen present (1) only foramen present (2) both absent (3)
Coding for Ichthyosauria: 3
Discussion. – See above, character 127.
- 102** Entepicondylar foramen present (0) absent (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 128.
- 103** Humerus: with robust heads and a short shaft (0) short and robust without a distinct shaft (1) slender with long shaft (2)
Coding for Ichthyosauria: 0
Discussion. – Within the Ichthyosauria, the Lower Triassic *Thaisaurus* (MAZIN et al. 1991) shows the most basal humerus morphology, which corresponds to the plesiomorphic state of this character.
- 104** Olecranon process: large, proximal articulation facet of ulna faces medially (0) small, proximal articulation facet faces proximally (1)
Coding for Ichthyosauria: ?
Discussion. – As ichthyosaurs do not possess an olecranon, this character can not be assessed.
- 105** Manual phalangeal formula: 23453 or higher (0) 23443 (1) 23333 or less (2) (modified)
Coding for Ichthyosauria: 0
Discussion. – Hyperphalangy of the manus is one of the most characteristic features of the entire Ichthyosauria. It is therefore assumed that the plesiomorphic state or a modification thereof was present in the ichthyosaurian grundplan.
- 106** Dorsolateral shelf on iliac blade absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – Even in *Utatusaurus* (MOTANI et al. 1998), the most basal ichthyosaur for which a pelvis is known, there is no dorsolateral shelf of the iliac blade. This condition is thus assumed for the ichthyosaurian grundplan.

- 107** Iliac blade: low with long posterior process (0) dorsally expanded, distally flaring (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 134.
- 108** Acetabular buttress: small, overhangs acetabulum only moderately (0) large, overhangs acetabulum strongly (1)
Coding for Ichthyosauria: 0
Discussion. – If at all, then only a small buttress of the ilium above the acetabulum is found in ichthyosaurs, as demonstrated by *Utatusaurus* (MOTANI et al. 1998), and this condition is therefore also assumed for the grundplan of the group.
- 109** Oblique ventral ridge on femur present (0) absent (1)
Coding for Ichthyosauria: 1
Discussion. – An oblique ventral ridge of the femur is lacking in all ichthyosaurs. It is considered likely that this is could be a result of their marine adaptations and connected to the general reduction of the hind limbs in the group. The character is thus of doubtful relevance for ichthyosaurs.
- 110** Femoral proximal articulation: antero-posteriorly long (0) round (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 137.
- 111** Great trochanter of femur absent (0) present on posterior edge of femur (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 111.
- 112** Femoral shaft: short and broad (0) long and slender (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 139.
- 113** Carpus and tarsus short and broad (0) long and slender (1)
Coding for Ichthyosauria: 0
Discussion. – All ichthyosaurs possess a short and compact carpus and tarsus. This is most probably a direct result of their limbs being turned into flippers for aquatic locomotion, but it could also have been inherited from their ancestors. As with many other characters of the ichthyosaurian limbs, it is therefore highly difficult to evaluate the relevance of this one.
- 114** Astragalus absent (0) incorporates incompletely fused tibiale, intermedium and perhaps centrale 4 (1) without traces of a compound origin (2)
Coding for Ichthyosauria: 2
Discussion. – See above, character 148.
- 115** Tibio-astragalar joint flat (0) tibial ridge fits into astragalar groove (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 147 (differently formulated but of equal meaning).
- 116** Astragalus and calcaneum separate (0) fused (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 149.
- 117** Medial pedal centrale present (0) absent (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 158.
- 118** Number of distal tarsals five (0) four or less (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 153.
- 119** Fifth pedal digit longer than first digit (0) more slender and no longer than first digit (1)
Coding for Ichthyosauria: 1
Discussion. – See above, character 159.
- 120** Metapodials non-overlapping (0) overlapping (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 160.
- 121** Pedal phalangeal formula: 2,3,4,5,4 or 3 or higher (0) 2,3,4,4,3 (1) 2,3,3,4,3 or less (2) (modified)
Coding for Ichthyosauria: 0
Discussion. – See above, character 161.
- 122** Ratio between length of mt I and mt IV: at least 0, 5 (0) less than 0, 5 (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 157.
- 123** Dorsal dermal ossifications absent (0) present (1)
Coding for Ichthyosauria: 0
Discussion. – See above, character 163.
- 124** Posterior margin of skull roof roughly straight (0) with a single, median embayment (1), embayed bilaterally (2)
Coding for Ichthyosauria: 1
Discussion. – Even very basal ichthyosaurs such as *Utatusaurus* (MOTANI et al. 1998) or *Grippia* (MOTANI 2000a) clearly show a sagittal emargination of the posterior margin of the skull roof. This is also typical for all later and more highly derived ichthyosaurs.
- 125** Atlantal neural arch possesses (0) or lacks (1) an epiphysis.
Coding for Ichthyosauria: 1
Discussion. – An epiphysis of the atlantal neural arch has never been observed in any ichthyosaur. It can therefore be assumed to have been absent in the grundplan of the group.

