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The Ichthyosauria

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With 44 figures and 1 table

Abstract

The phylogeny of the Ichthyosauria is investigated on the basis of 128 characters of the cranial and postcranial anatomy. Previous attempts are discussed and, as far as considered appropriate, their results are included in the analysis. Ichthyosaur taxonomy on the suprageneric, generic and specific level is discussed.

The following new suprageneric taxa are introduced: Hueneosauria taxon nov. and Toretocnemidae fam. nov. The following new genera and species are erected: *Phantomosaurus* gen. nov. for "*Shastasaurus*" *neubigi*, *Callawayia* gen. nov. for "*Shastasaurus*" *neoscapularis*, and *Rotundopteryx hulkei* gen. et sp. nov. for postcranial material previously ascribed to the omphalosaurid *Pessopteryx nisseri*. An overview of all valid genera and species of ichthyosaurs, including modern diagnoses, is presented.

The genera *Himalayasaurus*, *Tibetosaurus*, *Pessosaurus*, *Macropterygius* and *Pachygonosaurus* are dismissed as nomina dubia, the ichthyosaurian status of *Isfjordosaurus* is questioned. The genus *Protoichthyosaurus* is regarded as a junior subjective synonym of *Ichthyosaurus*. *Excalibosaurus* is referred to *Eurhinosaurus*. *Otschevia* is referred to *Brachypterygius*. *Plutoniosaurus* and *Simbirskiasaurus* are referred to *Platypterygius*, and *Paraophthalmosaurus*, *Undorosaurus*, *Yasykovia*, *Khudiakovia* and *Mollesaurus* are referred to *Ophthalmosaurus*. The occurence of the genus *Mikadocephalus,* hitherto exclusively known from the Grenzbitumenzone of Monte San Giorgio, in the Tschermakfjellet Formation of Spitsbergen is demonstrated.

The new phylogeny agrees well with hitherto published versions in general, but differs in many important details. *Thaisaurus*, ignored in previous works, appears to be the most basal ichthyosaur known. The mixosaurids are clearly less derived than the cymbospondylids. *Wimanius* is their sister taxon. The shastasaurids are not monophyletic but form a set of successive outgroups to the Parvipelvia. *Toretocnemus* and *Qianichthyosaurus* form a monophyletic family Toretocnemidae at the base of the Longipinnati. The post-Triassic ichthyosaurs form a very stable monophylum, the Neoichthyosauria Sander, 2000, the temnodontosaurids are the most basal forms of this clade whereas *Suevoleviathan* is the sister-group of the Thunnosauria. *Ichthyosaurus* is less derived than *Stenopterygius*. *Caypullisaurus* and *Ophthalmosaurus* are sister-taxa.

Zusammenfassung

Die Stammesgeschichte der Ichthyosaurier wird aufgrund von 128 Merkmalen des Schädel- und Postcranialskeletts untersucht. Frühere Versuche zum Thema werden diskutiert und deren Ergebnisse, soweit angemessen, in der Analyse mitberücksichtigt. Die Taxionomie der Ichthyosaurier auf der supragenerischen, generischen und spezifischen Ebene wird diskutiert.

Die folgenden neuen supragenerischen Taxa werden eingeführt: Hueneosauria taxon nov. und Toretocnemidae fam. nov. Die folgenden neuen Genera und Spezies werden aufgestellt: *Phantomosaurus* gen. nov. für "*Shastasaurus*" *neubigi*, *Callawayia* gen. nov. für "*Shastasaurus*" *neoscapularis* und *Rotundopteryx hulkei* gen. et sp. nov. für postcraniales Material, das bisher dem Omphalosauriden *Pessopteryx nisseri* zugeordnet wurde. Eine Übersicht aller validen Genera und Spezies der Ichthyosaurier mit modernen Diagnosen wird gegeben.

Die Genera *Himalayasaurus*, *Tibetosaurus*, *Pessosaurus*, *Macropterygius* und *Pachygonosaurus* sind nomina dubia. Der Status von *Isfjordosaurus* als Ichthyosaurier wird in Frage gestellt. Die Gattung *Protoichthyosaurus* wird als jüngeres subjektives Synonym von *Ichthyosaurus* betrachtet, *Excalibosaurus* wird zu *Eurhinosaurus* und *Otschevia* zu *Brachypterygius* verwiesen. *Plutoniosaurus* und *Simbirskiasaurus* werden zu *Platypterygius* gestellt. *Paraophthalmosaurus*, *Undorosaurus*, *Yasykovia*, *Khudiakovia* und *Mollesaurus* werden zu *Ophthalmosaurus* verwiesen. Das Vorkommen von *Mikadocephalus*, bisher ausschliesslich aus der Grenzbitumenzone des Monte San Giorgio bekannt, wird in der Tschermakfjellet Formation von Spitzbergen nachgewiesen.

Die neue Phylogenie stimmt generell recht gut mit früheren Versuchen überein, unterscheidet sich aber in vielen wesentlichen Details. *Thaisaurus*, von früheren Bearbeitern weitgehend ignoriert, erweist sich als basalster bekannter Ichthyosaurier. Die Mixosauriden sind weit weniger abgeleitet als die Cymbospondyliden. Ihr Schwestertaxon ist *Wimanius*. Die Shastasauriden sind kein Monophylum, sondern repräsentieren eine Reihe von Außengruppen der Parvipelvia. *Toretocnemus* und *Qianichthyosaurus* bilden eine monophyletische Familie Toretocnemidae an der Basis der Longipinnati. Die post-Triassischen Formen gehören einem sehr gut begründeten Monophylum Neoichthyosauria Sander, 2000 an, dessen basalste Familie die Temnodontosauriden sind. *Suevoleviathan* ist die Schwestergruppe der Thunnosauria. *Ichthyosaurus* ist weniger abgeleitet als *Stenopterygius*; *Caypullisaurus* und *Ophthalmosaurus* sind Schwestertaxa.

Preface

Der *Ichthyosaurus*

Es rauscht in den Schachtelhalmen,
verdächtig leuchtet das Meer,
da schwimmt mit Tränen im Auge
ein *Ichthyosaurus* daher.

Ihn jammert der Zeiten Verderbnis,
denn ein sehr bedenklicher Ton
war neuerlich eingerissen
in der Liasformation.

Der *Plesiosaurus*, der Alte,
er jubelt in Saus und Braus,
der *Pterodactylus* selber
flog neulich betrunken nach Haus.

Der *Iguanodon*, der Lümmel,
wird frecher zu jeglicher Frist,
schon hat er am hellen Tage
die Ichthyosaura geküsst.

Mir ahnt eine Weltkatastrophe,
so kann es ja länger nicht gehn;
was soll aus dem Lias noch werden,
wenn solche Dinge geschehn.

So klagt der *Ichthyosaurus*,
da ward es ihm kreidig zumut;
sein letzter Seufzer verhallte
im Qualmen und Zischen der Flut.

Es starb zu derselbigen Stunde
die ganze Saurierei,
sie kamen zu tief in die Kreide,
da war es natürlich vorbei.

Und der uns hat gesungen
dies petrefaktische Lied,
der fand's als fossiles Albumblatt
auf einem Koprolith.

Joseph Viktor von Scheffel, 1856

Contents

1. Introduction

The ichthyosaurs, a major group of superficially fish- or dolphin-like secondarily aquatic amniotes of the Mesozoic, are known from a wealth of well-preserved material from the Lower Triassic to the early Upper Cretaceous (Cenomanian), including numerous virtually complete skeletons, some with soft tissue preservation or the remains of embryos in the body cavities of pregnant females. Isolated bones and even some skeletons have been known to paleontologists since the 18th century and the first more complete remains were described and figured at the beginning of the 19th century.

The Staatliches Museum für Naturkunde, Stuttgart (SMNS) holds one of the world's largest collections of ichthyosaur specimens, including numerous holotypes and uniquely well-preserved skeletons, particularly from the Middle Triassic and Lower Jurassic of southern Germany, but also from other parts of the world. This study was therefore initiated by our work in the Stuttgart collection as well as in the nearby Tübingen collection (GPIT), which is the second largest in Germany. The data obtained there were then complemented by personal studies of numerous ichthyosaur specimens in the collections of other institutions and – in a few cases – by the literature.

From very early in the history of research on the ichthyosaurs it has been clear that they form a particular "order" of fossil tetrapods, not easily comparable even to other secondarily aquatic "reptiles", like the sauropterygians, and that their mixture of apparently primitive and highly derived characters makes it hard to place them into existing classifications. Influenced by religious belief, but also by accurate anatomical observation, 19th century English author Thomas Hawkins (1840) even went so far as to erect a new Regnum for the ichthyosaurs (and plesiosaurs as well), which he called the "Gedolim Taninim".

Because of the puzzling problem of the position of ichthyosaurs within vertebrates, the interest of phylogenetically oriented workers mainly focussed on the origin of the group, and numerous papers have been written, proposing numerous amniote and non-amniote groups as possible ichthyosaur ancestors. The most recent contributions to this discussion are those by MAISCH (1997a, 1998b) and MOTANI et al. (1998). Whereas MAISCH advocated a non-diapsid and probably parareptilian origin of ichthyosaurs, based on several important characters of the cranial skeleton which seem to contradict a close relationship between ichthyosaurs and diapsids, MOTANI et al. (1998) performed a much more inclusive cladistic analysis which resulted in ichthyosaurs being classified as a primitive diapsid group within the Neodiapsida.

The purpose of this paper is not to enter into this long-standing discussion, but to propose a robust in-group phylogeny for the Ichthyosauria. The goal of this excercise is twofold: first, we want to set up a workable framework of ichthyosaurian interrelationships which can be used as a reliable basis for further investigations on these animals, e. g. on their palaeobiogeography, functional morphology or the evolution of particular anatomical structures. Second, we want to clearly establish character polarity in ichthyosaurs and thus open the way for a detailed reconstruction of the ichthyosaurian grundplan, which is certainly needed before any further meaningful research on the origin of ichthyosaurs can be carried out.

2. Previous work

Ichthyosaur in-group phylogeny has, so far, received little attention. The first published explicitly phylogenetic systematic attempt, using common derived characters (synapomorphies) to indicate relationships was made by MAZIN (1982). Unfortunately MAZIN's phylogeny was to a large extent based on only one complex of the skeleton, namely the forefins and more explicitly so the meta-and autopodial parts (number of fingers and the like). This is a result of the long-standing tradition, going back to LYDEKKER (1889), KIPRIJANOFF (1881) and VON HUENE (1922), who divided the ichthyosaurs into two subgroups, one with a normal or supernormal number of digits in the forefin, of which two articulated with the intermedium of the proximal tarsal row (Latipinnati VON HUENE, 1948), and one with a usually subnormal number of digits, of which only one articulated with the intermedium (Longipinnati VON HUENE, 1948). This simple subdivision has been used right into the 1970ies (MCGOWAN 1972b, 1974a, b) and even today is still found in some works, although, particularly after the studies of MCGOWAN (1976) and APPLEBY (1979) it has become clear and generally accepted that this simple typological and quite artificial classification scheme does not reflect natural relationships within Ichthyosauria.

GODEFROIT (1993a, 1994) was the first to question MAZIN's phylogeny (which was repeated, rather uncritically, by RIESS 1986) by introducing characters of other parts of the skeleton, in this case the skull and pelvic girdle, to resolve the three-taxon-statement *Ichthyosaurus*, *Stenopterygius* and *Ophthalmosaurus*. It was important that he could show that, despite apparently closer resemblances in forefin morphology between *Ichthyosaurus* and *Ophthalmosaurus*, overall information supported a sister-group relationship between *Ophthalmosaurus* and *Stenopterygius*. This analysis was somewhat extended and the results corroborated by FERNÁNDEZ (1999).

DAL SASSO & PINNA (1996) published a data matrix and phylogenetic analysis of the large-growing Middle to Upper Triassic ichthyosaurs usually grouped as Shastasauridae. It must be noted that this analysis is mainly the result of the late J. M. CALLAWAY's Ph. D. Thesis which, unfortunately, remained unpublished. The main shortcoming of this analysis is, that, except *Grippia longirostris*, it did not take any of the more plesiomorphic Triassic and particularly none of the post-Triassic ichthyosaurs into account, but only "shastasaurs", including several very ill-known taxa, such as *Pessosaurus polaris* HULKE, 1873, a taxon recently regarded as a nomen dubium by SANDER & FABER (1998). The outcome therefore, of course, had to be a monophyletic Shastasauridae. Classification done by DAL SASSO & PINNA (1996) is not in accordance with phylogenetic taxonomy. The subfamily Cymbospondylinae which they propose for *Himalaysaurus*, *Shonisaurus* and *Cymbospondylus* is paraphyletic in their cladogram.

A more inclusive attempt to resolve ichthyosaur in-group phylogeny was published by MAISCH & MATZKE (1997a) in the course of the description of the newly discovered genus *Mikadocephalus*. This data matrix contained some uninformative (autapomorphous) characters (in order to establish the monophyly of the terminal generic taxa) and two have turned out to be non-independent (MOTANI 1999b). The codings for *Mixosaurus* have in part turned out to be incorrect because of the then very limited knowledge of the genus. Nevertheless, the resulting phylogeny was the first to be based largely on characters of the cranial skeleton and to include both Triassic and post-Triassic, well-known ichthyosaurs. The Jurassic ichthyosaurs were demonstrated to be a robust monophylum, with the included Triassic taxa *Mikadocephalus*, *Cymbospondylus* and *Mixosaurus* as successive sister groups. Within Jurassic forms the old longipinnate-latipinnate orthodoxy was completely abandoned and the arch-longipinnate genus *Temnodontosaurus* was shown to be the most plesiomorphic post-Triassic ichthyosaur, whereas, corroborating GODEFROIT's (1993a, 1994) results, the longipinnate *Stenopterygius* and the latipinnates *Ophthalmosaurus icenicus* and *Ophthalmosaurus natans* were grouped in one family.

A small analysis of the relationships of post-Triassic ichthyosaurs was done by MAISCH (1998a), but it relied on a very small set of characters (some of which were again uninformative) insufficient to resolve the phylogeny completely. The most important results were that, again, *Temnodontosaurus* was more primitive than any of the latipinnate forms and that two monophyletic family-group taxa, the Leptonectidae (containing *Leptonectes* and *Eurhinosaurus*) and the Stenopterygiidae (containing *Stenopterygius* and *Ophthalmosaurus*) could be recognized.

MOTANI (1998b) did a small analysis of the relationships of *Utatsusaurus*, *Grippia* and *Mixosaurus* and was able to demonstrate that the latter two are more closely related to each other than either is to *Utatsusaurus*. This analysis suffers from the shortcoming that, again, it is exclusively based on forefin characters, but its results are corroborated by the analyses of more extensive data sets (MOTANI 1999b and this study).

MOTANI (1999b) published a very inclusive phylogenetic analysis of the Ichthyosauria. It was based on a set of 105 characters and included the majority of well-known ichthyosaur taxa. As will be seen, his results are at variance with those presented here in several important points, but there are also a very large number of significant agreements. It should be noted in this context, that the initial phylogenetic studies of us were uninfluenced by those of MOTANI and vice versa. Nevertheless, a significant number of characters have been found to be identical or at least very similar in the two analyses. Several characters of MOTANI (1999b) have been taken from his phylogeny as they were not included in our data matrix before publication of his paper, and we have indicated this in every instance. Several characters of MOTANI (1999b) were found by us to be unsuitable for use in our phylogenetic analysis for different reasons. These are treated in a separate section below and a justification for the exclusion of these characters is given in every case. Some of the codings of characters for individual taxa are also at variance, as expectable, and we have discussed this as well in the character discussion below. By the synthesis of our own newly found characters and those proposed by the previous workers, particularly MOTANI (1999b), we have arrived at a set of 128 characters, of which about 40 are essentially new. This is the most inclusive, and therefore probably the most reliable attempt to resolve ichthyosaur phylogeny carried out so far. By no means can it be regarded as the final word on the question, but it is certainly a major advance towards a robust and fully resolved phylogeny of the Ichthyosauria, the most ancient and most extraordinarily adapted of all marine "reptiles", living or fossil.

3. Methods and material

Characters chosen were not weighted. Reversals and convergencies were treated as equally likely. Character polarity was defined by using the basal terrestrial tetrapods *Limnoscelis*, *Captorhinus* and the early diapsid *Youngina* as outgroups for comparison. The data set was analyzed by implementation of the software package Paup* 4.0b4a for Windows (SWOFFORD 1998). The data were subjected to both a branch and bound and a heuristic search using the options ‚stepwise addition' and ‚random search' with 10000 replicates. In all cases six most parsimonious trees were obtained which were subjected to a bootstrap analysis with the heuristic search option in effect and with 1000 replicates to evaluate the statistical significance of each clade.

33 ichthyosaur genera were found to be so completely known or showing such important character states that they could be included in the phylogenetic analysis, whereas the others are too incompletely known or described, showing such a small percentage of characters that their inclusion in the analysis would probably be premature and yielding rather insignificant results. The genera chosen, as well as those ichthyosaur genera which were excluded, are all discussed below in the section on "The genera of ichthyosaurs". The majority of taxa was personally investigated by at least one of us, largely based on original material, but in some cases only by the aid of high fidelity casts. The taxa and specimens investigated personally for this study are listed here in stratigraphical order:

Lower Triassic

Utatsusaurus hataii (casts of holotype and additional specimens, courtesy of Dr. R. MOTANI)
Grippia longirostris (casts of holotype – lost in second world war – and additional specimens, courtesy of Dr. R. MOTANI)
Chaohusaurus geishanensis (original material at Nanjing and Beijing, including holotype)
Parvinatator wapitiensis (cast of holotype, courtesy of Dr. E. L. NICHOLLS)
Rotundopteryx hulkei (Original material at Paris)

Middle Triassic

Mixosaurus cornalianus (original material at Zürich, Tübingen, Stuttgart, Berlin, London)
Mixosaurus kuhnschnyderi (original material at Zürich, including holotype)
Phalarodon nordenskioeldii (personal observation of original material at Berkeley, Zürich, Paris)

Contectopalatus atavus (personal observation of specimens in Tübingen, Stuttgart, Ingelfingen, Berlin, including lectotype at Tübingen)
Wimanius odontopalatus (holotype at Tübingen)
Cymbospondylus petrinus (original material at Berkeley)
Cymbospondylus buchseri (material at Zürich, including holotype)
Phantomosaurus gen. nov. *neubigi* (holotype at Munich)
Mikadocephalus gracilirostris (holotype at Tübingen and material at Zürich)

Upper Triassic

Toretocnemus californicus (holotype at Berkeley)
Toretocnemus zitteli (holotype at Berkeley)
Qianichthyosaurus zhoui (privately held specimen)
Shastasaurus alexandrae (material at Berkeley, including holotype and types of *S. osmonti* and *S. altispinus*)
Callawayia gen. nov. *neoscapularis* (cast of holotype, courtesy of Dr. C. McGowan and Dr. R. Motani)
Shonisaurus popularis (material at Berlin in Nevada)
Californosaurus perrini (material at Berkeley, including holotype)

Lower Jurassic

Temnodontosaurus trigonodon (material at Tübingen, Stuttgart, Holzmaden, Dotternhausen, Coburg, Ansbach, Berlin, Munich, Paris, Banz, including holotype at Banz)
Temnodontosaurus platyodon (material at London, Bristol, Tübingen, Stuttgart, Paris)
Stenopterygius quadriscissus (numerous specimens, e. g. in Tübingen and Stuttgart, including lectotype at Tübingen)
Stenopterygius hauffianus (numerous specimens, e. g. Tübingen, Stuttgart, including lectotype at Tübingen)
Stenopterygius longifrons (numerous specimens, e. g. Tübingen, Stuttgart)
Stenopterygius megalorhinus (numerous specimens, e. g. Tübingen, Stuttgart, Berlin, Paris)
Leptonectes tenuirostris (specimens at Tübingen, Berlin)
Leptonectes solei (holotype at Bristol)
Excalibosaurus costini (holotype at Bristol)
Eurhinosaurus longirostris (many specimens at Stuttgart, Tübingen, Holzmaden, Dotternhausen, Munich, Paris, London)
Ichthyosaurus communis (specimens in London, Bristol, Stuttgart, Tübingen, Göttingen, Hannover)
Ichthyosaurus intermedius (specimens at Bristol, Stuttgart)
Ichthyosaurus breviceps (specimen at Tübingen, undescribed)
Ichthyosaurus cf. *I. conybeari* (specimen at Coburg, undescribed)
Suevoleviathan integer (specimens at Tübingen, Stuttgart, Coburg)
Suevoleviathan disinteger (holotype in Stuttgart, specimen in Berlin)

Middle to Upper Jurassic

Aegirosaurus leptospondylus (specimens in Stuttgart and Munich)
Brachypterygius extremus (specimen in Bristol)
Ophthalmosaurus icenicus (specimens in Tübingen, Stuttgart, London, Frankfurt)

Cretaceous

Platypterygius hercynicus (holotype in Halle)
Platypterygius sp. (specimen in Munich)

Of the genera included in the phylogenetic analysis, we had to rely exclusively on the literature only in the cases of *Thaisaurus* (Mazin et al. 1991), *Hudsonelpidia* (McGowan 1991, 1995), *Macgowania* (McGowan 1991, 1996a), and *Caypullisaurus* (Fernández 1997, 1998)

Institutional abbreviations

BMNH – Natural History Museum, London.
GPIT – Institut und Museum für Geologie und Paläontologie der Universität Tübingen.
SMNS – Staatliches Museum für Naturkunde Stuttgart.
PIMUZ – Paläontologisches Institut und Museum der Universität Zürich.
ROM – Royal Ontario Museum, Toronto.
TMP – Tyrrell Museum of Paleontology, Drumheller, Alberta.
UCMP – University of California Museum of Paleontology, Berkeley.

4. Character discussion

For the analysis we chose only such characters which show little intraspecific variation in ichthyosaur genera and little individual variation in ichthyosaur species. We also avoided to include characters which are strongly affected by ontogenetic changes although this was not always possible. When relevant ontogenetic changes of characters have been recorded, this is explicitly stated in the character discussions below. We largely did not use proportional characters of the cranial skeleton, as these are variable even within well-established ichthyosaur genera, but we chose to include several proportional characters of the postcranium, which were found to be more constant, probably because they are related to fundamental changes in the pattern of locomotion.

As ichthyosaurs are secondarily aquatic animals and at least the derived members of the group certainly used an axial suboscillatory or even axial oscillatory mode of locomotion, using the well-developed lunate tailfin as means of propulsion (BRAUN & REIF 1985; REIF & WEISHAMPEL 1986; MCGOWAN 1992; LINGHAM-SOLIAR & REIF 1998), many parts of the skeleton, particularly the girdles and limbs, show a large amount of reduction, either in size or complexity of the individual elements. It was therefore impossible to avoid the inclusion of a large amount of characters which may to a certain extent be related to the secondarily aquatic adaptation of ichthyosaurs and are at closer inspection reductional characters. As there is no doubt that the ichthyosaurs are monophyletic, and as it has to be assumed that adaptation to living in the marine environment increased during the phylogeny of the group, this is probably not so much a problem for the assessment of ichthyosaur ingroup phylogeny. It clearly is problematic if one wants to discuss ichthyosaur origins, but this is beyond the scope of the present paper.