4. Conclusions

The main results of the phylogenetic analyses can be summarized as follows. First, it is evident that they provide simultaneous support for two contradictory ideas on the origin and systematic position of ichthyosaurs. On one hand, ichthyosaurs might be interpreted as relatively basal diapsids, not too far from the equally partially aquatic eosuchians, corroborating the results of CALDWELL (1996), MOTANI et al. (1998) and MÜLLER (2003, 2004). On the other hand, they can be seen as nested within the Parareptilia, forming a secondarily aquatic branch of that group. If the first scenario is correct, the metapsid temporal opening of the ichthyosaurs would be homologous to the fenestra supratemporalis of diapsids. If the second scenario is true, it was formed convergently. Temporal fenestrations are in fact not rare at all in parareptiles and are found in a variety of taxa, including the Millerettidae, *Acleistorhinus*, Lanthanosuchidae, *Australothyris*, Bolosauridae as well as some procolophonians. Homology of all these temporal fenestrations remains doubtful (MODESTO et al. 2009; TSUJI & MÜLLER 2009). Even if ichthyosaurs originally possessed a complete lower temporal opening, this would not in itself be sufficient evidence to deny a parareptilian origin of the group, as a lower temporal fenestra has been

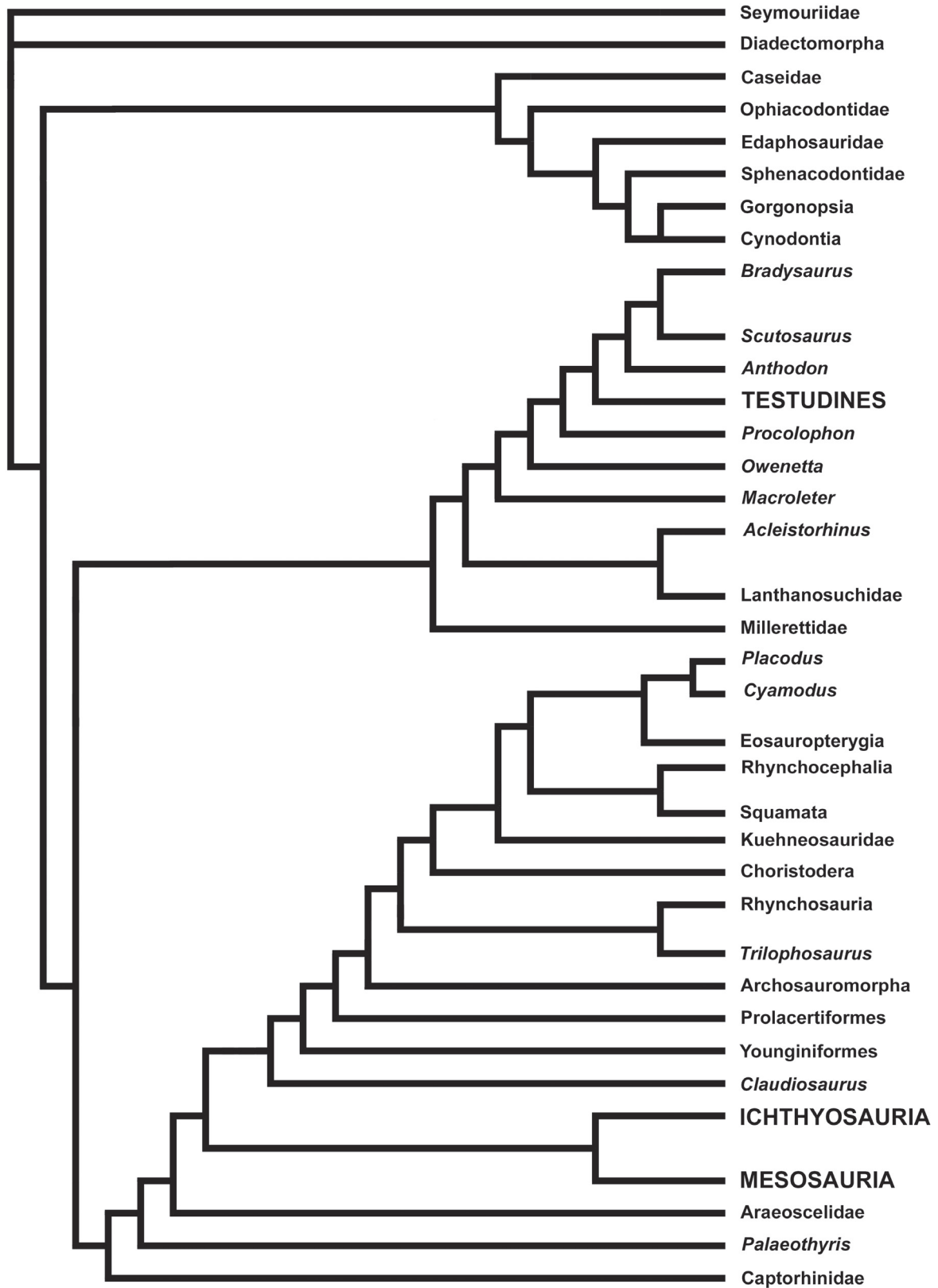


Fig. 1. Cladogram of the Amniota, based on the data matrix of LAURIN & REISZ (1995), including ichthyosaurs. On the following pages the data matrix is provided as a table.

hypothesized as an autapomorphy of the Procolophonomorpha (MODESTO et al. 2009). The metapsid temporal fenestra has, however, not been recorded in Parareptilia so far (but it is equally not found in Diapsida).

Arguments for both hypotheses on the origin of ichthyosaurs have been discussed in the recent literature (CALDWELL 1996; MAISCH 1997a, 1998c; MAISCH & HUNGERBÜHLER 1997b, 2001; MAISCH & MATZKE 2002b; MOTANI et al. 1998; MOTANI 1999c, 2000a; MÜLLER 2003, 2004). Both views find some support by introducing ichthyosaurs into the two analyses.

The opinion that ichthyosaurs are nested within diapsids is suggested by the analysis of the data matrix of DE BRAGA & RIEPPEL (1997) (see MOTANI et al. 1998) respectively its modified version published by RIEPPEL &

REISZ 1999 (this study). The analysis (a heuristic search was considered appropriate due to the size of the matrix) was carried out with the aid of PAUP*4b10 for Windows (SWOFFORD 2002). It resulted in a single most parsimonious tree with a length of 704 steps, a consistency index of 0.30 and a retention index of 0.643 (Fig. 1). The homoplasy index of 0.70 is remarkable as being very high.

As MOTANI et al. 1998 and I have used slightly different codings for the Ichthyosauria, it is no surprise that they also hold somewhat different positions in the resulting cladograms. While they appear as sister-group of the Sauria in the study of MOTANI et al. 1998, they are here the sister-group of the Mesosauria and, together with those, form the sister-group of the Neodiapsida. The mesosaurs were here introduced for the first time into the data matrix