4. 1. Characters of MOTANI (1999b) excluded from the analysis

Most of the characters which were introduced by MOTANI (1999b) are also found – at least in a modified form – in our analysis. If formulations of characters were found to be at variance, we usually stuck to our own definitions except in a few cases. A minor number (21) of MOTANI's characters were, however, excluded from the present analysis, because of a variety of reasons. Nine characters (11, 20, 21, 24, 36, 50, 51, 74, and 78 of MOTANI) are useful only if one choses the same outgroup taxa as MOTANI (1999b). They define relationships within these outgroup taxa respectively between them and ichthyosaurs. They have in themselves no bearing on ichthyosaur ingroup phylogeny and exclusion of these characters from our analysis therefore does not alter the results for the ingroup.

Two characters employed by MOTANI were at closer inspection found to be correlated. These are characters 57 (correlated to character 75) and character 98 (correlated to character 96). They are correlated in such a way that the derived state for character 57 always implies the derived state for character 75, and the derived state for character 98 always implies the derived state for character 96. Characters comparable to these have been included in our analyis but only one of each of the correlated group with simplified definition.

One character (33) is an autapomorphy for the ichthyosaur clade here regarded as a single genus *Eurhinosaurus*, and therefore redundant (uninformative) for our analysis. Its exclusion does not change the topology.

Another character (66) was also omitted, as the two alternative derived states are only encountered in one genus each (*Shastasaurus* and *Ichthyosaurus* respectively) and the character is therefore uninformative. Furthermore the character is extremely variable in *Ichthyosaurus* (compare e. g., MCGOWAN 1974b, where the derived state is present in the right, but the plesiomorphic state in the left forefin of the same individual).

Three characters (3, 65, 73) have been found to show considerable variation within genera and even species, and therefore do not meet the criteria for character eligibility enumerated above. Character 3 (presence or absence of maxilla-naris contact) is, according to our observations, coded incorrectly for *Eurhinosaurus* (0 instead of 1) and *Ophthalmosaurus* (1 instead of 0). The character is variable intragenerically within *Suevoleviathan*, and intraspecifically variable in *Stenopterygius quadriscissus.* As this character was originally introduced by ourselves (MAISCH & MATZKE 1997a) we feel even more justified to exclude it from the new analysis. Its inclusion (with the corrections enumerated above) would not change tree topology. Character 65 (anterior notch of radial absent or present) is intragenerically and intraspecifically variable, e. g. in *Stenopterygius*. Its very patchy distribution (cf. codings in MOTANI 1999b) speaks against a high phylogenetic information content, anyway, and its exclusion does not change the topology.

The derived state of character 73 (Manual digits S4–5 present) is autapomorphous for *Suevoleviathian* and convergently shown by some individuals of *Stenopterygius*. It is therefore an individual variation within this latter genus with no phylogenetic information content.

Characters 34 (snout extremely slender) and 54 (humerus relative width) are unfortunately not clearly defined, as it remains unclear what is implied by the terms “extremely slender” and “relative width” and they were therefore also excluded.

Character 5 (absence of nasal-naris contact) was excluded for two reasons. First it is correlated to the presence of a very long processus supranarialis of the premaxilla (MOTANI’s character 1), second it is only unequivocally known in *Cymbospondylus*. Whether the specimen UCIP 27141–27146, interpreted as *Shonisaurus* by MOTANI (1999b) really belongs to that genus is questionable. A different interpretation is favoured by other authors (CALLAWAY & MASSARE 1989; MAISCH 2000), who attribute it to *Shastasaurus*. As this specimen is therefore apparently not unequivocally identifiable at the generic level, the coding for *Shonisaurus* is doubtful and the character is essentially an autapomorphy of *Cymbospondylus* and therefore redundant at the present state of knowledge.

A few characters are more problematic than these, which have been excluded for rather simple reasons. These remaining characters refer to interpretations of certain skeletal structures by MOTANI, which we interpret differently.

Character 13 claims an entrance of the squamosal into the margin of the temporal fenestra in *Utatsusaurus* and *Shastasaurus*. Preservation of the available skull material of *Utatsusaurus* is in our opinion insufficient to be certain about this character. In *Shastasaurus*, as demonstrated elsewhere (MAISCH 2000) the squamosal is clearly separated from the temporal fenestra. The skull reconstruction presented by MOTANI (1999b, figs. 2F, 3F) is incorrect in this point. In his skull reconstruction of *Cymbospondylus petrinus*, MOTANI (1999b, figs. 2C, 3E) shows an enormous contribution of the squamosal to the temporal fenestra, nevertheless *Cymbospondylus* is coded for the derived state in his data matrix. The coding is correct, whereas the reconstruction is wrong in this point (MAISCH 2000), there is no squamosal-temporal contact in *Cymbospondylus*. The loss of the squamosal in *Ichthyosaurus* is a paleontological myth (see MAISCH 1998b; MAISCH & MATZKE 2000 b), and the loss of this element in *Platypterygius* – if true – is therefore an uninformative autapomorphy of this genus. In the view of these facts, we decided to omit this character.

Character 23 refers to a lack of contact between jugal and quadratojugal in basal ichthyosaurs, which was later acquired as a synapomorphy by the more highly derived forms. We see no clear evidence from the published accounts or our own observations, that there is a lack of contact between these two bones in any known ichthyosaur. *Utatsusaurus* and *Grippia* are not well enough preserved to be certain about the structure of this extremely difficult region of the ichthyosaur skull, which has posed interpretation problems even in exceedingly well preserved material for a long time (MAISCH 1997a). Furthermore, a contact between jugal and quadratojugal is described in some other Lower Triassic ichthyosaurs (MAZIN 1982; NICHOLLS & BRINKMAN 1995; MAISCH 1998b; in press b). The character was therefore excluded, although it agrees with the phylogeny proposed here.

Character 48 (orientation of scapular axis and glenoid facet) suffers in our opinion from a misunderstanding of homologies of the ichthyosaur scapula. MOTANI assumes that the blade of derived ichthyosaur scapulae is homologous to the posterodorsal portion of the plesiomorphic ichthyosaur scapula (MOTANI 1999b, fig. 4). There is, however, in our view little evidence for this assumption. In our opinion the scapular blade of derived ichthyosaurs is homologous to the central portion of the plesiomorphic ichthyosaur scapula, whereas the anterior and posterior extensions are reduced. The scapula of *Shastasaurus alexandrae* shows a perfectly intermediate stage between the two extremes, in which part of the anterior (preglenoidal) and posterior (postglenoidal) portions are retained, but the shape of the derived ichthyosaur scapula is already approached. The so-called glenoid facet of the plesiomorphic ichthyosaur scapula contains a small articulation facet with the coracoid. The anteroproximal margins of the scapula in plesiomorphic and derived ichthyosaurs are therefore, contra MOTANI's interpretation, non-homologous. We therefore do not accept MOTANI's character 48. The same general comments apply to MOTANI's character 49, which is, however, in some aspects contained in our analysis (as enlargment of scapular and coracoidal glenoid and articulation facets respective to the size of the bone).

Character 81 (iliac anteromedial prominence present) is based on a misinterpretation of the ilium of *Suevoleviathan* (MAISCH 1998a, in press a, contra MOTANI 1999b), which bears a prominence which is non-homologous to that of *Cali-*

fornosaurus, as evidenced in MOTANI's and our phylogenies, where these two genera do not form a clade despite this alleged "synapomorphy".

4. 2. Characters of the skull

Only characters which are newly introduced here or formulated differently from MOTANI 1999b are discussed. For the characters taken from MOTANI's publication, the reader is referred to his paper for further information.

A data matrix for the phylogenetic analysis of the Ichthyosauria is given in Table 1 (pp. 156–160).

(1) Mode of tooth implantation largely pleurodont/subthecodont or thecodont (0) aulacodont (1) (modified from MAISCH & MATZKE 1997a, with inverted polarity).

The term aulacodont has been coined by MAZIN (1983a) for the peculiar mode of tooth implantation encountered in all post-Triassic ichthyosaurs. There, the teeth in the premaxilla, maxilla and dentary are set in deep, continuous grooves with no bony dissepiment inbetween individual tooth roots. This mode of tooth implantation is not known in any Triassic ichthyosaur, with the exception of the posterior part of the maxillary dentition of *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a) and possibly *Mixosaurus cornalianus* (MAISCH & MATZKE 1997b).

Utatsusaurus (MOTANI 1996, 1997b,c) and *Grippia* (MOTANI 1997b,c) largely show a subthecodont (in the case of *Utatsusaurus* pleurodont/subthecodont) mode of tooth implantation, as does *Mixosaurus cornalianus* (MAISCH & MATZKE 1997b; MOTANI 1997c), so this condition can be safely assumed to be plesiomorphic for ichthyosaurs. In several taxa of the "shastasaur grade" this tooth implantation is modified to a peculiar form of thecodonty, as it is seen in *Cymbospondylus* (MERRIAM 1908; MOTANI 1997b) and *Mikadocephalus* (MAISCH & MATZKE 1997a). The only mixosaurids in which such a mode of tooth implantation has been definitely recorded are *Contectopalatus* (MAISCH & MATZKE 1998b contra MOTANI 1997c), and *Phalarodon* (pers. obs.) but this is probably best interpreted as a synapomorphy of these genera. The aulacodont mode of tooth implantation is found in all Jurassic ichthyosaurs examined in the course of this study. It therefore is a valid synapomorphy of all post-Triassic ichthyosaurs.

(2) Maxillary and posterior dentary tooth roots rounded or subrectangular in cross section (0) mesiodistally elongated (1).

This character is exclusively useful for the ingroup phylogeny of the mixosaurids, as all other ichthyosaurs, as far as it is known, have roots of the maxillary and posterior dentary teeth which are rounded (the majority of forms) or subrectangular ("*Otschevia*" *pseudoscythia* and *Platypterygius*, EFIMOV 1998; BARDET 1990) in cross section. In the mixosaurids a rounded cross section of the roots is also found in the genus *Mixosaurus*, represented by *Mixosaurus cornalianus* (BESMER 1947; MAISCH & MATZKE 1997b; see Fig. 17) and *M. kuhnschnyderi* (BRINKMANN 1998a, b). In *Contectopalatus atavus* (FRAAS 1891; MAISCH & MATZKE 1998b) and *Phalarodon nordenskioeldii* (HULKE 1873; WIMAN 1910; MERRIAM 1910; VON HUENE 1916; MAZIN 1984; NICHOLLS et al. 1999) the roots of the posterior dentary teeth and maxillary teeth are distinctly elongated mediodistally (Fig. 17). In *Contectopalatus* they show deep lingual and labial grooves, which lend a number-8 cross-section to the tooth roots (MAISCH & MATZKE 1998b), whereas in *Phalarodon* the roots are laterally compressed (MERRIAM 1910; WIMAN 1910; NICHOLLS et al. 1999). This is here interpreted as a synapomorphy of *Contectopalatus* and *Phalarodon*.

(3) Crowns of teeth ornamented with distinct apicobasal striations (0) macroscopically smooth in apicobasal direction (1) (modified from MAISCH 1998b).

In almost all ichthyosaurs, including *Utatsusaurus* (MOTANI 1996), *Grippia* (MAZIN 1981b; MOTANI 1997b), *Cymbospondylus* (MERRIAM 1908), *Besanosaurus* (DAL SASSO & PINNA 1996), *Mikadocephalus* (MAISCH & MATZKE 1997a) and the large majority of post-Triassic taxa, the crowns of the teeth show distinct surface ornamentation of the enamel, expressed as apicobasally running grooves or ridges. The only known exceptions are the presumably Lower Triassic *Thaisaurus chonglakmanii* (MAZIN et al. 1991) and the Lower Jurassic taxa *Leptonectes tenuirostris* (MAISCH 1998a, 1999), *Eurhinosaurus costini* (pers. obs. MWM) and *E. longirostris* (MAISCH 1998a). In the Jurassic species the teeth are furthermore peculiar because of the largely almost entirely straight and very elongate and narrow tooth crowns (Fig. 17). The enamel of the teeth is macroscopically smooth and even if examined with a hand lens (magnification x 10) does not show any obvious indication of surface sculpture, except that there are circular wrinkles of the tooth crown enamel, best expressed towards the base of the crowns, in *Eurhinosaurus longirostris*. This feature is therefore interpreted as a valid synapomorphy of the Leptonectidae (the family-group taxon comprising *Leptonectes* and *Eurhinosaurus*, formally erected by MAISCH 1998a), homoplastically encountered in *Thaisaurus*.

Very little surface sculpture of the tooth crowns is also encountered in the specimens we studied of the Upper Jurassic *Aegirosaurus leptospondylus* and the taxon has been accordingly coded for the derived state. The rather short and robust teeth of *Aegirosaurus* are, however, very different from those of the leptonectids and the feature was certainly acquired convergently.

(4) Complete, well-developed dentition retained in adults (0) dentition strongly reduced in adults (1) (modified from GODEFROIT 1993a).

This character was used by GODEFROIT (1993a) and interpreted as a synapomorphy of *Stenopterygius* and *Ophthalmosaurus*. Whereas in the latter genus there is undoubtedly a tendency towards tooth reduction in adults (GILMORE 1905, 1906; ANDREWS 1910) this is not true in general for the genus *Stenopterygius* (FRAAS 1891; VON HUENE 1922; MCGOWAN 1979; MAISCH 1998c). In fact, it has only been recorded definitely in one of the four currently valid species of the genus (MAISCH 1998c), *Stenopterygius quadriscissus*, whereas *S. longifrons*, *S. hauffianus* and *S. megalorhinus* do not display a clear tendency towards tooth reduction in old age. The character was therefore abandoned in MAISCH's (1998a) analysis of the relationships of post-Triassic ichthyosaurs, as was the presence of a "supernumary bone" (GODEFROIT 1993a, 1994) in the cheek of *Stenopterygius* and *Ophthalmosaurus*, which, in fact, as demonstrated by MAISCH (1997a) and confirmed by MOTANI et al. (1998), is the squamosal, present in all ichthyosaurs, including *Ichthyosaurus* (MAISCH & MATZKE 2000b), with the only possible exception of *Platypterygius* (ROMER 1968; WADE 1990; MAISCH 1998b).

Closer inspection reveals, however, that GODEFROIT's use of tooth reduction as a character might be of some use to resolve the relationships of Middle Jurassic to Cretaceous ichthyosaurs. There is definitely no sign of tooth reduction in either *Brachypterygius* (MCGOWAN 1976), *Aegirosaurus* (BARDET & FERNÁNDEZ 2000) or *Platypterygius* (ROMER 1968; WADE 1984, 1990), which are thus plesiomorphic. In the newly described South American genera *Chacaicosaurus* (FERNÁNDEZ 1994) and *Caypullisaurus* (FERNÁNDEZ 1997, 1998) there is, however, evidently a clear tendency to reduce the dentition in adults, as no teeth are recorded in the otherwise complete and articulated type skull of *Chacaicosaurus cayi*, and known specimens of *Caypullisaurus bonapartei* have only some small teeth, reminiscent of old individuals of *Ophthalmosaurus*. This character is therefore provisionally used here. The situation in the genus *Stenopterygius* remains puzzling. *Stenopterygius* is, in fact, an assemblage of ichthyosaur species which is hard to define by autapomorphies (MAISCH 1998c used the general build of the fore- and hindfins, which are to a certain degree different from all other post-Triassic ichthyosaurs, but it is hard to define clear-cut autapomorphic traits in the fins as well). The possibility remains, that *Stenopterygius* is paraphyletic instead of monophyletic, and if the tooth reduction should be corroborated as a valid synapomorphy of *Ophthalmosaurus*, *Chacaicosaurus*, *Caypullisaurus* and *Stenopterygius quadriscissus*, the genus *Stenopterygius* will probably have to be subdivided. As *S. quadriscissus* is the type species (HUNGERBÜHLER 1994), a new generic name would be necessary for the remaining species. At the moment we take the conservative course to regard tooth reduction in *S. quadriscissus* as an autapomorphic homoplasy to the *Ophthalmosaurus*-*Caypullisaurus* group and assume that no tendency towards tooth reduction is found in the grundplan of the genus *Stenopterygius*. If further common derived traits between *S. quadriscissus* and the *Ophthalmosaurus*-*Caypullisaurus* group not shared by other *Stenopterygius* species should be discovered, taxonomic consequences might, however, be necessary.

(5) Replacement teeth appear outside pulp cavity (0) inside (1) (MOTANI 1999b, character 35).

(6) Posterior tooth crown conical (0) rounded (1) (MOTANI 1999b, character 38).

(7) Tooth size relative to skull width normal (over 0.1) (0) small (below 0.05) (1) (MOTANI 1999b, character 39).

(8) Maxillary tooth row single (0) multiple (1) (MOTANI 1999b, character 40).

(9) Processus subnarialis of premaxilla absent or very small (0) distinctive, reaches back for more than one third of the narial length (1).

In *Utatsusaurus hataii* as described and figured most recently by MOTANI et al. (1998) there apparently is only a very slight indication of a processus subnarialis of the premaxilla. Instead, the entire ventral narial margin is formed by the maxilla (MOTANI et al. 1998; see Fig. 1). In *Grippia longirostris* usually a very small processus subnarialis is figured (WIMAN 1933, VON HUENE 1943; MAZIN 1981b; MOTANI 2000; see Figs. 1, 10) which contributes somewhat to the ventral narial margin. In mixosaurids there is also only a very small processus subnarialis (MAISCH & MATZKE

1998b), and the same holds true for *Cymbospondylus petrinus* (MERRIAM 1908; see Figs. 3, 10).

In *Mikadocephalus gracilirostris*, the processus subnarialis of the premaxilla is extensive (MAISCH & MATZKE 1997a; see Fig. 3) and it must have contributed considerably to the ventral narial margin. The same holds true for most post-Triassic ichthyosaurs. In *Temnodontosaurus*, *Leptonectes*, *Eurhinosaurus*, *Ichthyosaurus* and all species of *Stenopterygius* (except for *S. longifrons*, GODEFROIT 1993a, 1994; MAISCH 1997a; see Fig. 7) the maxilla is even excluded from the external narial opening by the long subnarial process of the premaxilla which reaches back to meet the processus ventralis anterior of the lacrimal. In *Suevoleviathan disinteger* (MAISCH 1998a; see Fig. 5) and in *Stenopterygius longifrons* the maxilla contributes to the ventral margin of the naris, but still there is a processus subnarialis of considerable size which makes up almost half of the ventral narial margin. In the Middle to Upper Jurassic genus *Ophthalmosaurus*, articulated material shows a long processus subnarialis, although, as correctly pointed out by GILMORE (1905, 1906; see Fig. 8) and ANDREWS (1910), the maxilla contributes substantially to the ventral narial margin. GILMORE (1906) shows a surprisingly small processus subnarialis for *Ophthalmosaurus natans*, but in view of its rare complete preservation in *Ophthalmosaurus icenicus* and many other ichthyosaurs this is possibly an artifact caused by breakage. At any rate the subnarial process indicated in GILMORE's figure is substantially larger than in any of the primitive Triassic ichthyosaurs and *Ophthalmosaurus* is therefore coded for the derived state with respect to this character.

(10) Processus supranarialis of premaxilla distinctly present (0) very small or absent (1) (modified from MAISCH & MATZKE 1997a).

In *Utatsusaurus hataii* as drawn by MOTANI et al. (1998, fig. 1) there is an extensive processus supranarialis of the premaxilla which borders a considerable part of the dorsal narial margin. In *Grippia longirostris* the reconstructions presented by WIMAN (1933) and MAZIN (1981b) are quite indecisive on this point. However, the drawing of specimen SVT 201 by MAZIN (1981b, fig. 3) clearly shows a typically bifurcated posterior margin of the premaxilla, with a small processus subnarialis and an even larger processus supranarialis. It is therefore quite plausible to assume that the premaxilla of *Grippia longirostris* was very similar to that of *Utatsusaurus hataii* with respect to the processus supranarialis (see Fig. 1), an interpretation confirmed by the recent study of MOTANI (2000) and pers. obs. of specimen SVT 201.

In the Mixosauridae the situation is much different. The premaxilla forms little more than the anterior narial margin in these ichthyosaurs, and although there usually is a very small processus subnarialis, there never is any indication of a processus supranarialis. This definitely holds true for *Mixosaurus cornalianus* (MAISCH & MATZKE 1997b, 1998b; see Fig. 2), *Mixosaurus kuhnschnyderi*, and *Contectopalatus atavus* (MAISCH & MATZKE 1998b; see Fig. 2), and the same situation is found in *Phalarodon nordenskioeldii* (MERRIAM 1910; see Fig. 2), so the reduction of the processus supranarialis of the premaxilla appears to be a common derived feature of all mixosaurids.

Other Triassic ichthyosaurs usually have well-developed supranarial processes. The structure is particularly extensive in many of the taxa usually grouped as "Shastasauridae", namely in *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 3), *Shas-*

tasaurus alexandrae (CALLAWAY & MASSARE 1989; MAISCH 2000 contra MOTANI 1999b; see Fig. 3), *Callawayia neoscapularis* (MCGOWAN 1994) and *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996; see Fig. 3). It is, however, certainly quite small in *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a; see Fig. 3).

In all known Jurassic ichthyosaurs at least a small processus supranarialis is developed. It is of unusually extensive size only in *Ichthyosaurus breviceps* (see Fig. 6), where it reaches back posteriorly up to the anterior margin of the orbit to establish a sutural contact with the prefrontal (pers. obs.). This is certainly a specific autapomorphy. In all other Jurassic ichthyosaurs examined, the supranarial process of the premaxilla is much shorter and does not extend posterior to the border of the external naris. Nevertheless the unusual condition in *Ichthyosaurus breviceps* shows, that the very long processus supranarialis seen in some "shastasaurids" and usually interpreted as an autapomorphy of this family shows some homoplasticity within ichthyosaurs, which strengthens our case that "shastasaurids" are not a monophyletic family but a grade of ichthyosaur evolution between mixosaurids and the post-Triassic forms.

(11) Processus postnarialis of maxilla large and distinctive (0) tiny or absent (1) (from MAISCH & MATZKE 1997a).

A very distinctive feature of most Triassic ichthyosaurs is the possession of a narrow dorsal extension of the maxilla posterior to the external narial aperture, which was termed processus postnarialis by MAISCH & MATZKE (1997a). It is known to occur both in *Utatsusaurus hataii* (MOTANI et al. 1998; see Fig. 1) and *Grippia longirostris* (WIMAN 1929, 1933; MAZIN 1981b; MOTANI 2000 contra VON HUENE 1943, 1956; see Fig. 1). In *Utatsusaurus* the processus is reconstructed as rather staight and directed largely posteriorly by MOTANI et al. (1998, fig. 2). From re-examination of a good cast of the specimen it seems, however, more plausible to us, that it was directed more dorsally and somewhat recurved, as in most other Triassic ichthyosaurs where it occurs.