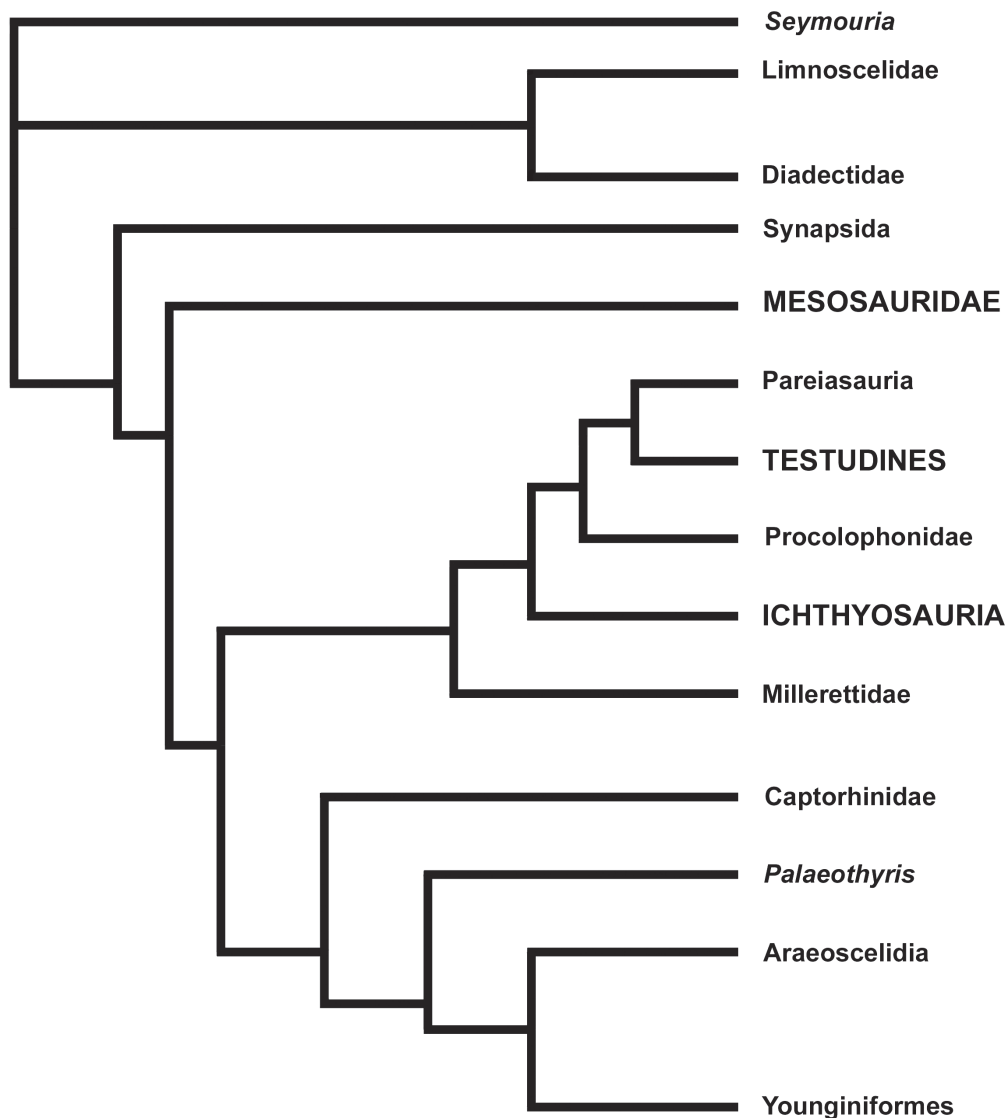


Fig. 2. Cladogram of the Amniota, based on the data matrix of REISZ & RIEPPEL (1999) including mesosaurs and ichthyosaurs.

of DE BRAGA & RIEPPEL (1997). Their inclusion may also have affected the topological position of ichthyosaurs and aid in explaining the differences between the two cladograms (MÜLLER 2004 provided interesting observations on the effects of taxon inclusion and exclusion in large amniote data matrices that are quite comparable).

The idea that ichthyosaurs have their origin among the Parareptilia is supported by their inclusion into the data matrix of LAURIN & REISZ (1995), as modified by MODESTO (1999). A “branch and bound”-analysis with the aid of PAUP*4b10 for Windows resulted in a most parsimonious tree with a length of 318 steps, a consistency index of 0.5377 (without uninformative characters: 0.5304), and a retention index of 0.574 (Fig. 2). Again, the homoplasy index of 0.4623 (without uninformative characters: 0.4696) is quite high. In the resulting cladogram, ichthyosaurs are the sister-group of a clade formed by Procolophonia (Pareiasauria + Testudines). The monophyly of the parareptilian groups including ichthyosaurs and turtles, seems to be quite well supported in this analysis. The clade including pareiasaurs, procolophonians and turtles has a bootstrap value of 100, that including also ichthyosaurs one of 78, they both belong to the best supported clades. All other groups are significant at the 50% threshold (which is not even remotely true for the analysis of RIEPPEL & REISZ 1999). The mesosaurs, however, do not show any closer relations to ichthyosaurs in this phylogeny, and their similarities must in this case be explained as convergences due to secondary aquatic adaptations.

Of course it may be regarded as questionable whether this result still has any value with view to the massive amount of new data that has accumulated on parareptiles since the publication of the analysis of LAURIN & REISZ (1995) 15 years ago. In the case of potential diapsid interrelationships of ichthyosaurs, the work of MÜLLER (2003, 2004) has provided more modern and exhaustive data, but parareptilian relationships of ichthyosaurs have, a priori, not been considered in any recent analysis. In order to do this (and to counter potential arguments that parareptilian relationships of ichthyosaurs may only be supported by outdated data-sets) the latest parareptile data matrix of MODESTO et al. (2009), which basically depends on the work of MÜLLER & TSUJI (2007), was analysed as well, including ichthyosaurs. A heuristic search with PAUP* 4b10 yielded 30 most parsimonious trees (3 in the original analysis without ichthyosaurs) with a length of 428 steps (400 originally), a CI of 0.30995 (0.43 originally) and an RI of 0.6743. In this analysis, ichthyosaurs form a polytomy with *Eunotosaurus*, the millerettids and the Procolophonomorpha (including *Australothyris*, the Lanthanosuchoidea, Bolosauridae, *Nyctiphruetus* and Procolophonia, which encompasses the Pareiasauridae). Ichthyosaurs show no close relationships to the eureptilian and diapsid taxa included (*Palaeothyris*, Captorhinidae, Areaoscelid-

ia, Younginiiformes). Again there is also no close relationship of ichthyosaurs to mesosaurs, as well. Ichthyosaurs therefore hold a very similar position in the cladogram resulting from the data matrix of MODESTO et al. (2009) respectively MÜLLER & TSUJI (2007) than they do in the original analysis of LAURIN & REISZ (1995).

The coding for ichthyosaurs for the analysis of MODESTO et al. (2009) is: 01010 10001 01111 20000 11100 10120 11201 10001 0101? 00010 ???00 11001 10000 21101 01010 0?010 01001 00000 10010 11100 02010 00?01 01001 01100 02001 10000 10011 00.

A disadvantage of the analysis of LAURIN & REISZ (1995) is, as it was also noted by RIEPPEL & REISZ (1999), that it has its focus on basal amniotes and parareptiles, as do more recent analyses like those of MÜLLER & TSUJI 2007 and MODESTO et al. 2009, which basically expanded on the original work of LAURIN & REISZ (1995). RIEPPEL & REISZ (1999) fail to notice, however, that the analysis of DE BRAGA & RIEPPEL (1997) suffers from similar and probably at least as significant problems. In its original form it was used to elucidate the relationships of sauropterygians and placodonts within the Diapsida, and therefore naturally had a focus on characters found in secondarily aquatic diapsids (RIEPPPEL 1994). Although the matrix of DE BRAGA & RIEPPEL (1997) is much more exhaustive, it nevertheless is based on and evolved from an original data set that takes the morphological peculiarities of aquatic diapsids into special account (and the same holds true to a certain extent for the more recent and more inclusive analyses of MÜLLER 2003, 2004).

In the view of these facts it is very tempting to assume that the phylogenetic position of notoriously difficult and highly autapomorphic groups such as the ichthyosaurs and turtles in these analyses does not remain unaffected by their respective genesis, original aim and particularly the choice of taxa (see also MÜLLER 2004). That the matrix of DE BRAGA & RIEPPEL (1997) puts much emphasis on convergences of secondarily aquatic amniotes is probably best illustrated by the unconventional position of mesosaurs (Fig. 2). That the choice of taxa is a considerable problem of both analyses is undeniably shown by the shifting position of turtles in both, as soon as the ichthyosaurs are included as a terminal taxon. The fact that the inclusion of a single taxon, with data sets staying completely identical to the original analyses otherwise, affects the results in such a remarkable way, is certainly noteworthy.

At any rate, regardless which analysis is used, be it that of MOTANI et al. 1998 or those carried out here, they all invariably result in a sister-group relationship of turtles and pareiasaurs, as LEE (1996, 1997a, b) advocated it. This is in strong contrast to the suggestions of RIEPPEL & DE BRAGA (1996), DE BRAGA & RIEPPEL (1997), RIEPPEL & REISZ (1999), PLATZ & CONLON (1997), HEDGES & POLING (1999), CAO et al. (2000), ZARDOYA & MEYER (2001) or LI et al.