In *Grippia longirostris* the processus postnarialis is apparently a rather narrow splint of bone (WIMAN 1933; MOTANI 2000), but otherwise similar to *Utatsusaurus*. Mixosaurids have an extensive processus postnarialis, as it is seen e. g. in *Mixosaurus cornalianus* (VON HUENE 1949; MAISCH & MATZKE 1998b; see Fig. 2), *M. kuhnschnyderi* (BRINKMANN 1998a, b) and *Contectopalatus atavus* (VON HUENE 1916; MAISCH & MATZKE 1998b; see Fig. 2). In *Phalarodon nordenskioeldii* neither MERRIAM (1910) nor VON HUENE (1916) found a well-developed processus postnarialis (they both referred to the holotype of *Phalarodon fraasi* UCMP 9924 only), but one of the new specimens from British Columbia (TMP 89.126.7) is figured by NICHOLLS et al. (1999) as possessing a very long and well developed postnarial process, as in other mixosaurids. Personal re-examination of the holotype of *Phalarodon fraasi* showed that there is a long, narrow and extensive processus postnarialis which meets the prefrontal, as in all other mixosaurids (Fig. 2).

The Monte San Giorgio genera *Mikadocephalus* and *Wimanius* also have a long processus postnarialis (MAISCH & MATZKE 1997a, 1998a; see Figs. 2 and 3), and the structure also occurs in *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 3) and *C. buchseri* (pers. obs.), although it is considerably shorter than in *Mikadocephalus*.

In the holotype of *Besanosaurus leptorhynchus*, a postnarial process was not found by Dal Sasso & Pinna (1996), instead they claim that the lacrimal forms the posterior border of the external naris. The circumnarial region in the holotype is, however, apparently not very well preserved. An as yet undescribed skull (associated with a partial postcranium) in the Zürich collection (PIMUZ T 1895) referrable to *Besanosaurus* has the narial region much better preserved. It shows that Dal Sasso & Pinna are correct (Fig. 3). There is a processus postnarialis, which is however very small and does not extend beyond the dorsal narial border, similar to the situation seen in *Cymbospondylus petrinus*, although the processus postnarialis in the latter taxon is much more extensive anteroposteriorly (Fig. 3). The posterior border of the naris is formed by the nasal in *Besanosaurus leptorhynchus* (not the lacrimal as hypothesized by Dal Sasso & Pinna), which also contributes to the posterior narial margin in *Cymbospondylus petrinus*. *Besanosaurus* is the only ichthyosaur of the shastasaur grade in which a processus postnarialis of considerable size is lacking and, at least in this feature, it approaches the Jurassic ichthyosaurs more closely than *Mikadocephalus* does.

Jurassic ichthyosaurs universally lack a well developed postnarial process. A small flange is developed posterior to the naris in *Ichthyosaurus breviceps* (Fig. 6), but otherwise no comparable structures occur in any of the post-Triassic taxa.

(12) Maxilla excluded from (0) meets prefrontal (1).

This character is admittedly not totally independent of character (11), because if there is no processus postnarialis developed, there is little chance that maxilla and prefrontal meet externally. It is, however, not impossible that the two bones meet internally via the lamina orbitalis descendens of the prefrontal. In mixosaurids, for example, they meet much more extensively on the internal than on the external surface of the skull roof. We therefore chose to treat these two characters as independent, because a situation is conceivable where there is no postnarial process, but the prefrontal and maxilla are still in contact.

In *Utatsusaurus hataii* (Motani et al. 1998; see Fig. 1) and *Grippia longirostris* (Wiman 1929, 1933; Mazin 1981b; Motani 2000; see Fig. 1) there is no evidence for a contact between maxilla and prefrontal. In mixosaurids, however, the processus postnarialis of the maxilla establishes a sutural contact with the prefrontal on the external side of the skull roof (von Huene 1949; Maisch & Matzke 1998b; see Fig. 2) and an even more extensive overlap of the prefrontal onto the maxilla is found internally, where the lamina orbitalis descendens of the prefrontal reaches down almost to meet the sutural surface of the palatine, as it is seen in specimens of *Contectopalatus atavus.* In *Cymbospondylus petrinus* (Merriam 1908; see Fig. 3) and *C. buchseri* (Sander 1989) a prefrontal-maxillary contact does not exist, and the same is the case in *Shastasaurus alexandrae* (Merriam 1902; Maisch 2000; see Fig. 3). In *Mikadocephalus gracilirostris*, as particularly shown by articulated material in the PIMUZ, the very long and recurved processus postnarialis extends posterodorsally to meet the prefrontal as in mixosaurids (Maisch & Matzke 1997a, 1999; see Fig. 3). In none of the Jurassic ichthyosaurs is there a prefrontal-maxillary contact on the external side of the skull, and there is also no evidence for an internal contact between these two bones, so they have been coded with 0 for this character. The long postnarial process contacting the prefrontal is probably a homoplasy shared between the mixosaurids and *Mikadocephalus*. In *Besanosaurus leptorhynchus*, closely related to the latter genus, there is no maxillary-prefrontal contact (DAL SASSO & PINNA 1996). All other shastasaurid-grade ichthyosaurs are too incompletely known to assess this character with confidence.

(13) External naris placed largely dorsally (0) largely laterally (1).

The position of the external naris differs considerably between the Lower Triassic taxa *Utatsusaurus hataii* (MOTANI et al. 1998), *Grippia longirostris* (WIMAN 1928, 1933; VON HUENE 1943; MAZIN 1981b; MOTANI 2000) as well as the presumably Lower Triassic *Parvinatator wapitiensis* (NICHOLLS & BRINKMAN 1995) and all more derived ichthyosaurs.

In both *Utatsusaurus* and *Grippia* the naris is seen to an approximately equal extent in the dorsal and lateral views of the skull (Fig. 1). The reason for this is simply the very narrow build of the internarial bar, formed largely by the nasals and to a slight extent by the processus supranarialis of the premaxilla. In both *Utatsusaurus* and *Grippia* the internarial bar is only about as wide as the narial opening when the skull is seen in dorsal view. In the mixosaurids (MAISCH & MATZKE 1998b, 2000a, in press a; see Fig. 2) the external narial apertures are not only distinctly smaller than they are in either *Utatsusaurus* or *Grippia* and also situated somewhat further back (closer to the orbit), but they are also in a practically exclusively lateral position, so that when the skull is seen in dorsal view the narial openings are not exposed at all or only seen as narrow slits. The internarial bar, formed exclusively by the nasals in mixosaurids because of the reduction of the processus supranarialis of the premaxilla, is much wider than in the Lower Triassic taxa, about three or four times as wide as the narial opening is high.

In the ichthyosaurs of the shastasaur grade the configuration of the external naris is more or less well known in *Cymbospondylus petrinus* (MERRIAM 1908; see Figs. 3, 10), *Qianichthyosaurus zhoui* (LI 1999, clearly visible in fig. 1 b, p. 1331); *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a, 1999; see Fig. 3), *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996; see Fig. 3), *Shastasaurus alexandrae* (CALLAWAY & MASSARE 1989; MAISCH 2000; see Fig. 3), *Shonisaurus popularis* (CAMP 1980) and *Callawayia neoscapularis* (MCGOWAN 1994a). The best skull material is known for *Cymbospondylus*, *Mikadocephalus* and *Besanosaurus*. In all these three forms (MERRIAM 1908; DAL SASSO & PINNA 1996; MAISCH & MATZKE 1997a) the external narial openings are situated largely laterally, as in the mixosaurids, and the internarial bar is wide.

In the Jurassic ichthyosaurs, the same holds true for all taxa examined, in many taxa the snout at the level of the external narial openings is also not half-cylindrical, but a distinct ridge is formed betwen the dorsal and lateral surfaces of the nasal which accentuates the lateral placement of the naris even more, such as it is the case e. g. in three-dimensional crania of *Stenopterygius* and *Ichthyosaurus*, as well as in *Ophthalmosaurus* (ANDREWS 1910; SOLLAS 1916; MCGOWAN 1973; MAISCH 1998c; see Figs. 6, 7, 8).

Why the ichthyosaurs started with a more or less dorsally situated external narial opening which was displaced posteriorly and laterally instead of posterodorsally is somewhat mysterious. In a secondarily aquatic, long-snouted vertebrate one would either expect the nares to be placed far back on top of the skull, as in the Cetaceans, on an elevation of the rostrum, as in phytosaurs, or at the tip of the snout, as in crocodiles, pliosaurs or proterochampsids. An explanation might be, that the osseous narial opening of ichthyosaurs must not necessarily coincide with the position of the true narial opening, formed by soft tissue, in the living animal, and that the position of the osseous narial opening was constrained by some unkown reason to its apparently rather disadvantageous posterolateral position in ichthyosaurs. This matter surely deserves further investigation, the phylogenetic trend outlined above is, at any rate, obvious.

(14) Nasal short, reaches back to orbit (0) longer, reaches distinctly over orbit (1) (from MAISCH & MATZKE 1997a).

In *Utatsusaurus hataii* (MOTANI et al. 1998; see Fig. 10), *Chaohusaurus geishanensis* (MAISCH in press b) and *Grippia longirostris* (WIMAN 1933; MAZIN 1981b; MOTANI 2000; see Fig. 10) the nasals reach posteriorly only shortly beyond the anterior margin of the orbit. The same is true for the three mixosaurid genera *Mixosaurus* (VON HUENE 1949; MAISCH & MATZKE 1997b, 1998b), *Phalarodon* (MERRIAM 1910) and *Contectopalatus* (MAISCH & MATZKE 1998b; see Fig. 10).

In *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 10) the nasals extend extremely far posteriorly, up to the posterior end of the orbit and even contact the postfrontals. In *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a) the nasal is also considerably longer than in the more plesiomorphic taxa and extends up to the middle of the orbit. In *Besanosaurus leptorhynchus* the nasals are overgrown dorsally by a thin sheet-like anterior extension of the frontal, below which they also reach back, however, at least to the middle of the orbit (pers. obs.). In *Shonisaurus popularis*, CAMP (1980, fig. 4) reconstructs also a very long nasal, reaching posteriorly almost up to the foramen parietale. In *Shastasaurus alexandrae* (MERRIAM 1902; MAISCH 2000; see Fig. 10) the nasals are not as long, but also reach back almost to the middle of the orbit, and their posterior margins are strongly weathered in the single known skull so that they can be assumed to have been even somewhat longer originally.

In the post-Triassic ichthyosaurs the nasals are universally long and extend posterior beyond the middle of the orbit. In some taxa, such as *Temnodontosaurus trigonodon* (MAISCH 1997a, 1998c) and *Stenopterygius longifrons* (GODEFROIT 1993a, 1994; MAISCH 1997a, 1998c; see Fig. 12) they even contact the parietals and separate the frontals from the postfrontals externally.

(15) Continuous high sagittal crest on nasal, frontal and parietal absent (0) present (1).

The mixosaurids are characterised, as first explicitly pointed out by MAISCH & MATZKE (1998b) and MOTANI (1999c), by the possession of a unique, high dorsal sagittal crest on top of the skull roof, formed by the nasals, frontals and parietals. This structure is present in *Mixosaurus cornalianus* (MAISCH & MATZKE 1998b; see Fig. 2), *M. kuhnschnyderi* (BRINKMANN 1998b), *Phalarodon nordenskioeldii* (where it was already noted by MERRIAM 1910, see also NICHOLLS et al.1999; see Fig. 2) and it is particularly well developed in the large-growing *Contectopalatus atavus* (EDINGER 1935; MAISCH & MATZKE 1998b, 2000a, in press a; see Figs. 2, 10). A similar structure is not known in any other ichthyosaur and therefore the sagittal crest constitutes a valid autapomorphy of the Mixosauridae. In the presumed sister taxon of the mixosaurids, *Wimanius odontopalatus*, only the nasal is known of the median skull roof elements and it shows no indication of a sagittal crest (MAISCH & MATZKE 1998a, 1999; see Fig. 2), so this taxon has been coded with a 0 for this character, even though it cannot be excluded that a crest was present on the frontal and parietal bones.

In *Cymbospondylus petrinus* there is also a relatively high sagittal crest on top of the skull roof (MERRIAM 1908; see Figs. 3, 10), but this is exclusively formed by the supratemporal and parietal and therefore was with certainty acquired independently from the mixosaurids. It also does not extend onto the interorbital skull roof (where it reaches to the level of the external narial aperture or even beyond in mixosaurids) but is restricted to the spatium intertemporale.

No post-Triassic ichthyosaur shows any indication of a true sagittal crest.

(16) Excavatio internasalis absent (0) present (1).

The excavatio internasalis (a term coined by MAISCH 1997b) is a depression situated on the dorsal surface of the skull at the level of the orbitonarial bar. It is not known in any Triassic ichthyosaur, but is present in *Temnodontosaurus* (MAISCH & HUNGERBÜHLER 1997a; MAISCH 1998c), *Leptonectes* (MAISCH 1999), *Eurhinosaurus* (pers. obs.), *Suevoleviathan* (MAISCH 1998a), *Ichthyosaurus* (MCGOWAN 1973; MAISCH 1997b; MAISCH & MATZKE 2000b) and all the Middle Jurassic to Cretaceous genera in which the skull is known completely enough. Sometimes a small foramen is found in the depth of the excavatio internasalis, called the internasal foramen by MCGOWAN (1973). WADE (1984) suggested that an unknown organ, possibly serving for echolot orientation, was situated within the excavatio internasalis, but in our opinion the structure of the middle ear and otic capsule of derived ichthyosaurs, which do not show any of the adaptations for echolot orientation displayed by Cetaceans, strongly contradict this view. Maybe the structure was in some way related to olfaction, a sense which, judging from the few internal moulds of the skull roof available (MCGOWAN 1973; MAISCH & MATZKE 1997a) was probably well developed in ichthyosaurs.

(17) Frontal about as large as the parietal or larger (0) distinctly smaller (1).

In *Utatsusaurus hataii* (MOTANI et al. 1998; see Fig. 10) the frontal is a very extensive element which makes up the largest portion of the interorbital skull roof. Its absolute size is even considerably larger than that of the parietal. In *Chaohusaurus geishanensis* (MAISCH in press b) and *Thaisaurus chonglakmanii* (MAZIN et al. 1991), frontal and parietal are of approximately the same size. In *Grippia longirostris* (WIMAN 1933; MAZIN 1981b; see Fig. 10) the frontal is shown too small in the old skull reconstructions. The best-preserved specimen, the holotype, destroyed in World War II, shows a big frontal (WIMAN 1928; VON HUENE 1943) only slightly smaller than that of *Utatsusaurus*. This is confirmed by the observations of MOTANI (2000). In mixosaurids the frontal is also a very large element. Its skull roof component is larger than that of the parietal and it forms a very substantial part of the high sagittal crest (MAISCH & MATZKE 1998b, 2000a, in press a).

In *Cymbospondylus petrinus* (MERRIAM 1908; VON HUENE 1916; see Fig. 10) the frontal is, despite the long posterior extent of the nasals, still an element as large as the parietal in dorsal view, particularly because it extends posterolaterally to form part of the anterior margin of the temporal opening (this also shows that the posterior extension of the nasals and the size of the frontals are independent characters !).

In *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a) the frontals are rather small elements and were probably even to some extent overlapped by the nasals dorsally. In *Besanosaurus leptorhynchus*, the frontals are larger, particularly because of the development of a dorsal sheet which overlaps the nasal (in contrast to the situation in most other ichthyosaurs).

In the post-Triassic taxa, the dorsal exposure of the frontals is universally much restricted by the overlap of the nasals anteriorly and the postfrontals laterally, and the frontals thus contribute less to the dorsal external skull roof than in the Triassic forms, *Mikadocephalus* being, however, apparently closest to the post-Triassic taxa with respect to this character among well-known Triassic ichthyosaurs.

(18) Frontal widest position located posteriorly (0) at nasal suture (1) (MOTANI 1999b, character 15).

(19) Frontal excluded from (0) contributes to foramen parietale (1) (from MAZIN 1982).

The foramen parietale, as in most tetrapods where it occurs, is probably primitively enclosed entirely within the parietals in ichthyosaurs. This character state is displayed by *Utatsusaurus hataii* (MOTANI et al. 1998; see Figs. 1, 10), *Chaohusaurus geishanensis* (MAISCH in press b; see Fig. 1) and *Grippia longirostris* (WIMAN 1928, 1933; MAZIN 1981b; MOTANI 2000; see Fig. 1). In the mixosaurids examined, the foramen parietale is situated extremely far back on the skull, almost at the posterior end of the crista sagittalis, and is enclosed entirely within the parietals as well (VON HUENE 1916; MAISCH & MATZKE 1998b contra MOTANI 1999c, Fig. 10). A surprising exception among basal ichthyosaurs is *Thaisaurus chonglakmanii*, in which, according to MAZIN et al. 1991, the foramen parietale is situated at the fronto-parietal suture.

In *Cymbospondylus petrinus* (MERRIAM 1908; VON HUENE 1916, Fig. 10) the frontals form the anterior margin of the foramen parietale, in *C. buchseri* the situation might be similar (SANDER 1989), but is unclear because of bad preservation. In *Mikadocephalus gracilirostris* the foramen parietale is also enclosed by both frontals and parietals, the former forming the anterior margin of the opening only (MAISCH & MATZKE 1997a). In *Shonisaurus popularis* (CAMP 1980) and *Shastasaurus alexandrae* (MERRIAM 1902; VON HUENE 1916; MAISCH 2000; see Fig. 10) there also is a frontal contribution to the foramen parietale. *Besanosaurus leptorhynchus* is the only known ichthyosaur which definitely lacks a foramen parietale. It was not found by DAL SASSO & PINNA (1996) in the holotype specimen, and the referrable skull PIMUZ T 1895, which preserves the frontal/parietal contact in good state, also shows no trace of it.

In post-Triassic ichthyosaurs the situation is similar in all taxa examined. The frontal universally forms the anterior margin of the foramen parietale as well as the lateral margin to a variable degree. The parietal is restricted to the posterior and posterior lateral or even the posterior margin of the opening in all the post-Triassic forms.

(20) Parietal ridge absent (0) present (1) (MOTANI 1999b, character 17).

(21) Prefrontal-postfrontal contact absent (0) present (1) (MOTANI 1999b, character 8).

(22) High supraorbital crest on prefrontal and postfrontal absent (0) present (1).

In the mixosaurids, the prefrontal and postfrontal form a continuous, high and narrow crista supraorbitalis above the orbit, which continues posteriorly onto the anterior portion of the ramus anterior of the supratemporal. This crista supraorbitalis borders the anterior terrace of the temporal fenestra (a term coined by MOTANI 1999b), which is exceedingly large in mixosaurids, laterally.

The structure is well developed in *Mixosaurus cornalianus* (MAISCH & MATZKE 1997b, 1998b), *M. kuhnschnyderi* (pers. obs.), *Contectopalatus atavus* (MAISCH & MATZKE 1998b, 2000a; see Fig. 10) and *Phalarodon nordenskioeldii* (NICHOLLS et al. 1999) and therefore constitutes a valid autapomorphy of the Mixosauridae.

In no other ichthyosaur, be it Triassic or post-Triassic, has a similar structure been observed so far.

(23) Anterior orbital margin irregular (0) of regularly rounded shape (1).

The anterior orbital margin of *Utatsusaurus hataii* is complicated by a lamina of the prefrontal which reaches into the orbit for some distance (MOTANI et al. 1998; see Figs. 1, 10), a situation somewhat reminiscent of the much bigger prefrontal shield seen in Middle and Upper Jurassic mesosuchian crocodiles of the family Metriorhynchidae.

The same situation is found in *Grippia longirostris* (WIMAN 1933; MAZIN 1981b; MOTANI 2000; see Figs. 1, 10) and in *Chaohusaurus geishanensis* (MAISCH in press b; see Fig. 1) and is therefore assumed to represent the primitive condition in ichthyosaurs. Maybe it had some protective function for the eyes in these very early ichthyosaurs.

In mixosaurids, the taxa of the shastasaur grade and all post-Triassic forms the anterior margin of the orbit is universally rather evenly rounded, at any rate the distinctive prefrontal extension of the primitive forms is absent.

(24) Postorbital contributes to lateral external margin of temporal fenestra (0) is excluded from temporal fenestra by postfrontal and supratemporal (1).

According to existing interpretations of skull structure, the postorbital contributes to the external lateral margin of the temporal fenestra in both *Utatsusaurus hataii* (MOTANI et al. 1998; see Figs. 1, 10) and *Grippia longirostris* (WIMAN 1928, 1933; MAZIN 1981b; MOTANI 2000; see Figs. 1, 10), as well as in *Thaisaurus chonglakmanii* (MAZIN et al. 1991) and *Parvinatator wapitiensis* (NICHOLLS & BRINKMAN 1995; see Fig. 1), where the postorbital contribution is particularly extensive. The situation remains unclear in *Chaohusaurus* (MAISCH in press b; see Fig. 1). In mixosaurids the external lateral margin of the temporal fenestra is formed exclusively by the postfrontal and supratemporal, which meet each other, overlapping the dorsalmost extension of the postorbital. This situation has been observed in *Mixosaurus cornalianus* (MAISCH & MATZKE 1998b; see Fig. 2) and *Contectopalatus* *atavus* (MAISCH & MATZKE 1998b; see Fig. 2) and is also described for *Phalarodon nordenskioeldii* (NICHOLLS et al.1999; see Fig. 2).

In *Cymbospondylus petrinus* (MERRIAM 1908; VON HUENE 1916; MAISCH 2000; see Figs. 3, 10) the postorbital is also excluded from the external lateral margin of the temporal fenestra by a long and narrow ramus anterior of the supratemporal and an unusually long postfrontal which extends far back onto the cheek region. It nevertheless contributes to the internal lateral margin of the temporal fenestra. The same general pattern can be observed in *C. buchseri* and appears to be characteristic of the genus *Cymbospondylus* in general.

In *Mikadocephalus gracilirostris*, the posterior extent of the postfrontal is surprisingly small in the holotype, as was already noted by MAISCH & MATZKE (1997a). The articulated skull in the PIMUZ collection shows, that the postorbital widely intervenes between the postfrontal and supratemporal, the latter also having a rather small ramus anterior (Fig. 3). *Mikadocephalus* is surprisingly primititive in this respect.

In *Shastasaurus alexandrae* (MERRIAM 1902; MAISCH 2000; see Figs. 3, 10) the postorbital forms the anterior two thirds of the internal margin of the temporal fenestra and also appears just to reach the temporal fenestra externally (MAISCH 2000). At any rate a clear postfrontal-supratemporal contact is lacking in the single known specimen, and the genus has therefore been coded with a 0. The same pattern seems to be present in *Besanosaurus leptorhynchus* (pers. obs. of PIMUZ specimens; see Fig. 3), although in this instance evidence is rather scanty.

In the post-Triassic ichthyosaurs the postorbital is universally externally overlapped by the postfrontal and the ramus anterior of the supratemporal, which meet in an extensive suture. Its posterior lamina is also mostly largely hidden beneath the squamosal. The situation in *Ophthalmosaurus*, described in detail by MAISCH (1998b; see Fig. 8) can be taken as representative in at least a general way for all post-Triassic ichthyosaurs.

(25) Supratemporal without (0) with anterodorsal sheet overhanging temporal fenestra (1).

In mixosaurids the supratemporal develops an extensive anterodorsal sheet-like lamina which overhangs most of the temporal opening and is medially connected to the parietal portion of the high sagittal crest. As noted by MAISCH & MATZKE (1998b) the reason that the true size and position of the temporal fenestra in mixosaurids escaped notice for such a long time is, that in dorsoventrally flattened specimens, where normally one would expect to see the temporal fenestra quite well, the supratemporal sheet is squashed over the fenestra and hides it from view. The anterodorsal temporal sheet occurs equally in *Mixosaurus cornalianus* (MAISCH & MATZKE 1998b; see Fig. 2), *M. kuhnschnyderi* (pers. obs.), *Contectopalatus atavus* (MAISCH & MATZKE 1998b; see Figs. 2, 10), where it is most conspicuously developed, and *Phalarodon nordenskioeldii* (NICHOLLS et al. 1999; see Fig. 2).

In *Cymbospondylus petrinus* there is a high dorsal lamina of the supratemporal which borders the temporal fenestra posteriorly (MERRIAM 1908; VON HUENE 1916; see Figs. 3, 10), but it is not expanded anterodorsally and does not hide large parts of the temporal fenestra when the skull is seen in dorsal view. A similar structure appears to be present in *C. buchseri* as well, but preservation is not adequate to assess this beyond doubt in the holotype.

In other ichthyosaurs no similar structures have ever been recorded. It is therefore evident, that the anterodorsal supratemporal sheet consitutes a valid autapomorphy of the Mixosauridae.

(26) Anterior terrace of temporal fenestra present (0) absent (1).

A peculiar characteristic of all adequately known Triassic ichthyosaurs is the fact, that the anterior and, in parts, the medial margin of the temporal fenestra are formed by areas of the skull roof depressed below the general level. These depressed areas have been termed "anterior terraces of the temporal fenestrae" by MOTANI (1999b). They are most conspicuously developed in the mixosaurids and were interpreted as additional areas of attachment for the jaw adductor muscles by MAISCH & MATZKE (1998b, 2000a, in press a).

A smaller anterior terrace is already found in *Utatsusaurus hataii* (MOTANI et al. 1998; see Fig. 10), where it is formed by the frontal, postfrontal and parietal. The same applies to *Grippia longirostris* (MOTANI 2000). The situation remains unknown in the other Lower Triassic taxa.

In *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 10) there is an extensive anterior terrace, largely formed by the postfrontals, parietals and the posteriorly expanded frontals. A much smaller one, formed again by the parietal, postfrontal and also the frontal is found in *Shastasaurus alexandrae* (MERRIAM 1902; MAISCH 2000; see Fig. 10) and in *Mikadocephalus gracilirostris* (pers. obs. of PIMUZ specimens).

In no post-Triassic ichthyosaur is there any indication of an anterior terrace. Instead, the anterior margin of the temporal fenestra, formed by postfrontal and parietal, is always perfectly level with the rest of the skull roof.

(27) Posterior margin of skull roof deeply indented (0) moderately indented (1).

A character which is obviously correlated to the relative position of the orbit and the temporal fenestra is the shape of the posterior margin of the skull roof seen in dorsal view. In primitive ichthyosaurs, the temporal fenestra is largely situated in a postorbital position, so that the skull roof bones forming the walls of the adductor chamber extend further posteriorly than the skull table. This yields a sagittaly deeply indented shape to the posterior margin of the skull.

The plesiomorphic condition is found in *Utatsusaurus hataii* (MOTANI et al. 1998; see Fig. 10), *Grippia longirostris* (WIMAN 1933; MAZIN 1981b; MOTANI 2000; see Fig. 10), *Chaohusaurus geishanensis* (MAISCH in press b), all mixosaurids, *Cymbospondylus petrinus* (MERRIAM 1908; VON HUENE 1916; see Fig. 10) and *Shastasaurus alexandrae* (MERRIAM 1902; MAISCH 2000; see Fig. 10).

In *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a), *Callawayia neoscapularis* (E. L. NICHOLLS, pers. comm.) and in all the post-Triassic ichthyosaurs the posterior margin of the skull is only more slightly indented and the occipital rami of the parietals which meet the occipital rami of the supratemporals diverge at a much lower angle. This is the result of the more supraorbital position of the temporal fenestra in all these taxa.

(28) Main body of quadratojugal largely situated laterally (0) posteriorly (1).

In almost all ichthyosaurs, the main body of the quadratojugal (wether largely exposed or covered by the adjacent elements of the cheek) is situated in a more or less lateral position and at least part of it (and, with the squamosal removed, nearly all of it) is well seen in a lateral view of the skull. In the leptonectids, comprising the Lower Jurassic genera *Leptonectes* and *Eurhinosaurus*, the postorbital segment of the skull is extremely shortened and the relationships of the bones have considerably changed in correlation to this (Fig. 5). The position of the eyes in leptonectids is also different from other ichthyosaurs, as it is most extremely seen in the highly derived *Eurhinosaurus longirostris* (Fig. 11). They are not only of remarkably large size, but also directed anteriorly to a certain extent. The result of this is, that the cheek bones in part form a posterior wall of the enormously enlarged orbit, and the quadratojugal, which is the most posteroventral element of the cheek, is rotated to a position which restricts its exposure practically entirely to the occipital surface of the skull. This is the reason why it is almost never well exposed in the usual, laterally flattened leptonectid specimens, although it is not a particularly small bone and in fact much less covered by the squamosal and postorbital than in, e. g. *Stenopterygius* or *Ophthalmosaurus*. This re-organization of the postorbital skull segment, best expressed with respect to the position of the quadratojugal, is a valid autapomorphy of the Leptonectidae.

(29) Quadratojugal with (0) without (1) distinctly offset processus quadratus.

The processus quadratus (a term introduced by MAISCH & MATZKE 1997a) is a posteroventral extension of the quadratojugal at the posterior surface of which a sutural facet for contact with the quadrate is found. It borders the quadrate foramen ventrally. It is of very variable shape in ichthyosaurs, and this might, at least to a certain extent, be correlated to the length of the postorbital skull segment. Just how far-reaching this correlation is has, however, yet to be determined by more intense investigation. This is not a problem for the present analysis, because we have not used the length of the postorbital skull segment as a character. The reason for this is, that it was found to be strongly variable ontogenetically and even within quite closely related taxa, and, furthermore, that it is totally arbitrary to define the character states because the length of the postorbital skull segment shows almost continuous variation among known ichthyosaurs.

In the undoubtedly most primitive ichthyosaurs known, the published information on the cheek is very scanty and we also see reasons to express some doubt about several of the published descriptions and illustrations. In *Utatsusaurus hataii* (contra MOTANI et al. 1998) the shape of the quadratojugal is not definitely known. It appears that *Grippia longirostris* (WIMAN 1933; MAZIN 1981b; MOTANI 2000) lacks a well developed processus quadratus. As MAISCH (1998b) already pointed out, there is, however, the possibility that the bone usually labelled as "quadrate" in the illustrations of the skull of *Grippia* is, in fact, the processus quadratus of the quadratojugal. The cheek region of *Parvinatator wapitiensis*, as illustrated by NICHOLLS & BRINKMAN (1995), lends support to this notion, as it shows a quadratojugal largely covered by the big squamosal but with a well developed and clearly offset processus quadratus, not unlike the "quadrate" of *Grippia* (Fig. 1). The same situation is found in an unnamed specimen from the Lower Triassic of Spitsbergen (MAZIN 1981a). In *Chaohusaurus geishanensis*, to the contrary, the processus quadratus is inconspicuous (MAISCH in press b; see Fig. 1).

As long as we had no opportunity to see WIMAN's original material, we had, however, to rely on published information and therefore coded *Grippia* as possessing a small processus quadratus.

In the mixosaurids the processus quadratus is universally short, even in *Contectopalatus atavus*, the species with the relatively longest postorbital segment of the skull (MAISCH & MATZKE 1998b; see Fig. 2). The probable sister-taxon of mixosaurids, *Wimanius odontopalatus*, has, however, a long and well developed processus quadratus (MAISCH & MATZKE 1998a, 1999; see Fig. 2).

In *Cymbospondylus petrinus* (MERRIAM 1908; VON HUENE 1916; see Fig. 3) the quadratojugal is an extensive bone and its processus quadratus is an elongate structure, clearly set off from the main body of the bone and expanded posteriorly for contact with the quadrate. The same general configuration of the quadratojugal is seen in *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a, 1999; see Fig. 3), the holotype of *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996; see Fig. 3) and in *Phantomosaurus neubigi* (labelled as "quadrate" by SANDER 1997). In other Triassic ichthyosaurs the quadratojugal is very little known, if at all.

In the post-Triassic forms, the quadratojugal possesses a processus quadratus, but it is never as clearly offset from the main body of the bone as it is, e. g. in *Cymbospondylus* or *Mikadocephalus*. In *Ichthyosaurus* (SOLLAS 1916; ROMER 1968; MCGOWAN 1973; MAISCH 1997b; MAISCH & MATZKE 2000b; see Fig. 6), the quadratojugal possesses a medium-sized, hook-shaped processus quadratus. It is also hook-shaped, but larger, in both *Temnodontosaurus* (FRAAS 1913; see Fig. 13) and the leptonectids. In available specimens of *Suevoleviathan* the processus quadratus is very short and inconspicuous (MAISCH 1998a, in press a; see Fig. 5) , and the same is the case in *Stenopterygius* (MAISCH 1997a; see Fig. 7), and *Ophthalmosaurus* (MAISCH 1998b; ANDREWS 1910; GILMORE 1905, 1906; see Fig. 8).

(30) Quadratojugal large, about as large or larger than the squamosal in external lateral view (0) small, largely covered by squamosal and postorbital (1).

This character is as problematic as the preceding one, because of our very incomplete knowledge of and the possibility of misinterpretations in the published accounts on *Utatsusaurus* and *Grippia*. In *Utatsusaurus*, MOTANI et al. (1998) reconstruct a quadratojugal of quite respectable size with an external lateral exposure similarly large as that of the squamosal. The cheek region of *Grippia longirostris* poses the problems of interpretation already pointed out above. If the interpretation of MAISCH (1998b), namely that the so-called "quadrate" is in fact the quadratojugal, was correct, this would mean that the bone traditionally interpreted as a product of fusion between quadratojugal and squamosal in *Grippia* (e. g. MAZIN 1981b, 1982) is in fact a large squamosal. The cheek region would in this case be extremely similar to *Parvinatator wapitiensis* (NICHOLLS & BRINKMAN 1995) and the quite far-fetched explanation of the unique condition of the cheek in *Grippia* as a product of fusion of two cheek elements (unrecorded in any other ichthyosaur), suggested by MAZIN (1981b) would become unnecessary. In this case, *Grippia longirostris* would have to be coded for the derived state of the character (as the allegedly large quadratojugal in *Utatsusaurus* is supposedly primitive). In *Chaohusaurus geishanensis* the quadratojugal and squamosal are quite comparable in size (MAISCH in press b; see Fig. 1) and the same appears to be the case in *Wimanius odontopalatus* (MAISCH & MATZKE 1998a, 1999; see Fig. 2).

In the mixosaurids, information on the cheek region is much more adequate and at least in *Mixosaurus cornalianus* (MAISCH & MATZKE 1998b; see Fig. 2) and *Contectopalatus atavus* (MAISCH & MATZKE 1998b; see Fig. 2) its configuration is definitely known. In both these taxa the quadratojugal is a small element and the same appears to be the case in *Phalarodon nordenskioeldii* (NICHOLLS et al. 1999, although their interpretation of the cheek region of this species appears to us extremely problematic in some points; see Fig. 2).

In *Cymbospondylus* several in part contradictory reconstructions of the cheek region have been presented (MERRIAM 1908; VON HUENE 1916; CAMP 1980; SANDER 1989; MASSARE & CALLAWAY 1990), but all agree that the quadratojugal is an extensive element, which has been confirmed by personal observation of the Berkeley specimens (MAISCH 2000; see Fig. 3). In *Mikadocephalus* (MAISCH & MATZKE 1997a; pers. obs. of PIMUZ specimens; see Fig. 3) it is clear from the shape and size of the quadratojugal and squamosal (unfortunately not preserved together in articulation in any of the specimens) that the cheek region was similar to *Cymbospondylus* in this respect, and the same holds true for *Besanosaurus* (DAL SASSO & PINNA 1996; pers. obs. of PIMUZ specimens; see Fig. 3).

In the most plesiomorphic post-Triassic taxa, the quadratojugal is still extensively exposed on the lateral surface of the skull in *Temnodontosaurus* (MAISCH & HUNGERBÜHLER 1997b and in press; see Fig. 4) and on the posterolateral surface of the skull in the leptonectids. In *Suevoleviathan* (MAISCH 1998a, in press a; see Fig. 5), the quadratojugal is extensively covered by a long ventral extension of the squamosal and appears to be subdivided at cursory inspection. This is an autapomorphous situation, but clearly represents state 1 as the character was defined above. In *Stenopterygius* (MAISCH 1997a; see Fig. 7), *Ophthalmosaurus* (MAISCH 1998b; see Fig. 8), *Aegirosaurus* (pers. obs. of SMNS and Munich specimens; see Fig. 8) and *Ichthyosaurus* (MAISCH & MATZKE 2000b; see Fig. 6) the quadratojugal is almost entirely covered by the postorbital and squamosal, so that little more than the processus quadratus is visible in lateral view. This situation, which, again, might be in some way correlated to the enlargement of the eyes and shortening of the postorbital skull region, is clearly derived. The cheek region is less well known in other post-Triassic ichthyosaurs. In *Platypterygius* the squamosal appears to be entirely lost (ROMER 1968; WADE 1984, 1990; see Fig. 9).

(31) Squamosal large, well integrated component of the cheek (0) superficially attached plate easily lost postmortally or entirely lost (1).

As already pointed out in the character discussions above, the cheek region of the most plesiomorphic ichthyosaurs is very problematic in several repects. In *Utatsusaurus hataii* MOTANI et al. (1998; see Fig. 1) reconstructed a big squamosal, covering about half of the cheek region, which was probably also a major component of this part of the skull. In *Grippia longirostris* the squamosal is either fused to the quadratojugal or even more extensive than envisaged by WIMAN (1933) and MAZIN (1981b), so that it is certainly a well integrated component of the cheek. In *Chaohusaurus geishanensis* (MAISCH in press b; see Fig. 1) the squamosal is also a large element, tightly sutured to the quadratojugal, and the same is the case in *Parvinatator wapitiensis* (NICHOLLS & BRINKMAN 1995; see Fig. 1).

In the mixosaurids, as best seen in *Contectopalatus atavus* and *Mixosaurus corna-*

lianus (MAISCH & MATZKE 1998b, 2000a, in press a; see Fig. 2) the squamosal is a very extensive element which leaves little room for the quadratojugal along the posteroventral margin of the cheek. It is a large, rectangular plate of bone and is tightly sutured to the supratemporal dorsally and the postorbital anteriorly.

In *Cymbospondylus petrinus*, according to the interpretations of MERRIAM (1908) and VON HUENE (1916) (see also MAISCH 2000 and Fig. 3), the same is true, whereas in *C. buchseri* the squamosal (contra SANDER 1989, the squamosal in his fig. is the dorsal portion of the postorbital) and the quadratojugal are detached from the rest of the skull and lost in the holotype (the postorbital skull segment of *C. buchseri* must therefore have been considerably longer than reconstructed by SANDER 1989, making this species more similar in skull proportions to the type-species, *C. petrinus*). In the type of *Shastasaurus alexandrae* (MERRRIAM 1902; MAISCH 2000; see Fig. 3) and the complete skeleton (PIMUZ T 4376, Fig. 3) of *Mikadocephalus gracilirostris* and the referred skull of *Besanosaurus leptorhynchus* in the Zürich collection (Fig. 3), the squamosal is still tightly attached to the supratemporal dorsally and the postorbital anteriorly, whereas the quadratojugal is apparently lost. This is the reverse of the situation in many Jurassic ichthyosaur specimens, where the squamosal is easily detached from the rest of the skull (MAISCH 1998b; MAISCH & MATZKE 2000b), whereas the quadratojugal is tightly integrated into the cheek.

In *Temnodontosaurus* (MAISCH & HUNGERBÜHLER 1997b and in press; see Fig. 4) the squamosal is still an extensive bone with a tight sutural contact to the supratemporal and it is never lost from articulated skulls, and the same holds true for the leptonectids and *Suevoleviathan* (MAISCH 1998a, fig. 5). In the latter genus the squamosal is even unusually large because of the development of an extensive ventral flange which overlaps part of the quadratojugal and reaches down to or near to the ventral margin of the cheek (an autapomorphous situation unknown in other ichthyosaurs so far).

In *Ichthyosaurus*, *Stenopterygius*, *Aegirosaurus* and *Ophthalmosaurus* the squamosal is a very thin, superficial, triangular plate of bone which lacks any strong sutural attachment to the surrounding or underlying skull elements, and is therefore easily lost from or overlooked in even otherwise well preserved and articulated material (MAISCH 1998b; MAISCH & MATZKE 2000b). This situation is characteristic of the derived post-Triassic ichthyosaurs. In *Platypterygius* a separately ossified squamosal has yet to be unequivocally identified, and it may be that the element was entirely lost in this highly derived and stratigraphically youngest ichthyosaur (Fig. 9).

(32) Ramus occipitalis of supratemporal absent or small (0) well developed (1) (MOTANI 1999b, character 22).

(33) Maximum skull length in adult less than (0) or more than 400 mm (1).

This admittedly very simple character has proved to show a reliably constant distribution among well known ichthyosaurs consistent with the topology resulting from the other characters, so it is provisionally included.

Utatsusaurus and *Grippia*, as well as the other Lower Triassic forms (*Parvinatator*, *Thaisaurus*, *Chaohusaurus*) are all obviously relatively small ichthyosaurs with skulls universally smaller than 400 mm total length. The same is true for *Mixosaurus* and *Phalarodon nordenskioeldii*.

In all ichthyosaurs of the shastasaur grade where the skull is at least reasonably well known, *Mikadocephalus*, *Besanosaurus*, *Cymbospondylus*, *Shonisaurus*, *Shastasaurus*, size ranges universally exceed 400 mm, often very considerably. The same is true for all the post-Triassic taxa, not only those included in the phylogeny but also the less well-known genera. There is obviously a trend in ichthyosaur evolution not only to increase the size of the skull with respect to overall body size (as discussed below) but also to increase overall size. This trend reaches its peak first in some of the Triassic forms, namely *Cymbospondylus* and *Shonisaurus*, then in the Lower Jurassic *Temnodontosaurus* and finally in the Cretaceous *Platypterygius*, all animals with overall sizes considerably larger than 6 m. After the evolution of the first ichthyosaur giants in the Middle Triassic, there are no really small ichthyosaurs (comparable to most of the Middle Triassic mixosaurids) anymore.

(34) Interpterygoid vacuities slit-like or absent (0) well developed with medial margin of pterygoid markedly concave (1) (from MAISCH & MATZKE 1997a).

In *Utatsusaurus hataii* the pterygoid is generally similar to that of mixosaurids (VON HUENE 1916; MAISCH & MATZKE 1997b; 1998b) except for the presence of a well developed transverse flange (see below). There is no indication of large interpterygoid vacuities and the medial margins of the pterygoids are more or less straight. *Chaohusaurus geishanensis* (MAISCH in press b; see Fig. 14) possesses similar pterygoids which, however, unlike the mixosaurids, do not cover the basis cranii entirely and do not have a totally straight medial margin. In fact the situation is closely comparable to, e. g. *Shastasaurus* or *Cymbospondylus* in these basal taxa, but different from that in the mixosaurs.

The palate of *Grippia longirostris* is much less well known, but from the available evidence (WIMAN 1933; see Fig. 14) it appears that the pterygoid in this species was quite similar to that of *Utatsusaurus hataii*. Nevertheless, the basis cranii and its relations to the palate are not known in these two forms. A total absence of interpterygoid vacuities, as in the mixosaurids, is also indicated in the little known taxon *Wimanius odontopalatus* (MAISCH & MATZKE 1998a; see Fig. 14).

The shastasaur grade ichthyosaurs (other than *Mikadocephalus*; see Fig. 15) in which the palate is adequately known, namely *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 15), *C. buchseri* (pers. obs. of undescribed PIMUZ material), *Phantomosaurus neubigi* (SANDER 1997; see Fig. 15) and *Shastasaurus alexandrae* (MERRIAM 1902; MAISCH 2000; see Fig. 15) show a widely exposed basis cranii and small interpterygoid vacuities, but the palate is still largely closed anterior to the basal plate of the parabasisphenoid.

In *Mikadocephalus gracilirostris* and all post-Triassic taxa, as we already discussed previously (MAISCH & MATZKE 1997a), the interpterygoid vacuities are large, which is reflected, e. g. in the deeply concave medial border of the pterygoid bone. This feature is also shared by *Callawayia neoscapularis* (MCGOWAN 1994a; pers. obs. of cast of holotype).

(35) Processus posteromedialis pterygoidei present (0) absent (1) (from MAISCH & MATZKE 1997a).

The processus posteromedialis (a term introduced by MAISCH & MATZKE 1997a) is a peculiar structure on the posterior border of the pterygoid observable only in

Triassic ichthyosaurs. It is a more or less extensive bony flange which extends posteriorly from the point where the ramus quadratus of the pterygoid is attached to the main body of the bone. In *Utatsusaurus hataii* a small but well developed processus posteromedialis is present and this structure is therefore very probably plesiomorphic for ichthyosaurs, as we proposed previously (MAISCH & MATZKE 1997a). It is known in mixosaurids, such as *Contectopalatus atavus* (VON HUENE 1916; MAISCH & MATZKE 1998b; see Fig. 15), *Phalarodon nordenskioeldii* (NICHOLLS et al. 1999; see Fig. 14) and *Mixosaurus cornalianus* (MAISCH & MATZKE 1997b; it should be noted in this context that the small knob-like expansion at the posterior end of the processus posteromedialis observed by us in one particular specimen of the species has not been found in any other specimen so far, and it might be an individual anomaly or pathology instead of a diagnostic character).

In shastasaurid-grade ichthyosaurs, the processus posteromedialis is known in *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 15), *C. buchseri* (pers. obs. of undescribed PIMUZ material) and *Shastasaurus alexandrae* (MERRIAM 1902; MAISCH 2000; see Fig. 15). Whereas it is huge in both species of *Cymbospondylus* and extends posteriorly even beyond the level of the condylus occipitalis, it is considerably shorter and also wider in *Shastasaurus alexandrae* (MERRIAM 1902; see Fig. 15) but probably broken in the single known specimen. It was suggested by MAISCH & MATZKE (1998b) that the processus posteromedialis was an additional area of attachment for the internal (pterygoideus) adductor musculature.

In *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a; see Fig. 15) and in all post-Triassic ichthyosaurs the processus posteromedialis is completely absent.

(36) Processus transversus pterygoidei present (0) absent (1).

In *Utatsusaurus hataii* a well developed, anterolaterally oriented processus transversus pterygoidei is present. In *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 15) this structure is still developed, but less conspicuous than in *Utatsusaurus* and directed rather posterolaterally. There is some indication that a processus transversus was also retained in *Grippia longirostris* (WIMAN 1933; MOTANI 2000; see Fig. 14), but evidence is scanty. The situation remains unclear in other Lower Triassic forms.

In mixosaurids (VON HUENE 1916; MAISCH & MATZKE 1997b, 1998b; NICHOLLS et al. 1999; see Figs. 14, 15) and *Wimanius odontopalatus* (MAISCH & MATZKE 1998a; see Fig. 14) the posterolateral margin of the pterygoid is gently rounded and a processus transversus is completely absent. The same is the case in *Shastasaurus alexandrae* (MERRIAM 1902; MAISCH 2000; see Fig. 15), *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a; see Fig. 15), *Callawayia neoscapularis* (MCGOWAN 1994a) and all the post-Triassic taxa in which the palate is adequately known.