(2008), among others, who, on the basis of morphological and molecular data, assume a diapsid origin of turtles (see, however, WERNEBURG & SÁNCHEZ-VILLAGRA (2009) on recent developmental evidence that advocates a more basal position of turtles). The analysis of RIEPPEL & REISZ (1999) fails to satisfactorily demonstrate such a relationship, as shown above, as did the original analysis of DE BRAGA & RIEPPEL (1997), as shown by LEE (2001). Concerning the DNA-data I have always asked myself what the DNA of a parareptile would look like if we were able to analyse it. As these creatures disappeared at the end of the Triassic we will probably never know. However, it must be asked if DNA-data can have that much relevance for the evaluation of the relationships between extant organisms and completely extinct groups, like the pareiasaurs and procolophonians. The inherent difficulty to assess character polarity in DNA-data is another point that must be borne in mind. At any rate, the analysis of DNA will a priori always result in a closest relationship of turtles with one of the extant amniote monophyla, and very probably not the synapsids, which leaves only the Diapsida or one of its subgroups. The relevance of results that are therefore without much of an alternative from the beginning may be questioned in a very general way (see also LEE 2001 for a critical discussion on this topic).

This critique is also applicable to soft-tissue characters. We have almost no idea about the soft-part anatomy of parareptiles. We have no means to judge whether they or one of their subgroups developed structures of, e. g., the musculature and/or the circulatory system similar to those found in archosaurs and turtles. It has recently been suggested that some parareptiles invented an impedance matching ear convergent to other amniotes (MÜLLER & TSUJI 2007). This may be viewed as an indication that we have to be very careful not to overemphasize even complex similarities between extant taxa, and to consider that all characters, even supposedly very unique ones, can be potentially acquired convergently. The data presented here, at any rate, are exclusively supportive of the opinion of LEE (1993, 1994, 1996, 1997a, b, 2001), who considers the turtles as the sister-group of the Pareiasauria within the Parareptilia. They also support – in a more general way – the idea of LAURIN & REISZ (1995), who also regarded turtles as parareptiles, although as the sister-group of the Procolophonia. They are in line with recent suggestions of WERNEBURG & SÁNCHEZ-VILLAGRA (2009), based on developmental evidence, who suggest that turtles may be the sister-group of extant diapsids. I do not declare that I “believe” in a parareptilian origin of turtles. In fact a multitude of recent, largely exclusively molecular analyses strongly points towards a sister-group relationship of turtles and archosaurs, a fact that has to be acknowledged (but see LEE 2001). I only have to state that exclusively morphology-based phylogenetic data sets that alleg-

edly support a diapsid relationship of turtles fail to do so at closer scrutiny.

Getting back to the ichthyosaurs, and to more general problems as well: the remarkable discrepancy between the systematic position of ichthyosaurs in the two analyses (and their derivatives, such as the analyses of MÜLLER 2003, 2004 and MODESTO et al. 2009), as well as the fact that inclusion of ichthyosaurs (respectively ichthyosaurs and mesosaurs) in the analyses alters their original topology to such an extent as to even destroy the formerly best-supported monophyla (like Procolophonia + Testudines of LAURIN & REISZ 1995) makes one suspicious towards the eventual usefulness of these data matrices (and their subsequent extensions) for elucidating the relationships of highly derived and morphologically unique groups. A detailed discussion of these issues is, however, beyond the scope of the present paper, as it would involve a detailed argumentation pro and contra pattern cladistics versus HENNIGIAN phylogenetic systematics.

For the time being the origin and phylogenetic relationships of ichthyosaurs have to be honestly labelled as “unknown”. The results presented here have the single merit that they hopefully demonstrated inherent weaknesses of important and influential analyses that still serve as the basis for morphology-based reconstruction of large-scale amniote phylogeny. Neither do they offer any clue regarding the origin of ichthyosaurs, nor do they contribute anything decisive to the ongoing debate concerning the origin of turtles. But they definitely show that other pattern-cladistic analyses that claimed to do so did not do this either.