(37) Pterygoid teeth present (0) absent (1) (MOTANI 1999b, character 44).

(38) Processus postpalatinalis pterygoidei absent (0) present (1) (from MAISCH & MATZKE 1997a).

In all Triassic ichthyosaurs in which the palate is known, with the noteworthy exception of *Cymbospondylus*, *Utatsusaurus* and possibly *Grippia* which retain a well developed transverse flange of the pterygoid, as discussed above, and in the large majority of Jurassic forms, including *Suevoleviathan* and *Eurhinosaurus*, the palatine extends back in the palate along the lateral margin of the pterygoid up to the fenestra subtemporalis, of which it forms the anterior border.

The only exceptions known are *Stenopterygius* (OWEN 1881; GODEFROIT 1993a, 1994; MAISCH 1998c; see Fig. 16), and *Ophthalmosaurus* (GILMORE 1905; ANDREWS 1910; see Fig. 16), in which a posterolateral extension of the pterygoid is present which excludes the palatine from the anterior border of the fenestra subtemporalis. This is here called the processus postpalatinalis pterygoidei (see also MAISCH & MATZKE 1997a; MAISCH 1998a, c; MAISCH & HUNGERBÜHLER in press). It must be noted that a processus postpalatinalis is also shown by MERRIAM (1902, pl.13) to be present in *Shastasaurus alexandrae*, but MAISCH (2000) has shown that this is incorrect.

(39) Basioccipital peg absent (0) present (1) (MOTANI 1999b, character 29).

(40) Area extracondylaris of basioccipital extensive (0) strongly reduced (1) (MOTANI 1999b, character 30).

(41) Basis cranii largely formed by parasphenoid (0) basisphenoid (1) (modified from MAISCH & MATZKE 1997a).

The structure of the basis cranii remains unknown in *Utatsusaurus* and *Grippia*. In *Chaohusaurus geishanensis* (MAISCH in press b; see Fig. 14) and mixosaurids it is formed largely by the parasphenoid, the basal plate of which extends as a posteriorly produced collar of bone beneath the basioccipital (MAISCH & MATZKE 1997b). The same is true for the shastasaur-grade ichthyosaurs *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a), *Shastasaurus alexandrae* (MERRIAM 1902; see Fig. 15), *Cymbospondylus buchseri* (pers. obs.), *C. petrinus* (MERRIAM 1908; see Fig. 15) and *Phantomosaurus neubigi* (pers. obs.; see Fig. 15). In other Triassic taxa this region of the skull is, if at all, very inadequately known.

The situation in *Callawayia neoscapularis* (MCGOWAN 1994a; pers. obs. of holotype cast) is remarkably different from that in other Triassic forms. Here, the parasphenoid is restricted to the processus cultriformis and a narrow central strip of bone underlying the basisphenoid, which is well ossified. Much the same arrangement is seen in the most basal post-Triassic ichthyosaur *Temnodontosaurus* (FRAAS 1913; VON HUENE 1931b; see Fig. 16).

In the Jurassic ichthyosaurs the basisphenoid, which is still a small ossification in *Mikadocephalus gracilirostris*, situated on the dorsal surface of the parasphenoid (MAISCH & MATZKE 1997a), has expanded considerably, whereas the parasphenoid contribution to the basis cranii is almost restriced to the formation of the processus cultriformis. There is, in summa, a very basic reorganisation of the basis cranii observable from Middle Triassic to post-Triassic ichthyosaurs.

(42) Carotid foramen unpaired in parasphenoid (0) paired in para- or basisphenoid (1) unpaired in basisphenoid (2) (modified from MAISCH & MATZKE 1997a).

Of course if the basis cranii is largely formed by the parasphenoid the arteria carotis interna has to enter the cranial cavity through this bone, and this is the situation found in *Chaohusaurus geishanensis* (MAISCH in press b; see Fig. 14), mixosaurids (VON HUENE 1916, MAISCH & MATZKE 1997b), *Cymbospondylus buchseri*, *Phanto-*

mosaurus neubigi (Fig. 15) and *Mikadocephalus gracilirostris*. In *Shastasaurus alexandrae* (Merriam 1902; Maisch 2000; see Fig. 15) and *Cymbospondylus petrinus* (Merriam 1908; see Fig. 15) the situation is puzzling, as there is no carotid foramen visible in ventral view of the skull. It is therefore conceivable, that the carotis entered the cranial cavity between the parasphenoid and the basioccipital in these two taxa. Admittedly, preservation of the available specimens is not adequate to make a definite statement on this problem possible.

Whereas the foramen arteria carotis interna posterius is a large, unpaired opening in *Chaohusaurus geishanensis* (Maisch in press b; see Fig. 14) and both *Contectopalatus atavus* (von Huene 1916; Maisch & Matzke 1998b; see Fig. 15) and *Mixosaurus cornalianus* (Maisch & Matzke 1997b), it is paired in all the other Triassic ichthyosaurs known, as it is in most basal tetrapods and amniotes.

From the condition seen in e.g. *Cymbospondylus buchseri* or *Mikadocephalus*, the one displayed uniquely by *Callawayia* in the Triassic and *Temnodontosaurus* among post-Triassic forms can rather easily be derived. In *Temnodontosaurus* the foramen arteria carotis interna posterius is a paired structure, situated on both sides of the very narrow parasphenoid which extends back on the undersurface of the basisphenoid almost to the posterior end. Ossification of the lateral portions of the parasphenoid has been obviously already restricted in *Temnodontosaurus*, but the sagittal portion of the basal plate is still well ossified and thus the foramina are paired. Exactly the same configuration is observable in *Callawayia neoscapularis* (McGowan 1994a). In all other post-Triassic ichthyosaurs, namely *Suevoleviathan* (Fraas 1891), *Eurhinosaurus* (Fig. 16), *Ichthyosaurus* (Sollas 1916; McGowan 1973; see Fig. 16), *Stenopterygius* (Fig. 16), *Ophthalmosaurus* (Gilmore 1905; Andrews 1910; Appleby 1956; see Fig. 16) and *Platypterygius* (Wade 1990) the carotid foramen is an unpaired structure and the parasphenoid has its posterior termination along its anterior margin, being thus almost completely restricted to the processus cultriformis.

(43) Base of processus cultriformis wide, gently grading into basal plate (0) distinctly narrowed, well offset from basal plate (1).

This is another character unknown in *Utatsusaurus*, *Grippia* or any other lower Triassic ichthyosaur, except *Chaohusaurus geishanensis* (Maisch in press b; see Fig. 14), which shows the plesiomorphic state. In the mixosaurids (von Huene 1916; Maisch & Matzke 1997b) the rather short processus cultriformis is not clearly set off from the basal plate of the parasphenoid but merges gently and uninterruptedly with it at its posterior termination.

Much the same is observable in *Shastasaurus alexandrae* (Merriam 1902; Maisch 2000; see Fig. 15), *Cymbospondylus buchseri*, *C. petrinus* (Fig. 15) and *Phantomosaurus neubigi* (Sander 1997; see Fig. 15).

In *Callawayia neoscapularis* (McGowan 1994a) and all of the post-Triassic ichthyosaurs in which the parabasisphenoid is known, the processus cultriformis is very slender and clearly set off from the basal plate of the parabasisphenoid (Fig. 15, 16). It is conceivable, but by no means certain from the available evidence, that this is correlated to the size-reduction of the posterior portion of the parasphenoid, which is also found in these taxa. At present it has been regarded as best to retain this character as independent. If it is omitted from the analysis, there is no change in tree topology.

(44) Basis cranii well exposed between pterygoids (0) completely covered by pterygoids (1) (from Maisch & Matzke 1997a, but with inverted polarity).

In *Utatsusaurus hataii* the basis cranii was certainly largely, but not completely covered by the pterygoids and it was probably even more widely exposed in *Grippia longirostris* (Wiman 1933) and certainly in *Chaohusaurus geishanensis* (Maisch in press b; see Fig. 14). In the mixosaurids, as first demonstrated by von Huene (1916) in *Contectopalatus atavus* and later by Maisch & Matzke (1997b) in *Mixosaurus*, the basis cranii is entirely covered by the pterygoids, which meet each other in the midline for practically their entire length (Fig. 15). The same can be inferred from the shape of the pterygoid described in *Phalarodon nordenskioeldii* (Nicholls et al. 1999; see Fig. 15) and *Wimanius odontopalatus* (Maisch & Matzke 1998a; see Fig. 15). In the ichthyosaurs of the "shastasaur grade", as far as their ventral skull surface is adequately known, the basis cranii is universally well exposed. This is the case in *Mikadocephalus gracilirostris* (Maisch & Matzke 1997a; see Fig. 15), *Shastasaurus alexandrae* (Merriam 1902; Maisch 2000; see Fig. 15), *Callawayia neoscapularis* (McGowan 1994a), *Phantomosaurus neubigi* (Sander 1997; see Fig. 15), *Toretocnemus zitteli* (pers. obs. of holotype), *Cymbospondylus petrinus* (Merriam 1908; see Fig. 15) and *C. buchseri*, and it is of course also the case in all the post-Triassic taxa.

Outgroup comparison shows that the situation in mixosaurids is most probably derived. Neither in basal diapsids (to which ichthyosaurs belong according to current orthodoxy) nor in parareptiles (to which ichthyosaurs are most probably related according to Maisch 1998c and in our own opinion) is the basis cranii ever completely covered by the pterygoids. This state is only found in placodonts and nothosauroid sauropterygians among known diapsids, to which ichthyosaurs are probably not closely related (Motani et al. 1998). It therefore appears safe to assume, that at least some space was left open between the posterior quarters or thirds of the pterygoids (depending on the length of the posteromedial processes) to expose the basis cranii to a level somewhat in front of the basipterygoid articulation in the primitive ichthyosaurian condition. This is suggested by the situation seen in *Utatsusaurus*, *Grippia* and *Chaohusaurus*.

We therefore coded mixosaurids as derived with respect to this character. The only other known ichthyosaur which, from the shape of its pterygoid, clearly approaches the mixosaurid condition is the tantalizingly fragmentary *Wimanius* (Maisch & Matzke 1998a), and it therefore appears now that this animal is more closely related to mixosaurids than assumed by Maisch & Matzke (1998a), at least if character polarity is correctly assessed for this feature.

(45) Coronoid ossification large and laterally flattened (0) very narrow, elongate splint of bone or absent (1).

Utatsusaurus hataii possesses a rather large, laterally flattened coronoid (Motani et al. 1998) which is situated on the medial dorsal surface of the surangular quite in advance of the coronoid eminence. This is taken here as the primitive condition, as rather wide, plate-like coronoid elements are generally found in diadectomorphs, basal diapsids and parareptiles.

In *Mixosaurus cornalianus* the coronoid is already a rather narrow but still plate-like bone, whereas it is unusually large in *Shonisaurus popularis* (Camp 1980, fig. 18 a). In *Mikadocephalus gracilirostris* (Maisch & Matzke 1997a) the coronoid is much reduced to a very elongate and narrow splint of bone. The same is found in the post-Triassic forms *Ichthyosaurus* (McGowan 1973), *Temnodontosaurus* (von Huene 1931b) and *Stenopterygius* (pers. obs. of several specimens in SMNS). In other post-Triassic taxa the coronoid is as yet unknown and it might even have been totally lost in most derived post-Triassic ichthyosaurs.

(46) Angular small in lateral view, only well visible for less than one third of the mandibular length (0) distinctly larger (1).

This is another phylogenetically useful character of the ichthyosaurian mandible, which is otherwise largely of a very uniform build or only shows autapomorphous features. In *Utatsusaurus hataii* (Motani et al. 1998; see already Shikama et al. 1978; see also Fig. 1) the lateral exposure of the angular is restricted to the posteriormost portion of the mandible and already ends quite a distance posterior to the anterior orbital margin. Particularly the posterodorsal external lamina of the angular, which takes part in the lateral surface proper of the mandible is exceedingly small. In *Grippia longirostris* the same situation is found (Wiman 1929, 1933; Motani 2000; see Fig. 1 contra Mazin 1981b, where it is not clear on what new evidence deviating from Wiman's description his reconstruction of a big angular in fig. 6 is based), as it is also the case in *Parvinatator wapitiensis* (Nicholls & Brinkman 1995; see Fig. 1) and *Chaohusaurus geishanensis* (Maisch in press b; see Fig. 1).

In all the mixosaurids the angular is quite comparably small (Fig. 2). In *Mikadocephalus gracilirostris* the posterodorsal external lamina of the angular is also small (Maisch & Matzke 1997a; see Fig. 2) and the contribution of the bone to the lateral mandibular surface is, as shown by the articulated referred specimen in the PIMUZ, almost as restricted as in *Utatsusaurus*. In *Cymbospondylus petrinus* (Merriam 1908; von Huene 1916; see Fig. 3) and in *C. buchseri* (Sander 1989) the angular is, in contrast, an element of much larger size and its lateral exposure extends well anterior to the orbital margin, as in a Jurassic or Cretaceous ichthyosaur. This is one of the very few features in which *Mikadocephalus gracilirostris* (Fig. 3) is more plesiomorphic than other shastasaur-grade ichthyosaurs, except *Shastasaurus alexandrae* (Fig. 3), which has a quite comparable angular (Maisch 2000). *Besanosaurus leptorhynchus* (Dal Sasso & Pinna 1996; see Fig. 3) has a larger angular than *Mikadocephalus*, although it is not as extensive as in *Cymbospondylus*, whereas *Shonisaurus popularis* (Camp 1980) appears to be quite similar to *Cymbospondylus* in this character. The extensive lateral exposure of the angular of *Cymbospondylus* and *Shonisaurus* probably was acquired convergently to the post-Triassic ichthyosaurs, because other characters support a closer relationship of *Mikadocephalus* to the latter.

In all post-Triassic forms the angular is widely exposed and seen as a large element on the lateral mandibular surface. It usually reaches to or beyond the anterior orbital margin. The only exception is, to some extent, *Eurhinosaurus longirostris* (Fig. 5), but only because there the length of the entire mandible is autapomorphously shortened, but relative to the other mandibular bones the angular is as largely exposed on the lateral side of the lower jaw in *Eurhinosaurus* as in other post-Triassic forms.

(47) Articular transversely wide with dorsally deeply concave retroarticular portion (0) transversely narrow (1).

The articular remains unknown or very little known in the Lower Triassic taxa. In the holotype of *Parvinatator wapitiensis* (NICHOLLS & BRINKMAN 1995) there is, however, a long and dorsally curved retroarticular process which has a transversely concave dorsal surface which in all probability is formed by the articular.

In the Middle Triassic taxa *Mixosaurus cornalianus*, *Cymbospondylus petrinus* (MERRIAM 1908) and *Shastasaurus alexandrae* the articular is, despite of the great size difference, of rather uniform shape. It is a transversely wide element with a long, wide and strongly concave retroarticular portion. The same appears to be true for *Phantomosaurus neubigi* (SANDER 1997; pers. obs. of holotype) but as the articular is not completely exposed in the single specimen, there remains some uncertainty.

In *Callawayia neoscapularis* (pers. obs. of cast of holotype), *Mikadocephalus gracilirostris* (MAISCH & MATZKE 1997a), *Shonisaurus popularis* (CAMP 1980) and all post-Triassic genera in which the articular is known, it is transversely narrow and the retroarticular portion is not deeply concave, instead the dorsal margin is rather straight or only very slightly concave.

(48) Skull/body ratio distinctly less than 1/2 (0) about 1/2 or more (1).

This is another rather grossly defined character which, nevertheless, shows a distribution among well known ichthyosaurs which indicates some phylogenetic relevance. In *Utatsusaurus hataii*, as reconstructed by MOTANI et al. (1998) the skull makes up only little more than one third of the length of the presacral vertebral column. In *Chaohusaurus* the same is true for the larger known specimens. It is clear, that this character is very variable ontogenetically and can only be sensibly applied to mature and fully grown individuals.

In *Grippia longirostris* no complete skeleton is known, and this makes assessment of this character quite difficult. The specimen TMP 89.127.3 previously referred to this genus (BRINKMAN et al. 1992) preserves a considerable part of the postcranial skeleton in articulation up to presacral 30. If one assumes at least 40 presacrals, about the same number as in *Utatsusaurus*, the skull (which is, unfortunately, not completely preserved but the length of which can be roughly estimated) and body show a quite similar ratio. Nevertheless, a re-investigation of the specimen by MOTANI (1998a) makes it appear uncertain whether it was correctly attributed to the genus *Grippia* by BRINKMAN et al. Of the Spitsbergen material none is sufficiently articulated, and so it remains rather uncertain whether *Grippia* is correctly coded with 0 in our data matrix, although from the little evidence available it appears more plausible.

The mixosaurids have large heads which are about half as long as the body, as shown by the numerous well articulated specimens in the PIMUZ, GPIT and SMNS collections. In this character – as in some others, such as the shortening of the postorbital skull and the maxilla – they show surprising convergent resemblance to some of the derived post-Triassic ichthyosaurs.

In the shastasaur-grade ichthyosaurs, particularly *Cymbospondylus* and *Besanosaurus*, the skull is very small if compared to the body, only about one quarter of the presacral length. This is in strongest possible contrast to *Mikadocephalus gracilirostris*, where the skull, as demonstrated by the beautiful articulated skeleton in the PIMUZ, is more than half the length of the presacral vertebral column. As the length of the skull is only about 100 mm less than in the holotype of *Besanosaurus leptorhynchus*, this is certainly not a difference attributable to ontogenetic variation, but a valid distinguishing character of the two genera and, in fact, between *Mikadocephalus* and any of the other well-known "shastasaurs".

In all post-Triassic ichthyosaurs the skull makes up about one half of the presacral length or more. In the Leptonectidae, with their extremely elongated premaxillary rostrum, the skull is even only a little shorter than the entire body. It is therefore obvious that there is a big proportional difference between the plesiomorphic Triassic forms (except for the uniquely specialised mixosaurids) and the post-Triassic ichthyosaurs and *Mikadocephalus*.

4. 3. Characters of the axial skeleton

(49) Atlas pleurocentrum anteriorly convex (0) deeply concave (1).

In *Utatsusaurus hataii* the pleurocentrum of the atlas is convex on one and concave on the other side (pers. obs.). This suggests that, as in *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 18c) the condylus occipitalis of the basioccipital was concave in this taxon. An anteriorly convex atlas pleurocentrum has also been described by MERRIAM (1908; see Fig. 18p) in *Shastasaurus*. This is, to some extent, surprising, as the basioccipital in the single known skull of *Shastasaurus alexandrae* appears to be strongly convex (MERRIAM 1902). The specimen is, however, strongly damaged and it is conceivable that the condylus occipitalis was, indeed, saddle shaped rather than rounded. A saddle-shaped condylus is also present in *Phantomosaurus neubigi* (pers. obs. of holotype).

In the mixosaurids, the condylus occipitalis is strongly convex and the atlas pleurocentrum, which has so far not been described, therefore must be assumed to be deeply concave to form a functional articulation. In this respect the mixosaurids again appear to have developed a trait of more highly derived ichthyosaurs convergently.

In other shastasaur-grade ichthyosaurs, the atlas-axis complex is very inadequately known. The basioccipitals of *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996), *Callawayia neoscapularis* (MCGOWAN 1994a) and *Mikadocephalus gracilirostris* are, however, strongly convex and imply a concave atlantal pleurocentrum, which has also been described in *Shonisaurus popularis* (CAMP 1980).

In the post-Triassic taxa, the basioccipital, where known, usually bears a well developed, strongly posteriorly protruding, convex, sometimes almost hemispherical condylus occipitalis and the atlas pleurocentrum is, accordingly, deeply concave anteriorly.

(50) Atlas and axis separated (0) co-ossified in adult (1).

The cervical vertebral column is not very well known in many Triassic ichthyosaurs. SHIKAMA et al. (1978) indicate, that the atlas and axis are separate in *Utatsusaurus hataii* and without evidence to the contrary this must be accepted. In *Grippia longirostris* the situation is again not very clear. The Spitsbergen material does not preserve good cervical remains, but the specimen figured by WIMAN (1933, fig. 4) apparently preserves the atlas and axis which seem to be independent from each other. The referred specimen from British Columbia the generic assessment of which was questioned by MOTANI (1998a) shows well separated atlas and axis vertebral centra, so all in all available evidence points to a separate ossification of these elements in *Grippia* as well.

In *Cymbospondylus* the cervical vertebral column is well known in *C. petrinus* (MERRIAM 1908, Fig. 18c), and there the atlas and axis are completely separate, as they are also in *Shastasaurus* (MERRIAM 1908, Fig. 18p). In *Mikadocephalus* the same holds true, and the elements are also described as separate in *Shonisaurus* (CAMP 1980). In mixosaurids there is also no co-ossification of the first cervical vertebrae in either *Mixosaurus* or *Phalarodon* (NICHOLLS et al. 1999). The situation in *Contectopalatus* is unknown, because no cervical material is at present referrable with certainty to this genus.

Even in the most plesiomorphic post-Triassic ichthyosaur known, *Temnodontosaurus*, the atlas and axis are co-ossified in adults (FRAAS 1913) although they are still largely recognisable as individualised elements and are usually separate in juveniles (HAWKINS 1840; see Fig. 19a). The same appears to hold true for the leptonectids and *Suevoleviathan*, although in the latter genus the situation is not particularly clear and could be interpreted differently (MAISCH 1998a). An as yet undescribed, large skull of *Suevoleviathan* in the Berlin collection (MAISCH in press a) indicates, however, that probably all known examples of the genus are juveniles or at maximum subadults and there is no reason to assume that in adults there was no tight co-ossification of the elements as in all other Jurassic ichthyosaurs. In *Ichthyosaurus*, *Stenopterygius* and *Ophthalmosaurus* the atlas and axis are universally co-ossified (Fig. 19g) into a massive block, and in the Cretaceous *Platypterygius* the third cervical centrum is usually included as well (BROILI 1907; KUHN 1957; see Fig. 19b).

(51) Zygapophyses in anterior thoracal neural arches paired (0) unpaired (1).

A feature long noticed in the literature (FRAAS 1891) is the fact, that at least in the cervical and anterior thoracal vertebral column of Triassic ichthyosaurs the zygapophyses are paired with articulatory facets which are inclined with respect to each other, whereas they are unpaired and the articulatory facets are confluent and rather flat in the post-Triassic forms. This feature was first noticed in neural arches ascribed to *Mixosaurus atavus* and nowadays identified as generically and specifically indeterminate mixosaurids (MAISCH & MATZKE 1998b).

In *Grippia longirostris* and *Utatsusaurus hataii* information is, of course, again very scanty, but because the anterior zygapophyses are universally paired in both mixosaurids and shastasaur-grade ichthyosaurs and this is also the case in all basal tetrapods and amniotes we have in this case considered it safe to assume that the plesiomorphic situation is also found in the Lower Triassic taxa.

In mixosaurids the paired zygapophyses are well exposed in many of the beautiful articulated PIMUZ skeletons and in shastasaur-grade ichthyosaurs they have been described e. g. by MERRIAM (1908) for *Shastasaurus* and *Cymbospondylus* (Fig. 18h–i, n–o) and by DAL SASSO & PINNA (1996) in *Besanosaurus*, and they are also present in *Mikadocephalus* and in *Phantomosaurus*. In all post-Triassic ichthyosaurs, including *Temnodontosaurus*, the zygapophyses of the entire vertebral column are simple, unpaired structures and this is interpreted here as an unequivocal synapomorphy of these forms (Fig. 19c-e).

(52) Number of cervical vertebrae less than 10 (0) 10 or more (1) (modified from Dal Sasso & Pinna 1996).

The number of cervical vertebrae is known with some certainty at least for the Lower Triassic taxa *Grippia* and *Utatsusaurus*. Wiman (1933) assumed that the neck of *Grippia longirostris* was very short and did not include much more than 5 vertebrae. In *Utatsusaurus*, Shikama et al. (1978) found only 7 cervicals as well, and the latest reconstruction of Motani et al. (1998) shows about 6–7 cervicals at maximum. The same number is encountered in the articulated specimens of *Mixosaurus* and *Phalarodon* (Nicholls et al. 1999) available.

In the ichthyosaurs of the shastasaur grade the neck region is usually much longer, and more than 10 cervical vertebrae are recorded in *Cymbospondylus* (Merriam 1908), *Shastasaurus* (Merriam 1908) and *Mikadocephalus*. In all the post-Triassic taxa the number of cervical vertebrae is less than 10, usually around 6 or 7, so this is one of the few characters that could support Shastasauridae to be monophyletic. As the outcome of our entire analysis has shown, this character is, however, easily outweighted by the numerous features which connect *Mikadocephalus* more closely to the post-Triassic ichthyosaurs.

(53) Rib articulation in thoracal series predominantly unicipital (0) exclusively bicipital (1) (modified from Dal Sasso & Pinna 1996).

In *Utatsusaurus*, *Grippia* and *Chaohusaurus*, as well as in the mixosaurids the rib articulation of the presacral series is largely unicipital (Wiman 1933; Shikama et al. 1978; Mazin 1981b; von Huene 1935), except for the cervicals and the region around the sacrum. The same holds true for the shastasaur-grade ichthyosaurs (Merriam 1902, 1908; Camp 1980; Sander 1989; Dal Sasso & Pinna 1996; see Fig. 18d–g) except that the circumsacral vertebrae are also unicipital in these forms.

In the Jurassic forms, all presacral vertebrae show double articulation facets and all rib heads are clearly subdivided in *Ichthyosaurus*, *Stenopterygius*, *Ophthalmosaurus* and *Platypterygius*. The more primitive genera *Temnodontosaurus*, *Leptonectes*, *Eurhinosaurus* and *Suevoleviathan* (see e. g. von Huene 1922, 1926a, 1931a, b; McGowan 1979; Maisch 1998a, c; see Fig. 19f) show a somewhat intermediate condition, because although most presacral vertebral centra show clearly subdivided articulatory facets, the rib heads are not bicephalic but the two articulatory facets are connected so that the ribs appear rather holocephalic, and this intermediate stage has also been coded as primitive in the present analysis. The character therefore does not refer to the presence of one or two articulatory facets on the vertebral centra, but to the presence or absence of clearly double-headed ribs.

(54) Anterodorsal rib facets confluent with anterior facet in at least some centra (0) not confluent (1) (Motani 1999b, character 101).

(55) Presacral vertebral count less than 50 (0) more than 50 (1) (modified from Dal Sasso & Pinna 1996).

The presacral vertebral count of *Utatsusaurus hataii* is known with certainty. Motani et al. (1998) describe about 40 presacral vertebrae (of which 6 or 7 are cervical, as pointed out above). In *Chaohusaurus geishanensis* (Motani et al. 1997) the number is also approximately 40, so this presacral vertebral count appears to be primitive for ichthyosaurs. In *Grippia longirostris* the presacral count is not known with certainty from the Spitsbergen material. The specimen described by BRINKMAN et al. (1992) from British Columbia preserves about 40 presacrals and the ribs show a considerable size decrease in the posteriormost preserved segments, so it is very probable that not much more than 40 presacrals were present. The taxonomic assignment of this individual has recently been doubted by MOTANI (1998a). The shape of the scapula and coracoid are, however, much more in agreement with *Grippia* as described by WIMAN (1933) than with *Utatsusaurus* as described and figured by SHIKAMA et al. (1978), so we think that it was probably correctly assigned to *Grippia* by BRINKMAN et al. (1992) and consequently we coded *Grippia* with 0.

In the mixosaurids, complete postcrania are known for the genus *Mixosaurus* (VON HUENE 1935) and the presacral count is somewhat higher than 50 in the specimens examined. The presacral count appears to be identical in *Phalarodon nordenskioeldii* (NICHOLLS et al. 1999), so the mixosaurids show a considerable increase in the number of presacral vertebrae when compared to the Lower Triassic forms.

The Middle to Upper Triassic ichthyosaurs of the shastasaur grade universally have rather high presacral counts, with the one exception of *Californosaurus perrini* (MERRIAM 1908), which only has about 45–50 presacrals and thus comes closest to the plesiomorphic condition on one and the condition in most post-Triassic forms on the other hand. In *Cymbospondylus petrinus* (MERRIAM 1908) 65 presacrals are recorded, *Besanosaurus leptorhynchus* shows 60 presacrals (DAL SASSO & PINNA 1996), whereas *Mikadocephalus gracilirostris* (although the trunk is much shortened in comparison to other shastasaur-grade taxa) has 65 presacrals. In *Shonisaurus popularis* CAMP (1980) only notes that more than 45 presacrals are present, the exact number is, however, apparently unknown, as it is in *Shastasaurus* where MERRIAM (1908) estimated about 50 presacrals to be present.

In the post-Triassic forms the vertebral counts are usually much lower. In the Lower Liassic *Temnodontosaurus platyodon*, VON HUENE (1922) recorded between 43 and 46 presacrals. In the Upper Liassic species *T. trigonodon*, there are between 42 and 46 presacrals according to VON HUENE (1922, 1931a), whereas MCGOWAN (1979) counted 45–49. In *Leptonectes tenuirostris* 47–49 presacrals were counted by MCGOWAN (1974b) and in *Eurhinosaurus longirostris* there are between 40 and 48 according to VON HUENE (1931a). In *Suevoleviathan* (MAISCH 1998a) between 42 and 44 presacrals are recorded. In *Ichthyosaurus* the presacral count has been recorded as between 41 and 44 (VON HUENE 1922). In *Stenopterygius* it usually is around 44–48 (VON HUENE 1922, 1931a). In *Ophthalmosaurus icenicus* the presacral count is around 40 according to ANDREWS 1910, but around 49 according to VON HUENE 1922, which equals the number recorded in *Ophthalmosaurus natans* (MERRIAM 1908). In *Platypterygius platydactylus*, BROILI (1907) found 54 presacral vertebrae, and this is the only post-Triassic ichthyosaur known in which the number of presacrals exceeds 50. This is, most probably, an autapomorphy of *Platypterygius platydactylus* instead of a retained plesiomorphy. In the Australian species *Platypterygius longmani* WADE (1990) recorded only 46 presacrals, which lends support to this hypothesis.

In summa the presacral counts of ichthyosaurs appear to be quite low, although higher than in any primitive terrestrial tetrapod, in the Lower Triassic forms, around 40, then increase considerably to a number around 50 in the mixosaurids and some shastasaur-grade forms, the extreme is reached by *Cymbospondylus*, *Besanosaurus* and *Mikadocephalus*, where the presacral count exceeds 60, whereas in the large majority of post-Triassic taxa the presacral count is between 42 and 49. The very long presacral vertebral colums of *Cymbospondylus*, *Mikadocephalus* and *Besanosaurus* might be viewed as indicative of close relationship. However, at least in the case of *Mikadocephalus* and *Cymbospondylus* the evidence from all regions of the skeleton strongly contradicts this interpretation. The example of *Platypterygius platydactylus* shows, that the number of presacral vertebrae can rapidly and significantly change in ichthyosaurs, even within one genus, and that it is, at best, a very rough guideline for phylogenetic inferences. In our view the very high presacral counts of the aforementioned ichthyosaurs probably only indicate, that these forms have taken the axial undulatory form of locomotion to an extreme, maybe even independently, and it might therefore characterise a certain grade of ichthyosaurian evolution rather than anything else. It is admittedly hard to conceive that the Jurassic forms with presacral counts lower than 50 could be derived from an animal like *Mikadocephalus* with 65 presacral vertebrae. Nevertheless features of the cranial skeleton, girdles and other parts of the vertebral column speak so much in favour of this hypopthesis, that we cannot accept a monophyletic Shastasauridae (which could be based only on few characters, including the elongated neck region and the high presacral count, which are even to some extent correlated features and not even found in all "shastasaurids") as a likely alternative hypothesis.

(56) Posterior dorsal centra shape cylindrical (0) discoidal (1) (MOTANI 1999b, character 97)

(57) Sacral rib(s) bicipital (0) unicipital (1) (modified from DAL SASSO & PINNA 1996).

The condition of the sacral ribs is not definitely known in *Utatsusaurus hataii* but from MOTANI et al.'s illustration (1998) it appears to us as if there were two proximal articulation facets. There are definitely two proximal articulation facets and clearly double headed sacral ribs in both *Grippia longirostris* (WIMAN 1933) and the mixosaurids (VON HUENE 1935).

In all the ichthyosaurs of the shastasaur grade of organization as well as in all post-Triassic forms the single sacral rib is unicipital and there is only one articulatory facet on the sacral vertebral centrum.

(58) Sacral ribs – two distinguishable (0) not distinguishable (1) (MOTANI 1999b, character 104).

(59) Caudal vertebral centra elongated (0) short (1).

In *Utatsusaurus hataii* (SHIKAMA et al. 1978; MOTANI et al. 1998), *Grippia longirostris* (WIMAN 1933; MAZIN 1981b) and *Chaohusaurus geishanensis* (CHEN 1985; MAISCH in press b) the vertebral centra of the caudal vertebral column anterior to the fin region are universally of elongated shape, as long as they are high or longer.

In the mixosaurids, all shastasaurid-grade ichthyosaurs and all post-Triassic forms, the caudal vertebral centra are without exception higher than they are long (Fig. 18 l–m). This is an unambiguous synapomorphy of mixosaurids and more highly derived ichthyosaurs.

(60) Middle caudal processus spinosi distinctly inclined anteriorly (0) vertical or inclined posteriorly (1).

In the middle caudal region, where the caudal peduncle transforms into the tailfin, the processus spinosi of the caudal vertebrae are inclined distinctly anteriorly in primitive Triassic ichthyosaurs. This condition is found in *Utatsusaurus hataii* (SHIKAMA et al. 1978; MOTANI et al. 1998); *Chaohusaurus geishanensis* (MAISCH in press b), *Grippia longirostris* (WIMAN 1933), and all mixosaurids in which the postcranial skeleton is known.

Among “shastasaurs”, *Cymbospondylus petrinus* (MERRIAM 1908) is the only genus which retains this plesiomorphic condition. In *Californosaurus perrini* (MERRIAM 1908), *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996) and *Mikadocephalus gracilirostris* the processus spinosi are already very short in this region and do not distincly slant anteriorly. In all post-Triassic taxa they are vertical or inclined posteriorly or so much reduced that their orientation cannot even be determined.

(61) Processus spinosi in anterior and middle caudal vertebrae very long and slender (0) short and wide (1).

The anterior and middle processus spinosi of the caudal vertebral column (those situated anterior to the tailfin) are remarkably elongate and narrow anteroposteriorly (higher and shorter than the vertebral centrum) in *Utatsusaurus hataii* (SHIKAMA et al. 1978; MOTANI et al. 1998), *Grippia longirostris* (WIMAN 1933), *Mixosaurus cornalianus* (REPOSSI 1902; MERRIAM 1908; WIMAN 1912; VON HUENE 1935), *Phalarodon nordenskioeldii* (WIMAN 1910; NICHOLLS et al. 1999), *Toretocnemus californicus* (MERRIAM 1908) and *Qianichthyosaurus zhoui* (LI 1999). The only known exception among basal ichthyosaurs is *Chaohusaurus geishanensis* (MAISCH in press b), which nevertheless retains quite high processus spinosi if compared to later forms.

In the shastasaurid-grade ichthyosaurs, they are wider anteroposteriorly and shorter. This is known in *Cymbospondylus petrinus* (MERRIAM 1908), *Californosaurus perrini* (MERRIAM 1908), *Shonisaurus popularis* (CAMP 1980), *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996) and *Mikadocephalus gracilirostris*. In none of these taxa are the processus spinosi higher than the vertebral centra and they are usually about as long anteroposteriorly as the centra are. The same is true, without exception, for the post-Triassic ichthyosaurs.

(62) Anterior dorsal neural spines normal (0) high and straight (1) (MOTANI 1999b, character 102).

(63) Ossified haemapophyses present (0) absent (1).

In all Triassic ichthyosaurs in which the caudal vertebral column is known, there are ossified haemapophyses present. In no post-Triassic ichthyosaur are there ossified haemapophyses (Fig. 18m). There are, however, cartilaginous haemapophyses present in *Eurhinosaurus longirostris* (VON HUENE 1928, 1931a) and haemapophyseal facets are also known to occur in *Leptonectes* (OWEN 1881), *Ichthyosaurus* (HAWKINS 1840; OWEN 1881), at least some caudals of *Ophthalmosaurus* (ANDREWS 1910) and *Temnodontosaurus* (VON HUENE 1922), so at least cartilaginous haemapophyses must also have been present in these taxa.

In *Suevoleviathan* and *Stenopterygius* (VON HUENE 1922; MAISCH 1998c) not even haemapophysial facets are present and they have never been recorded in any of the Upper Jurassic or Cretaceous forms so it can be safely assumed that in these taxa the haemapophyses were entirely reduced.

(64) Posterior gastralia present (0) absent (1) (MOTANI 1999b, character 105).

(65) Tail as long or longer than the rest of the body (0) distinctly shorter (1).

In *Utatsusaurus hataii* (MOTANI et al. 1998) the tail is as long as the skull and body combined and the same is true for *Chaohusaurus geishanensi* (MOTANI et al. 1997). Data are again inadequate for *Grippia longirostris*. In mixosaurids the tail is also at least as long as the body (VON HUENE 1935), so it appears safe to assume that in *Grippia longirostris* the tail was also of very considerable length, particularly as there is not the least indication of a well developed tailfin in this species (WIMAN 1933).

In *Cymbospondylus* the tail is incompletely known (MERRIAM 1908), but from the remaining portions of the caudal vertebral column it is evident that it was also at least as long as the body, as it is in both *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996) and *Mikadocephalus gracilirostris*.

In the Jurassic taxa the tail is also as long as the body or longer in *Temnodontosaurus*, *Leptonectes*, *Eurhinosaurus* and *Suevoleviathan* (VON HUENE 1922, 1926a), whereas it is distinctly shorter in *Ichthyosaurus*, *Stenopterygius*, *Ophthalmosaurus*, *Aegirosaurus* and *Platypterygius* (BROILI 1907; VON HUENE 1922; pers. obs.).

(66) No lunate tailfin (0) well developed lunate tailfin (1).

None of the known Triassic ichthyosaurs possesses a well developed lunate tailfin as it is found in the derived post-Triassic taxa. In *Temnodontosaurus* there was probably a tailbend, but it was not very strongly expressed, and the same is apparently true for *Leptonectes* (MCGOWAN 1989a, 1996). Probably the angle of the tailbend amounted to little more than 25° in these two genera. In *Eurhinosaurus* the situation is complicated (RIESS 1986; MCGOWAN 1990). Obviously, as RIESS (1986) demonstrated, several of the specimens of *Eurhinosaurus* have been tampered with during or after preparation and they appear to have originally lacked any indication of a well-developed tailbend. MCGOWAN (1990) later demonstrated, that a tailbend was probably present in *Eurhinosaurus*, but from our personal observations of numerous complete skeletons in the GPIT, SMNS and elsewhere we are certain that it was surely not as considerable as in the more derived taxa and probably did not exceed 25° as well.

In the articulated holotype of *Suevoleviathan disinteger* (VON HUENE 1926a; MAISCH 1998a) a well developed, rather steep tailbend is indicated and there is no evidence that the orientation of the postflexural segment of the tail has been changed during preparation, as there is in most specimens of *Temnodontosaurus* and *Eurhinosaurus* (pers. obs). It therefore appears safe to assume that *Suevoleviathan* (at least as a large animal) had a well-developed tailbend with an angle of more than 30°. In *Stenopterygius*, *Ichthyosaurus*, *Ophthalmosaurus*, *Aegirosaurus* and *Platypterygius* there is undoubtedly a well developed tailbend and all these animals possess a big lunate tailfin superficially reminiscent of that of certain fast swimming sharks and bony fish.

4. 4. Characters of the shoulder girdle and forelimb

(67) Interclavicle shape cruciform (0) triradiate (1) T-shaped (2) (MOTANI 1999b, character 45).

(68) Clavicle with expanded medial flange (0) slender and narrow medially (1).

The clavicle of basal ichthyosaurs, where known, usually exhibits a strong medial expansion in the form of a bony flange. This feature is known in *Chaohusaurus geishanensis* (MAISCH in press b), *Utatsusaurus hataii* (pers. obs. of cast of holotype), *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 20), *C. buchseri* (SANDER 1989) and the mixosaurids.

In all more highly derived ichthyosaurs, the clavicle is slender and rod-shaped medially.

(69) Scapular glenoid and coracoid facets very small (0) enlarged (1).

In the most plesiomorphic ichthyosaurs, the scapula is a wide and short bony plate with small facets for the glenoid and contact with the coracoid situated on a narrow bony peduncle. This situation is found in *Utatsusaurus hataii* (SHIKAMA et al. 1978), *Grippia longirostris* (WIMAN 1933; see Fig. 20), *Mixosaurus cornalianus* (REPOSSI 1902; WIMAN 1912; VON HUENE 1916; see Fig. 20) and *Phalarodon nordenskioeldii* (NICHOLLS et al. 1999; see Fig. 20). In all these taxa the contact surfaces are only about one fifth to one quarter of the greatest anteroposterior scapular length.

In the ichthyosaurs of the shastasaur grade, the contact surfaces for the coracoid and humerus are distinctly enlarged and not as clearly set off from the main body of the bone as they are in primitive forms. The only exceptions are *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 20) and *C. buchseri* (SANDER 1989), where the contact surfaces are also only about one quarter of the greatest anteroposterior scapular length.

In *Shastasaurus* (MERRIAM 1902, 1908; see Fig. 21), *Californosaurus* (MERRIAM 1908; see Fig. 21), *Besanosaurus* (DAL SASSO & PINNA 1996; see Fig. 20) and *Mikadocephalus gracilirostris* (Fig. 21) the contact surfaces are about one third or more of the greatest anteroposterior scapular length.

Because of the distinctly different shape of the scapula in post-Triassic ichthyosaurs, the contacts for coracoid and humerus in these forms amount to more than one half of the greatest anteroposterior length of the bone (Fig. 22).

(70) Anterior scapular process distinct and large (0) reduced or absent (1).

In the most plesiomorphic ichthyosaurs, a large portion of the scapula extends anterior to the contact surfaces for the coracoid and humerus, which are situated on a well-offset peduncle. This part of the scapula is here referred to as the anterior process. In *Utatsusaurus hataii* (SHIKAMA et al. 1978), *Grippia longirostris* (WIMAN 1933; see Fig. 20) and the mixosaurids (WIMAN 1910, 1912; VON HUENE 1916; see Fig. 20) this anterior process is extensive and about as long as the posterior process (postglenoidal portion) of the scapula.

Among the shastasaur-grade ichthyosaurs, only *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 20) and *C. buchseri* (SANDER 1989) retain an anterior process of respectable size, albeit already only about half as long as the posterior process (which is autapomorphously enlarged into a blade-like structure in *Cymbospondylus*). In *Shastasaurus* (Merriam 1902, 1908; see Fig. 21) and *Shonisaurus* (McGowan & Motani 1999; see Fig. 21) only a small anterior flange of the scapula is retained, which is even completely absent in *Besanosaurus leptorhynchus* (Dal Sasso & Pinna 1996; see Fig. 20), *Californosaurus perrini* (Merriam 1908; see Fig. 21), *Mikadocephalus gracilirostris* (Fig. 21) and *Callawayia neoscapularis* (McGowan 1994a; see Fig. 21).

None of the Jurassic or Cretaceous ichthyosaurs retains an anterior flange of the scapula (Fig. 22).

(71) Posterior scapular process distinct and large (0) reduced, middle portion of scapula transformed into elongate blade (1) (modified from Dal Sasso & Pinna 1996).

In the primitive forms *Utatsusaurus hataii* (Shikama et al. 1978), *Grippia longirostris* (Wiman 1933; see Fig. 20) and the mixosaurids (von Huene 1916; see Fig. 20) the postglenoidal part of the scapula is, as the anterior portion of the bone, drawn out into a posterior plate-like process. The same is found in *Cymbospondylus petrinus* (Merriam 1908; see Fig. 20) and *C. buchseri* (Sander 1989), where it is, autapomorphously, transformed into a blade-like structure with a straight lateral margin which meets the lateral margin of the anterior process in an oblique angle (in all other Triassic ichthyosaurs the lateral margin of the scapula is rounded or straight). In the other "shastasaurs", the posterior process is still present but not as large as in *Cymbospondylus*, instead, the scapula is transformed into a rather equidimensional element in typical *Shastasaurus* (Merriam 1902, 1908; see Fig. 21), *Californosaurus* (Merriam 1908; see Fig. 21), *Besanosaurus* (Dal Sasso & Pinna 1996; see Fig. 20) and *Mikadocephalus* (Fig. 21). The posterior margin of the scapula in all these forms is more or less deeply concave as a sign of reduction of the posterior process. In *Callawayia neoscapularis* (McGowan 1994a; see Fig. 21) and *Shonisaurus popularis* (Camp 1980; McGowan & Motani 1999; see Fig. 21) the reduction of the posterior process is almost completed. In the post-Triassic forms the anterior process is also completely reduced, all that remains of the scapula is the elongate, blade-like middle portion of the original element. This has a superficial resemblance to the scapula of terrestrial tetrapods, but, in fact, is the product of a long morphological transformation from the element of the *Utatsusaurus-Mixosaurus* type, which can be followed through the evolution of the "shastasaur" shoulder girdle almost step by step. This type of scapula is found in all Jurassic and Cretaceous ichthyosaurs and this again indicates that the little known "shastasaur" *Callawayia neoscapularis* (which certainly, as discussed below, merits to be put into a genus of its own) might be even closer to the origin of the Jurassic ichthyosaurs than *Mikadocephalus* or *Californosaurus*.

(72) Glenoid and scapular facets of coracoid very small (0) enlarged (1).

As the glenoid and coracoidal facets of the scapula, the scapular and glenoidal facets of the coracoid are very short in relation to the entire length of the bone and situated on a distinctly offset peduncle in the most primitive ichthyosaurs. The condition is known in *Utatsusaurus hataii* (Shikama et al. 1978), *Grippia longirostris*

(Wiman 1933; see Fig. 20) and the mixosaurids (Wiman 1910, 1912; von Huene 1916; see Fig. 20). The coracoid peduncle is only one fifth to one quarter of the anteroposterior length of the entire element.