In the case of the ichthyosaurs we know that they are amniotes, and that they are not synapsids. That is a certain progress with respect to some previous hypotheses, but a progress that has already been made long ago in pre-cladistic times and actually does not appear like a great achievement. Whether ichthyosaurs are diapsids, and if so, where exactly they have to be placed within the Diapsida, or whether they are parareptiles, and if so, whether they are related to mesosaurs or not, these are questions that remain as unresolved as one hundred years ago. I have severe doubts whether the creation of amniote supermatrices like that of HILL (2005) will help to resolve this issue, and would rather expect useful future results from a more modest, and hopefully more thoughtful, approach towards phylogeny. Personally I would still tend to derive ichthyosaurs from primarily anapsid forms, as I have suggested already in 1997 (MAISCH 1997a), but there is no compelling morphological evidence for either this or the alternative hypothesis of a diapsid origin. The only argument that may have some validity that I can momentarily think of is, that if ichthyosaurs were the sister-group of neodiapsids, their ghost-lineage would be much longer, because in that case the terminus post quem non for their origin would be the Upper Carboniferous. If they were the sister-group of

procolophonians and pareiasaurs (ignoring the turtles for that matter), it only reached back to the Middle Permian. With regard to the fact that the oldest known ichthyosaurs are still Smithian in age, this argument may have at least some weight, as ghost-lineages tend to become less and less credible the longer they get.

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Address of the author:

PD Dr. MICHAEL W. MAISCH, Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany

E-mail: michael.maisch@smns-bw.de

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Tab. 1. (continued)

Taxon	Characters																		
	11	11	11	11	12	12	12	12	12	12	12	13	13	13	13	13	13	13	14
Seymouriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diadectomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cascidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ophiacodontidae	0	0[1]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Edaphosauridae	0	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?
Sphenacodontidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gorgonopsia	1	1	0	0	1	0	0	1	2	0	0	0	1	0	0	0	1	1	0
Cynodontia	1	1	2	0	1	?	?	2	2	0	0	1	1	0	1	0	1	1	1
Captohinidae	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Palaeothyris	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Millerettidae	?	0	0	?	0	0	?	1	1	?	0	0	?	0	1	0	0	0	0
<i>Acleistorhinus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lanthanosuchidae	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Macroleter</i>	0	1	0	?	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0
<i>Bradysaurus</i>	0	1	1	?	1	0	0	0	2	2	0	0	1	0	0	1	1	0	0
<i>Scutosaurus</i>	0	1	1	?	1	0	0	0	2	2	0	0	1	0	0	1	1	0	0
<i>Anthodon</i>	0	2	1	?	1	0	0	2	2	0	0	1	0	0	1	0	0	1	0
<i>Procolophon</i>	0	1	0	?	1	0	0	2	1	0	0	0	1	0	0	1	0	0	0
<i>Owenetta</i>	?	?	?	?	1	0	0	?	1	0	1	?	?	?	?	?	?	?	?
Araucoscelidae	1	0	0	0	1	0	0	1	0	1[2]	0	0	0	0	0	0	0	0	0
<i>Claudiosaurus</i>	?	0	0	1	0	0	1	1	2	1	0	0	1	0	0	0	0	1	?
Younginiiformes	1	?	0	0	0	0	0	1	1	0[2]	0	0[1]	1	0	1	0	0	1	?
Kuehneosauridae	?	0	0	1	0	0	0	1	1	0	1	?	1	1	?	0	0	1	?
Testudines	0	2	2	?	0	1	0[1]	1	2	0[2]	1	0	1	1	0[1]	1	0	0	1
Rhynchocephalia	1	0	0	1	0	0	0	1	2	0	0	0	1	1	0	0	0	1	0[1]
Squamata	1	0	0	1	0	0	1	1	0[2]	1	0	0[1]	1	1	0	0	0	1	0[1]
Choristodera	?	?	0	1	0	0	0	1	0[2]	1	2	?	1	1	0	?	0	0	1
Rhynchosauria	?	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	1	0
Prolacertiformes	1	0	0	1	0	0	0	1	2	0	1	1[2]	1	1	0[1]	0	0	1	?
<i>Trilophosaurus</i>	?	1	0	1	0	0	0	1	2	0	1	0	0	0	0	0	0	1	1
Archosauriformes	1	0[1]	0	1	0	0[1]	0	1	1	1	0	1	1	1	0	0	1	0	0
<i>Placodus</i>	0	0	0	1	1	1	1	1	0	1	2	?	?	?	?	?	?	?	?
<i>Cyamodus</i>	0	0	0	1	1	1	1	1	0	1	2	?	?	?	?	?	?	?	?
Eosauropterygia	0	2	0	1	0	1	0[1]	1	0[1]	0[1]	1[2]	1	1	?	?	?	?	?	?
Mesosauria	0	0	0	1	1	1	1	1	2	1	0	0	1	0	0	0	0	0	0
Ichthyosauria	0	0	0	1	0	0	1	1	2	0	1	1	1	1	0	0	0	0	1