In the shastasaur-grade ichthyosaurs, the facets occupy a much larger portion of the medial margin of the coracoid and are not clearly offset from the rest of the bone. This is already the case in *Cymbospondylus petrinus* (Merriam 1908; see Fig. 20) and *C. buchseri* (Sander 1989), where the length of the facets amounts to approximately one third of the length of the entire element. In the more derived "shastasaurs" *Californosaurus* (Merriam 1908; see Fig. 21), *Shastasaurus* (Merriam 1902, 1908; see Fig. 21), *Besanosaurus* (Dal Sasso & Pinna 1996; see Fig. 21), *Mikadocephalus* (Fig. 21) and *Shonisaurus* (Camp 1980; see Fig. 21) they amount to about half the length of the element, and the same is true for the post-Triassic ichthyosaurs in general (Fig. 22).

(73) Coracoid with well rounded medial margin (0) with straight medial symphysis at least in adults (1).

In the largest majority of Triassic taxa the medial margin of the coracoid is well rounded. This is seen in *Utatsusaurus hataii* (Shikama et al. 1978), *Grippia longirostris* (Wiman 1933; see Fig. 20), *Mixosaurus cornalianus* (Wiman 1912; von Huene 1916; see Fig. 20), *Phalarodon nordenskioeldii* (Nicholls et al. 1999; see Fig. 20), *Cymbospondylus petrinus* (Merriam 1908; see Fig. 20), *C. buchseri* (Sander 1989), *Shastasaurus alexandrae* (Merriam 1902; see Fig. 21), *Californosaurus perrini* (Merriam 1908; see Fig. 21), *Besanosaurus leptorhynchus* (Dal Sasso & Pinna 1996; see Fig. 20) and *Mikadocephalus gracilirostris* (Fig. 21). The single exception is *Toretocnemus zitteli* (Merriam 1908), in which the coracoids form a distinct medial symphysis.

In *Callawayia neoscapularis* (McGowan 1994a; see Fig. 21) the medial margin of the coracoid is already quite straight, except for the middle portion, and in *Shonisaurus popularis* (Camp 1980; see Fig. 21) it is practically entirely straight so that the two elements form a long sagittal symphysis. This latter condition is universally found in adult post-Triassic ichthyosaurs (in juveniles the coracoids usually retain a rounded shape, Johnson 1979; Hungerbühler 1991).

(74) Coracoid with anterior extension longer than posterior one (0) with reduced anterior extension (1).

The preglenoidal portion of the coracoid is much longer than the postglenoidal portion in *Utatsusaurus hataii* (Shikama et al. 1978), *Grippia longirostris* (Wiman 1933; see Fig. 20) and the mixosaurids (Wiman 1912; von Huene 1916; see Fig. 20).

In the "shastasaurs", including *Cymbospondylus petrinus* and *C. buchseri* (Merriam 1908; Sander 1989; see Fig. 20), the anterior extension of the coracoid is just somewhat larger at maximum than the postglenoidal portion, in *Californosaurus* (Merriam 1908; see Fig. 21) it is distinctly smaller, whereas in *Shastasaurus* (Merriam 1902, 1908; see Fig. 21), *Besanosaurus* (Dal Sasso & Pinna 1996; see Fig. 20), *Mikadocephalus* (Fig. 21) and *Shonisaurus* (Camp 1980; see Fig. 21) it is about the same size or even somewhat larger. Despite this variation the condition in shastasaurs is always widely different from that in the primitive forms.

In the post-Triassic ichthyosaurs the postglenoidal portion of the coracoid is universally larger than the much reduced anterior extension (Fig. 22).

(75) Humerus with well differentiated and offset caput humeri (0) without well differentiated head (1).

The most primitive ichthyosaurs known universally possess humeri with a well differentiated and clearly offset caput humeri of almost terrestrial type, as it is most excellently demonstrated in *Mixosaurus cornalianus* (MAISCH & MATZKE 1998c; see Fig. 24). The humeri of *Grippia longirostris* (WIMAN 1933; see Fig. 24), *Utatsusaurus hataii* (MOTANI 1997a; see Fig. 24) and *Chaohusaurus geishanensis* (MOTANI & YOU 1998a, b; MOTANI 1999a; see Fig. 24) are principally similar. Of course the caput humeri is only well differentiated in adult animals (MAISCH & MATZKE 1998c; MOTANI & YOU 1998a).

All the shastasaurs, including *Cymbospondylus*, lack a well defined offset caput humeri at the proximal end of the humerus, and the same is true for the post-Triassic ichthyosaurs (Figs. 25–29).

(76) Humerus without (0) with well developed (1) secondarily reduced anterior flange (2) (from MOTANI 1998b).

The so-called anterior flange of the humerus is an autapomorphy of all ichthyosaurs, except *Thaisaurus* (MAZIN et al. 1991; see Fig. 24), not found in other tetrapods, with the exception of the Hupehsuchia (CARROLL & DONG 1991).

It is fully retained in *Utatsusaurus hataii* (MOTANI 1997a, 1998b, 1999a; see Fig. 24), *Chaohusaurus geishanensis* (MOTANI & YOU 1998a, b; see Fig. 24), *Grippia longirostris* (WIMAN 1933; MAZIN 1981b; MOTANI 1998b; see Fig. 24), *Isfjordosaurus minor* (WIMAN 1910; see Fig. 36 g-h), the mixosaurids *Mixosaurus* (MAISCH & MATZKE 1998c; see Fig. 24), *Phalarodon* (WIMAN 1910; NICHOLLS et al. 1999; see Fig. 25) and *Contectopalatus* (pers. obs. of specimen in SMNS), and in *Rotundopteryx hulkei* (WIMAN 1910; see Fig. 36 i-j), where the humerus has a convex anterior border. The single, very noteworthy exception is *Thaisaurus chonglakmanii* which lacks an anterior flange entirely (MAZIN et al. 1991; see Fig. 24).

The anterior flange is still distinctly present, although notched or concave anteriorly, in all the other Triassic shastasaur-grade taxa, including *Cymbospondylus* (MERRIAM 1908; SANDER 1989; see Fig. 25), *Shastasaurus* (MERRIAM 1902, 1908; see Fig. 25), *Shonisaurus* (CAMP 1980; see Fig. 25), *Besanosaurus* (DAL SASSO & PINNA 1996; see Fig. 25), and *Callawayia neoscapularis* (MCGOWAN 1994a; see Fig. 26). In *Mikadocephalus gracilirostris* the entire humerus is very modified into an almost round structure which is wider than long and has a convex anterior margin (WIMAN 1910; pers. obs. of PIMUZ specimens; see Figs. 25, 36 b, e). This is quite certainly an autapomorphous feature of the genus.

In *Hudsonelpidia brevirostris* (MCGOWAN 1995; see Fig. 26) and *Macgowania janiceps* (MCGOWAN 1996a; see Fig. 26), the anterior flange is almost entirely reduced and the humerus has a distinct shaft, as it is the case in all the post-Triassic genera in which the humerus is known (Figs. 26–29).

(77) Anterior margin of humerus straight, convex or with small central notch (0) markedly concave (1).

This character is not directly correlated to the presence or absence of the anterior flange, because in several taxa, such as *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 25), the anterior flange is well developed but the anterior margin of the humerus is nevertheless clearly concave.

In the most basal ichthyosaurs the anterior margin of the humerus is strongly convex or has a small central notch at maximum. The single exception – again – is *Thaisaurus chonglakmanii* (MAZIN et al. 1991; see Fig. 24). In *Utatsusaurus* (Fig. 24), *Chaohusaurus* (Fig. 24), *Grippia* (Fig. 24), the mixosaurids (Figs. 24–25) and all shastasaur-grade ichthyosaurs, with the exception of *Cymbospondylus petrinus* (Fig. 25), including *Callawayia neoscapularis* (MCGOWAN 1994a; see Fig. 26), the primitive condition is retained. The only Triassic ichthyosaurs which show the derived condition are *Hudsonelpidia* (MCGOWAN 1995; see Fig. 26) and *Macgowania* (MCGOWAN 1996a; see Fig. 26). All Jurassic and Cretaceous ichthyosaurs universally show the derived condition (Figs. 26–29).

(78) Humerus without or with incipient trochanter dorsalis (0) with well developed trochanter dorsalis (1).

The trochanter dorsalis (JOHNSON 1979), an additional area of muscle attachment found universally in Jurassic and Cretaceous ichthyosaurs (in the latter it is extremely conspicuously developed) is a structure not seen in the most primitive ichthyosaurs, *Utatsusaurus*, *Grippia*, *Chaohusaurus* or the mixosaurids (MOTANI 1997a, 1998b, 1999a; MOTANI & YOU 1998a, b; MAISCH & MATZKE 1998c). In the shastasaurs the dorsal surface of the largely flattened and plate-like humerus also shows little differentiation and there is no structure really comparable to the trochanter dorsalis (MERRIAM 1908; MOTANI 1999a), which therefore is a valid autapomorphy of the post-Triassic ichthyosaurs.

The only taxon in which a trochanter dorsalis might have been present – in this case certainly convergently – is *Toretocnemus zitteli* (MERRIAM 1903, 1908; see Fig. 25). The preservation of the single known specimen is, however, not very good and the humerus hard to interpret. There is, nevertheless, a distinct swelling on the dorsoproximal side and *Toretocnemus* has therefore been coded with a 1 for this character.

(79) Facet for radius on humerus distinctly larger than ulnar facet (0) of subequal size (1).

The primitive state for this character is shown by *Utatsusaurus hataii* (MOTANI 1997a, 1998b; see Fig. 24), *Chaohusaurus geishanensis* (MOTANI & YOU 1998a, b; see Fig. 24), *Grippia longirostris* (WIMAN 1933; MAZIN 1981b; MOTANI 1998b; see Fig. 24), the mixosaurids (e. g. MAISCH & MATZKE 1998c; see Figs. 24–25) and all the shastasaur-grade ichthyosaurs (Figs. 25–26), with the exceptions of *Toretocnemus zitteli* (MERRIAM 1903, 1908; see Fig. 25) which has the radial and ulnar facets almost equal in size, and *Mikadocephalus gracilirostris* (Figs. 25, 36b, e) in which the same appears to be the case.

(80) Distal end of humerus as wide as proximal end (0) enlarged with large radial facet (1) (from MOTANI 1998b).

This character is somewhat corellated to the preceding one, as this is probably a second evolutionary step in a transitional series – distal end of humerus narrow with small radial facet, distal end wide with very large radial facet, distal end wide with large radial and ulnar facet subequal in size. This is, however, an a posteriori inference from the phylogeny resulting from our analysis and we therefore decided to keep the two characters independent.

The primitive state is only found in *Utatsusaurus hataii* (MOTANI 1997a, 1998b; see Fig. 24) and *Isfjordosaurus minor* (WIMAN 1910; see Fig. 36 g-h), all other known ichthyosaur humeri correspond to the derived state (see MOTANI 1999a for a review).

(81) Humerus and zeugopodium as long or longer than manus (0) manus longer (1) (from MOTANI 1998b).

The plesiomorphic state for this character is only known to occur in *Utatsusaurus hataii* (MOTANI 1997a, 1998b; see Fig. 24). In all other ichthyosaurs in which the forefin is known, the length of the manus exceeds that of pro- and zeugopodium combined.

(82) Radius and ulna of elongate terrestrial shape (0) distinctly shortened (1) (modified from DAL SASSO & PINNA 1996).

The zeugopodial forelimb elements retain an essentially "terrestrial" elongate configuration with long diaphyses in the Lower Triassic taxa *Utatsusaurus hataïi* (SHIKAMA et al. 1978; MOTANI 1997a, 1998b; see Fig. 24), *Chaohusaurus geishanensis* (MOTANI & YOU 1998a, b; see Fig. 24), *Grippia longirostris* (WIMAN 1933; MAZIN 1981b; MOTANI 1998b; see Fig. 24), *Parvinatator wapitiensis* (NICHOLLS & BRINKMAN 1995; see Fig. 24) and *Thaisaurus chonglakmanii* (MAZIN et al. 1991; see Fig. 24).

Already in the mixosaurids the radius and ulna are much shortened and have lost a long and elongate diaphysis (REPOSSI 1902; WIMAN 1910, 1912; VON HUENE 1916; MAISCH & MATZKE 1998c; NICHOLLS et al. 1999; see Figs. 24–25), a trend which is only carried further in the shastasaur-grade and post-Triassic ichthyosaurs (Figs. 25–29).

(83) Radius/ulna relative size nearly equal (0) ulna much larger than radius (1) (MOTANI 1999b, character 64).

The derived state for this character is uniquely shown by the two Upper Triassic taxa *Callawayia neoscapularis* (MCGOWAN 1994a; see Fig. 26) and *Shonisaurus popularis* (CAMP 1980; MCGOWAN & MOTANI 1999; see Fig. 26). Even though it is a potential synapomorphy of the two, other skeletal characters indicate that it was possibly acquired convergently, as shown by the topology of the cladogram.

(84) Big spatium interosseum between radius and ulna present (0) only foramen or absent (1) (modified from Dal Sasso & Pinna 1996).

In the Lower Triassic forms, the mixosaurids and even the "shastasaurs", the radius and ulna retain a distinct shaft region, although, particularly in the latter group, it might be very short. Therefore a considerable spatium interosseum remains open between the two zeugopodial elements. In the post-Triassic taxa, radius and ulna contact each other for their entire length and the spatium interosseum is completely closed or, at maximum, as in *Leptonectes tenuirostris* (McGowan 1974a, 1989b; Godefroit 1992; see Fig. 27) a small foramen interosseum remains open.

(85) Posterior margin of ulna concave (0) convex or straight (1) (Motani 1999b, character 62).

(86) Anterior margin of radius concave (0) with notch or straight (1) (Motani 1999b, character 59).

(87) Proximal end of ulna much narrower than distal end (0) about equal in width (1).

In most basal ichthyosaurs, the proximal end of the ulna is distinctly narrower than the distal end. This is definitely the case in *Utatsusaurus*, *Grippia*, *Chaohusaurus* and *Parvinatator*. The width of the distal end is already somewhat reduced, but still more considerable than the proximal width, in the mixosaurids. In all more highly derived ichthyosaurs the proximal and distal margins of the ulna are about equal in width.

(88) Forefin primitive pentadactyl (0) first digit reduced (1) (from Motani 1999a).

This character was first pointed out by Motani (1999a). *Utatsusaurus*, *Chaohusaurus*, *Grippia*, *Thaisaurus* and *Parvinatator*, as well as the mixosaurids *Mixosaurus* and *Phalarodon* all retain the basic structure of a primitively pentadactyl tetrapod autopodium. The number of fingers decreases, however, to three or four in the shastasaurs, and this is most probably brought about by a reduction of the first, and in some forms probably the fifth digit. The first digit must also be reduced in the basal post-Triassic ichthyosaurs which, as *Temnodontosaurus*, *Eurhinosaurus*, *Leptonectes* or *Suevoleviathan* demonstrate, have at maximum three or four primary fingers. It is therefore clear that the reduction of the first digit is a valid synapomorphy of "shastasaurs" and post-Triassic forms.

(89) Forefin without accessories postaxial to fourth finger (0) with accessory digits postaxial to fourth finger (1).

In *Utatsusaurus*, *Chaohusaurus*, *Grippia* and probably *Thaisaurus* only five digits are present in the forefin. In *Mixosaurus cornalianus* and *Parvinatator* a very small additional (sixth) postaxial accessory, usually only represented in adults by a small neomorph distal to the pisiform, is present (Nicholls & Brinkman 1995; Maisch & Matzke 1998c; see Fig. 24), which in *Phalarodon nordenskioeldii* has transformed into a veritable accessory postaxial finger (Wiman 1910; Nicholls et al.1999; see Fig. 25).

In the "shastasaurs", as far as their fins are known (Figs. 25–29), there is no indication of any accessory fingers being developed, instead, the number of fingers is usually reduced to three and there is no reason to assume that these are not homologous to some of the primary digits, most probably digits 2–4.

In the post-Triassic forms, the most plesiomorphic genus, *Temnodontosaurus* (Fig. 26), shows three primary digits in the forefin and one postaxial accessory. This, taken together with the tridactyl forelimb prevailing in the shastasaurs, renders it plausible that the fourth postaxial finger often seen in *Temnodontosaurus* is a neomorph and that post-Triassic ichthyosaurs had only three primary fingers in the grundplan, a condition inherited from their shastasaur-grade ancestors. This, of course, means that all the additional digits displayed by the more highly derived post-Triassic ichthyosaurs – four to five in *Leptonectes* (Fig. 27), four and very rarely five in *Eurhinosaurus* (Fig. 27), four to five in *Suevoleviathan* (Fig. 27), five in *Stenopterygius* (Fig. 27), more than five in *Ichthyosaurus* (Fig. 27), *Ophthalmosaurus* (Fig. 28), *Platypterygius* (Fig. 29), *Brachypterygius* (Fig. 29), *Caypullisaurus* (Fig. 28), *Aegirosaurus* (Fig. 27) – are neomorphs which are not homologous to the primary fingers of the pentadactyl Lower Triassic and Middle Triassic forms.

The acquisition of at least one postaxial neomorph posterior to the fourth finger is a clear synapomorphy of all post-Triassic ichthyosaurs.

(90) Forefin primitive pentadactyl or with subnormal number of primary fingers (0) at least one accessory neomorphous postaxial digit additional to five primary fingers (1).

As discussed above, all ichthyosaurs either retain the primary number of five fingers, or they reduce their primary fingers and any additional ones have to be interpreted as secondary neomorphs. The only exception to this are *Parvinatator* (Fig. 24) and the mixosaurids *Mixosaurus* and *Phalarodon* (Fig. 24, 25), which, as mentioned above, develop an additional sixth digit posterior to the original five digits. Although the same condition has been assumed to be present in *Contectopalatus* (VON HUENE 1916) there is as yet no evidence in support of this hypothesis.

(91) Forefin without (0) with well developed preaxial accessory fingers (1).

In addition to postaxial accessories, preaxial accessories occur in some of the derived post-Triassic forms. These include *Brachypterygius* (BOULENGER 1904; VON HUENE 1922; MCGOWAN 1997b; see Fig. 29), *Ophthalmosaurus* (MCGOWAN 1997b; see Fig. 28), *Caypullisaurus* (MOTANI 1999a; see Fig. 28) and *Platypterygius* (e. g. BROILI 1907; KUHN 1946; MCGOWAN 1972a; WADE 1984, 1990; see Fig. 29).

This feature constitutes a valid synapomorphy of these four genera not encountered in any other known ichthyosaur, except *Stenopterygius* where it is a rare anomaly (pers. obs.).

(92) Manual phalangeal count 5 or less (0) seven or more (1) (MOTANI 1999b, character 77).

(93) Pisiform about as large as ulnare (0) much smaller or absent (1).

In the most basal ichthyosaurs in which the forefins are well known, the pisiform is a large element which is about the same size as the ulnare. This situation is found in *Utatsusaurus*, *Grippia*, *Chaohusaurus* and *Parvinatator*, the situation in *Thaisaurus* is unknown. The mixosaurids also retain the primitive condition, as is demonstrated by the forefins of *Mixosaurus* (MAISCH & MATZKE 1998c; see Fig. 24) and *Phalarodon* (WIMAN 1910; see Fig. 25). In all more highly derived ichthyosaurs, the pisiform is either much smaller than the ulnare, or it has been lost and is entirely absent.

(94) Zeugo- to autopodial elements flattened and plate-like (0) strongly thickened (1).

In most known ichthyosaurs the autopodial elements of the fore- and hindfins are, even if completely three-dimensionally preserved, much thinner than their maximum diameter. In the four derived post-Triassic genera *Ophthalmosaurus* (ANDREWS 1910; see Fig. 28), *Platypterygius* (BROILI 1907; MCGOWAN 1972a; WADE 1990; see Fig. 29); *Brachypterygius* (BOULENGER 1904; see Fig. 29) and *Caypullisaurus* (FERNÁNDEZ 1997, 1998; see Fig. 28) the zeugo- to autopodial elements of the fins are greatly thickened, sometimes thicker than their maximum diameter, a situation not found in any other ichthyosaur.

(95) Distal carpal I much smaller than distal carpal V or absent (0) of similar size or larger (1).

In the forefins of *Mixosaurus* (MAISCH & MATZKE 1998c; see Fig. 24) and *Phalarodon* (WIMAN 1910; see Fig. 25) the distal carpal 1 is very large, much larger or at least as large as the metacarpal 5. In the more primitive forms, such as *Utatsusaurus* and *Grippia*, the reverse is the case (Fig. 24), whereas the distal carpal 1 is lost in all the more highly derived ichthyosaurs. This character therefore appears to constitute a mixosaurid autapomorphy, yet it remains unknown in *Contectopalatus*.

(96) Distal carpals II-III much smaller than distal carpal IV (0) of comparable size (1).

In *Utatsusaurus* (MOTANI 1997a; see Fig. 24), *Grippia* (MOTANI 1998b; see Fig. 24), *Parvinatator* (NICHOLLS & BRINKMAN 1995; see Fig. 24), *Chaohusaurus* (MOTANI & YOU 1998a, b; see Fig. 24) and the mixosaurids, the distal carpals 2–3 are distinctly smaller than the fourth distal carpal. The situation remains unknown in *Thaisaurus*. In all more derived ichthyosaurs in which the situation is known, the three remaining distal carpals 2–4 are of comparable size. In Triassic forms this condition is present in *Toretocnemus* (MERRIAM 1908; see Fig. 25), *Qianichthyosaurus* (LI 1999), *Callawayia* (MCGOWAN 1994a; see Fig. 26), *Shonisaurus* (CAMP 1980; see Fig. 26) and *Macgowania* (MCGOWAN 1991, 1996a; see Fig. 26). Unfortunately it remains unknown in all other forms, which lack completely articulated forefins.

(97) Metacarpale I cylindrical (0) semilunate or rounded (1) (modified from MOTANI 1998b).

The primitive state for this character is among known ichthyosaurs exclusively recorded for *Utatsusaurus hataii* (MOTANI 1997a, 1998b; see Fig. 24) and *Parvinatator wapitiensis* (NICHOLLS & BRINKMAN 1995; see Fig. 24). In all other Lower Triassic to post-Triassic ichthyosaurs in which the first metacarpal is known, it is of either semilunate shape with a rounded anterior margin or completely rounded or rectangular.

(98) Metacarpals II-IV of elongate cylindrical shape (0) rounded (1)

In *Utatsusaurus hataii* (MOTANI 1997a; see Fig. 24), *Grippia longirostris* (MOTANI 1998b; see Fig. 24), *Chaohusaurus geishanensis* (MOTANI & YOU 1998a, b; MAISCH in press b; see Fig. 24), *Thaisaurus chonglakmanii* (MAZIN et al. 1991; see Fig. 24) and *Parvinatator wapitiensis* (NICHOLLS & BRINKMAN 1995; see Fig. 24), the metacarpal bones are very elongated, cylindrical elements with a long diaphysis. They are still longer than wide in the mixosaurids, but there they are already distinctly shortened, without a long shaft and also more flattened than in the Lower Triassic forms.

This trend is carried further in the "shastasaurs" and post-Triassic forms, where the metacarpals are rather equidimensional elements which lose their individuality and are hardly distinguishable other than by size from the carpals and phalanges.

(99) Metacarpal V with convex (0) straight or concave posterior margin or absent (1)

In basal ichthyosaurs, the fifth metacarpal has a distinctly convex posterior margin. This is the case in *Utatsusaurus* (MOTANI 1997a; see Fig. 24), *Grippia* (MOTANI 1998b; see Fig. 24), *Chaohusaurus* (MOTANI & YOU 1998a, b; MAISCH in press b; see Fig. 24), *Parvinatator* (NICHOLLS & BRINKMAN 1995; see Fig. 24) and the mixosaurids *Mixosaurus* (MAISCH & MATZKE 1998c; see Fig. 24) and *Phalarodon* (WIMAN 1910; see Fig. 25). In all more derived ichthyosaurs, the fifth metacarpal has a straight or concave posterior margin, or it is entirely lost, together with digit 5.

(100) Metacarpal V much larger than distal carpal IV (0) smaller or absent (1).

In the lower Triassic ichthyosaurs *Utatsusaurus* (MOTANI 1997a; see Fig. 24), *Grippia* (MOTANI 1998b; see Fig. 24), *Chaohusaurus* (MOTANI & YOU 1998a, b; see Fig. 24) and *Parvinatator* (NICHOLLS & BRINKMAN 1995; see Fig. 24) the fifth metacarpal is considerably larger than the distal carpal 4. Already in the mixosaurids *Mixosaurus* (MAISCH & MATZKE 1998c; see Fig. 24) and *Phalarodon* (WIMAN 1910; see Fig. 25), the fifth metacarpal is of comparable size to distal carpal 4. In all more highly derived ichthyosaurs, the fifth metacarpal is equally small or it is lost entirely (Figs. 25–29)

(101) Distal manual elements elongate (0) rounded (1) (from MOTANI 1998c).

In *Utatsusaurus hataii*, the distal phalanges of the manus retain perichondral ossification and are still notched (MOTANI 1997a, 1998b; see Fig. 24), as it is also the case in *Chaohusaurus* (MAISCH in press b; see Fig. 24) whereas they are rounded in *Grippia* (MOTANI 1998c; see Fig. 24), *Parvinatator* (NICHOLLS & BRINKMAN 1995; see Fig. 24) and *Mixosaurus* (MAISCH & MATZKE 1998c, Fig. 24), as well as all the more highly derived ichthyosaurs in which the forefins are known complete enough.

(102) Proximal manual phalanges elongate or hourglass shaped (0) rounded or rectangular (1).

In *Utatsusaurus* (Motani 1997a; see Fig. 24), *Parvinatator* (Nicholls & Brinkman 1995; see Fig. 24), *Chaohusaurus* (Motani & You 1998a, b; see Fig. 24) and *Grippia* (Motani 1998b; see Fig. 24) the proximal phalanges are much elongated and longer than wide. Already in the mixosaurids (Repossi 1902; Wiman 1910, 1912; Maisch & Matzke 1998c; Nicholls et al. 1999; see Figs. 24, 25) the proximal phalanges are much shortened, but most still retain a distinct hourglass shape with anterior and posterior notches (those of fingers II-V) and the same is found in *Toretocnemus* (Merriam 1903, 1908; see Fig. 25) and *Qianichthyosaurus* (Li 1999).

In all other ichthyosaurs where the proximal phalanges are known, they are of rectangular or rounded shape (see Motani 1999a for a review, Figs. 25–29).

4.5. Characters of the pelvic girdle and hindlimb

(103) Pelvis tripartite (0) bipartite with ischiopubic plate (1) (from Godefroit 1993a).

The pelvic girdle of plesiomorphic ichthyosaurs is universally tripartite. This is well established in *Utatsusaurus hataii* (Motani et al. 1998; see Fig. 30), *Grippia longirostris* (Wiman 1933; Mazin 1981b; see Fig. 30), *Phalarodon nordenskioeldii* (Wiman 1910; von Huene 1916, Nicholls et al. 1999; see Fig. 30), *Mixosaurus cornalianus* (Wiman 1912), *Mikadocephalus gracilirostris* (Fig. 31), *Cymbospondylus petrinus* (Merriam 1908; see Fig. 30; the pelvic girdle is unknown in *C. buchseri*), *Shastasaurus alexandrae* (Merriam 1908), *Californosaurus perrini* (Merriam 1908; see Fig. 31), *Toretocnemus californicus* (Merriam 1903, Fig. 30), *Shonisaurus popularis* (Camp 1980; see Fig. 31), *Temnodontosaurus trigonodon* (von Huene 1922; McGowan 1996c; see Fig. 31) and *T. platyodon* (Hawkins 1840), *Eurhinosaurus* (von Huene 1922, 1928, 1931a; see Fig. 32), *Leptonectes* (McGowan 1974a; 1989; 1996b, c; see Fig. 32), *Suevoleviathan* (von Huene 1926a; Maisch 1998a; see Fig. 32) and *Ichthyosaurus* (Hawkins 1840; Owen 1881; von Huene 1922; McGowan 1974b; see Fig. 32). In *Stenopterygius* (Fraas 1891; Wiman 1921; von Huene 1922, 1931a; see Fig. 32), *Ophthalmosaurus* (Andrews 1910; see Fig. 32), and *Aegirosaurus* (Bardet & Fernández 2000; see Fig. 32) the ischium and pubis are, in contrast, fused to an elongate bony plate even in small juveniles. A foramen oblongum (not homologous to the foramen obturatum in the pubis of more plesiomorphic ichthyosaurs) remains open between the two bones. A distal co-ossification of the ischium and pubis has been observed as a variation in *Leptonectes tenuirostris* (McGowan 1996c) and *Temnodontosaurus trigonodon* (McGowan 1996c), but no other ichthyosaurs show a complete proximal and distal fusion of the ischium and pubis, so this character is a valid synapomorphy of the family-group taxa Stenopterygiidae and Ophthalmosauridae.

(104) Ilium anterodistally expanded for articulation with two sacral ribs (0) less expanded, only articulating with one sacral rib (1).

The primitive state of this character is exclusively known, as pointed out by Motani et al. (1998), in *Utatsusaurus hataii* (Fig. 30). This taxon is the only ichthyosaur in which there appears to be substantial evidence for the presence of two well developed sacral ribs which both articulate distally with the ilium. The ilium is therefore strongly expanded anterodistally to provide enough space for the attachment of the sacral ribs. In *Grippia longirostris* (Wiman 1933; Mazin 1981b; see Fig. 30) the ilium is already much narrower distally and it is impossible to conceive that it was firmly connected with more than one sacral rib. A certain distal expansion of the ilium occurs in many ichthyosaurs, for example *Besanosaurus leptorhynchus* (Dal Sasso & Pinna 1996; see Fig. 31) and *Mikadocephalus gracilirostris* (Fig. 31), but this is always restricted to the distal margin of the bone and does not involve the distal half of the anterior margin as well.

The situation remains unknown in other Lower Triassic ichthyosaurs, such as *Thaisaurus*, *Chaohusaurus* and *Parvinatator*.

(105) Ischium plate-like and at least as long as broad (0) distinctly narrower (1).

In all the Triassic forms in which the pelvis is adequately known, the ischium is a rather flat, plate-like anteroposteriorly elongated element, and it is elongated dorsoventrally and considerably shortened in all the post-Triassic taxa. This rearrangement of the ventral pelvic bones is one of the most convincing synapomorphies of the post-Triassic ichthyosaurs which among Triassic forms is exclusively shared by *Hudsonelpidia brevirostris* (McGowan 1995; see Fig. 31).

(106) Pubis plate-like and at least as long as broad (0) distinctly narrower (1).

This character is as simple and striking as the preceding one. One of the major distinctions between all Triassic and all post-Triassic ichthyosaurs in which the pelvic girdle is known is the shape of the pubis. In the plesiomorphic condition, exhibited by all the Triassic taxa, except *Hudsonelpidia brevirostris* (McGowan 1995; see fig. 31) the pubis is a plate-like, wide, flat element whose anteroposterior elongation equals or is more considerable than the mediolateral diameter.

In all post-Triassic ichthyosaurs, the pubis is mediolaterally (or, better, dorsoventrally) elongate and slender. This is already the case in *Temnodontosaurus* (e. g. Hawkins 1840; von Huene 1922; see Fig. 31) and *Leptonectes* (Owen 1881; McGowan 1989b, 1996c; see Fig. 32), and it is universally the case in the more derived post-Triassic taxa.

(107) Pubis distinctly larger than ischium (0) of similar size or smaller than ischium (1).

The plesiomorphic condition of this character is neatly displayed by the Lower Triassic forms *Utatsusaurus hataii* (Motani et al. 1998; see Fig. 30) and *Grippia longirostris* (Wiman 1933; see Fig. 30). It is also true, particularly so, for *Phalarodon nordenskioeldii* (Wiman 1910; von Huene 1916; see Fig. 30) and *Mixosaurus cornalianus* (Wiman 1910, 1912). In the shastasaur-grade ichthyosaurs once again one perceives a gradual change towards the condition found in the Jurassic forms, hardly explicable if one assumes the “shastasaurids” to be a monophylum. In *Toretocnemus californicus* (Merriam 1905, 1908; see Fig. 30) and *Cymbospondylus petrinus* (Merriam 1908; see Fig. 30), the pubis is still considerably larger than the ischium and the same is true, at least slightly, in *Besanosaurus leptorhynchus* (Dal Sasso & Pinna 1996; see Fig. 31). In *Californosaurus perrini* (Merriam 1908; see Fig. 31), *Shastasaurus alexandrae* (Merriam 1908), *Mikadocephalus gracilirostris* (Fig. 31) and

Shonisaurus popularis (Camp 1980; see Fig. 31) the two elements are of approximately equal dimensions, although in the latter some variation is recorded and the pubis generally tends to be still a little larger.

In *Hudsonelpidia brevirostris* (Fig. 31), otherwise closest in pelvic structure to the post-Triassic taxa among Triassic ichthyosaurs, the plesiomorphic condition of this character is retained (McGowan 1995).

In the post-Triassic taxa the pubis is universally of the same size or distinctly smaller than the ischium (Figs. 31–32).

(108) Pubis and ischium meet medially in well defined symphysis (0) with strongly convex medial margins (1).

In *Grippia longirostris* (Wiman 1933; see Fig. 30), *Utatsusaurus hataii* (Motani et al. 1998; see Fig. 30), *Mixosaurus* and *Phalarodon* (Wiman 1910; see Fig. 30) a well defined medial symphysis is retained between the pubes and ischia. This is already reduced in *Toretocnemus californicus* (Merriam 1908; see Fig. 30) where, although the elements still meet in the midline, their medial margins are markedly convex. The same is universally the case in all more highly derived ichthyosaurs, where the pelvis is adequately known.

(109) Pubic foramen present and enclosed within pubis (0) posteriorly open or absent (1) (modified from Dal Sasso & Pinna 1996).

In the plesiomorphic condition, a foramen obturatum, as it is found in many other primitive tetrapods and amniotes, perforates the pubic plate close to its posterior margin in ichthyosaurs. It has been recorded in *Utatsusaurus hataii* (Motani et al. 1998; see Fig. 30), *Grippia longirostris* (Wiman 1933; Motani 2000; see Fig. 30); *Chaohusaurus geishanensis* (Maisch in press b; see Fig. 30), *Phalarodon nordenskioeldii* (Wiman 1910; see Fig. 30) and *Mixosaurus cornalianus* (Wiman 1912). In all these taxa, the foramen obturatum is closed posteriorly, at least in adults. The same condition is still found in *Cymbospondylus petrinus* (Merriam 1908; see Fig. 30) and *Toretocnemus californicus* (Merriam 1903, 1908; see Fig. 30) among the shastasaur-grade forms.

In all other “shastasaurs”, however, the foramen obturatum is open posteriorly. This is the case in *Besanosaurus leptorhynchus* (Dal Sasso & Pinna 1996; see Fig. 31), *Mikadocephalus gracilirostris* (Fig. 31), *Shastasaurus alexandrae* (Merriam 1908) and *Shonisaurus popularis* (Camp 1980; see Fig. 31). In *Californosaurus perrini* (Merriam 1908; see Fig. 31) the obturator notch, which is quite narrow and slit-like in the aforementioned taxa, has widened so considerably as to provide the entire posterior border of the pubis with a deeply concave outline. In *Hudsonelpidia* (McGowan 1995; see Fig. 31) and the post-Triassic ichthyosaurs (Figs. 31–32), there is no foramen obturatum in the pubis and the obturator nerve must have passed through the space left between the pubis and ischium. Only in the Stenopterygiidae and Ophthalmosauridae, where a co-ossified ischiopubis is found, a secondary foramen obturatum is formed which is, however, not situated within the pubis but between ischium and pubis and is therefore better neutrally called foramen oblongum.

(110) Distance between obturator foramen/incisure and distal margin of pubis large (0) small (1) absent (2).

In the basal forms *Utatsusaurus* (MOTANI et al. 1998; see Fig. 30), *Grippia* (WIMAN 1933; see Fig. 30), *Chaohusaurus* (MAISCH in press b; see Fig. 30), *Phalarodon* (WIMAN 1910; see Fig. 30), *Mixosaurus* (VON HUENE 1916), *Cymbospondylus* (MERRIAM 1908; see Fig. 30) and *Toretocnemus* (MERRIAM 1908; see Fig. 30) the distance between the pubic foramen and the distal margin of the pubis amounts to more than half of the width of the entire bone, whereas in all more highly derived ichthyosaurs (Figs. 31–32) the distance is either considerably smaller or the obturator foramen is entirely lost.

(111) Hindfins two thirds the length of the forefins or more (0) shorter (1) (modified from DAL SASSO & PINNA 1996).

In the most plesiomorphic well-known ichthyosaur, *Utatsusaurus hataii*, the hindfin is not particularly well known, but the femur is longer than the humerus which indicates that the hindfin was probably at least as well developed as the forefin. As in terrestrial tetrapods the forelimbs are almost universally shorter or only slightly longer than the hindlimbs, this can safely be assumed to be the plesiomorphic condition for ichthyosaurs. The hindfin of *Grippia longirostris* is, again, not very well known, but available evidence (WIMAN 1933; MAZIN 1981b) suggests, that it was not very much smaller than the forefin. This is definitely true for *Chaohusaurus geishanensis* (MAISCH in press b). In *Phalarodon nordenskioeldii* evidence is somewhat scanty, at least the hindfins appear to have been distinctly smaller than the forefins and WIMAN's (1910) assumption that it was probably only half the size of the forefin appears plausible. In *Mixosaurus cornalianus* this was certainly the case (VON HUENE 1935) and this is one of the features in which the small Middle Triassic family Mixosauridae parallels the highly derived representatives of the post-Triassic ichthyosaurs. One almost gets the impression as if the mixosaurids tried to prematurely achieve a similarly sophisticated degree of adaptation to the aquatic environment. They are certainly the most "specialized" of all Triassic ichthyosaurs.

In the shastasaur-grade forms, the fore and hindfins are often not very well known, particularly articulated and complete pairs of fins are practically non-existing in any of the known genera. Judging from the proportions of the stylo- and zeugopodial elements, which are usually preserved, it is however certain that *Cymbospondylus petrinus* (MERRIAM 1908) had very well developed and large hindfins, certainly two thirds the size of the forefins at least, and the same is suggested by the available material for *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996), *Mikadocephalus gracilirostris* and *Shonisaurus popularis* (CAMP 1980).

The post-Triassic ichthyosaurs start off with an array of forms where the hindfins are about two thirds of the length of the forefins, similar to the situation in shastasaurs. This condition is found in *Temnodontosaurus* (HAWKINS 1840; OWEN 1881; VON HUENE 1931a; MCGOWAN 1974a, 1979), *Eurhinosaurus* (VON HUENE 1922, 1928, 1931a, 1951, where the hindfins can be even slightly longer than two thirds) and *Suevoleviathan* (VON HUENE 1926a; MAISCH 1998a). The only exceptional genus appears to be *Leptonectes* (VON HUENE 1922; MCGOWAN 1974b, 1979, 1993) where the hindfin is usually only about half as long as the forefin and never seems to reach two thirds of the length of the forefin.

In the derived post-Triassic genera such as *Ichthyosaurus* (HAWKINS 1840; OWEN 1881; VON HUENE 1922; MCGOWAN 1974b), *Stenopterygius* (VON HUENE 1922, 1931a; MCGOWAN 1979), *Platypterygius* (KUHN 1946) and *Ophthalmosaurus* (ANDREWS 1910) the hindfins are much reduced and never reach nearly two thirds the length of the forefin. In the majority of specimens they are about half as long.

(112) Tibial facet of femur larger than fibular facet (0) subequal or equal in size (1).

In all Triassic ichthyosaurs in which the hindfin is adequately known, the tibial facet of the femur is considerably larger than the fibular facet. This is, e. g. exemplified by *Thaisaurus* (MAZIN et al. 1991; see Fig. 33), *Chaohusaurus* (MAISCH in press b; see Fig. 33) or *Phalarodon* (WIMAN 1910; see Fig. 33). The only known exception is *Hudsonelpidia* (MCGOWAN 1995) in which, as in all adequately known post-Triassic ichthyosaurs, the tibial and fibular facets are of quite comparable size,

(113) Tibia and fibula of elongate terrestrial shape (0) distinctly shortened (1).

In *Utatsusaurus hataii* (SHIKAMA et al. 1978; MOTANI et al. 1998), *Thaisaurus chonglakmanii* (MAZIN et al. 1991; see Fig. 33), *Chaohusaurus geishanensis* (MAISCH in press b; see Fig. 33) and *Grippia longirostris* (WIMAN 1933; MAZIN 1981b) the tibia and fibula are very slender, narrow and elongate bones which, apart from their distinct flattening, retain more or less the shape typically found in terrestrial tetrapods. The diaphyseal portions of these zeugopodial elements are already considerably shortened in *Mixosaurus* (REPOSSI 1902; VON HUENE 1935; see Fig. 33) and *Phalarodon* (WIMAN 1910; VON HUENE 1916; NICHOLLS et al. 1999; see Fig. 33) and this is equally true for the shastasaur-grade ichthyosaurs *Cymbospondylus petrinus* (MERRIAM 1908; see Fig. 33), *Californosaurus perrini* (MERRIAM 1908; see Fig. 34), *Shastasaurus alexandrae* (MERRIAM 1908; see Fig. 34), *Shonisaurus popularis* (CAMP 1980; see Fig. 34), *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996; see Fig. 34) and *Mikadocephalus gracilirostris* (Fig. 34), although in all these taxa the elements retain clear diaphyses and a distinctly elongate shape. In *Phantomosaurus neufigi* the zeugopodial elements might have been more elongate than in the other "shastasaur-grade" forms, but the single available hindfin is too incomplete to be certain about this.

In all the post-Triassic taxa, the tibia and fibula are short, plate-like, almost equidimensional and more or less rectangular elements which have lost any resemblance to the zeugopodium of a terrestrial tetrapod and any remnants of a diaphysis.

(114) Big spatium interosseum between tibia and fibula present (0) absent (1).

In all the Lower Triassic taxa in which the hindlimb is known, namely *Utatsusaurus* (SHIKAMA et al. 1978; MOTANI et al. 1998), *Grippia* (WIMAN 1933; MAZIN 1981b), *Chaohusaurus* (MAISCH in press c; see Fig. 33) and *Thaisaurus* (MAZIN et al. 1991; see Fig. 33), a big spatium interosseum remains open between the elongate zeugopodial elements. Although these are shortened in the more derived mixosaurids and shastasaur-grade forms (Figs. 33–34), the spatium interosseum remains distinctive in all these taxa, including even *Hudsonelpidia* (MCGOWAN 1995). In the post-Triassic forms (Fig. 35), the spatium interosseum is totally closed and there does not even remain a foramen open between the plate-like tibia and fibula.

(115) Fibula not fixed, being mobile relative to femur (0) fixed (1) (MOTANI 1999b, character 93 pars).

(116) Fibula posterior to femur (0) about the same level (1) (MOTANI 1999b, character 93 pars).

(117) Tibia anterior shaft complete or nearly complete (0) notch or largely reduced (1) absent (2) (MOTANI 1999b, character 92).

(118) Metatarsals elongate and slender (0) shortened (1).

In *Utatsusaurus hataii* (MOTANI et al. 1998), *Chaohusaurus geishanensis* (MAISCH in press b; see Fig. 33) and *Thaisaurus chonglakmanii* (MAZIN et al.1991; see Fig. 33) the metatarsals are elongate cylindrical bones with a distinct diaphysis, reminiscent of the homologous elements of the hindlimb of terrestrial tetrapods. Already in the mixosaurids (WIMAN 1910; VON HUENE 1916, 1935; see Fig. 33) these elements have largely lost their elongate shape and are hardly distinguishable from the phalanges of the digits. This trend is carried further in all the shastasaur-grade genera and post-Triassic forms (Figs. 34–35), where the metatarsals are rounded or rectangular elements indistinguishable from the tarsals or phalanges other than by position or size.

(119) Phalanges of hindfin elongate or hourglass-shaped (0) largely rounded or rectangular (1).

The hindfin of *Utatsusaurus hataii* is, apparently, very little known, but MOTANI et al. (1998) show it with hourglass-shaped, elongated posterior phalanges, at least in the proximal part of the hindfin. The same is found in *Chaohusaurus geishanensis* (MAISCH in press b; see Fig. 33), whereas in *Grippia longirostris* the autopodium of the hindfin is not known with certainty (WIMAN 1933; MAZIN 1981b).

In the mixosaurids, the posterior phalanges are also largely hourglass-shaped (REPOSSI 1902; WIMAN 1910; NICHOLLS et al. 1999; see Fig. 33), as it is also the case in *Toretocnemus* and *Qianichthyosaurus* (MERRIAM 1908, LI 1999; see Fig. 33). In all the shastasaur-grade ichthyosaurs in which the posterior phalanges are known and in all the post-Triassic genera, the phalanges are rounded or rectangular and never much longer than they are wide (Figs. 34–35).

(120) Number of toes 5 (0) less than 5 (1).

In the most basal Triassic ichthyosaurs in which the hindfins are well known, *Thaisaurus* (MAZIN et al. 1991; see Fig. 33), *Chaohusaurus* (MAISCH in press b; see Fig. 33), *Mixosaurus* and *Phalarodon* (WIMAN 1910; see Fig. 33), the complete number of five posterior digits is retained. In *Toretocnemus* (Fig. 33) the number has already decreased to three, and there is no evidence that any of the other shastasaur-grade forms possessed more than four toes. Three to four primary toes are also found in the post-Triassic taxa, such as *Temnodontosaurus*, *Leptonectes*, *Eurhinosaurus*, *Suevoleviathan* and *Stenopterygius* (Fig. 35).

4. 6. Main autapomorphies of the Ichthyosauria

(121) Premaxilla short (0) long premaxillary rostrum (1).

The premaxillaries are elongated to form a long, narrow rostrum in all known ichthyosaurs. Although the length of the rostrum is highly variable it is always at least 33 % of the entire skull length, and the snout up to the anterior orbital margin is always longer than 50 % of the entire skull length in all known ichthyosaurs. This feature is neither encountered in basal diapsids nor in parareptiles, diadectomorphs or seymouriamorphs. The only groups that parallel the ichthyosaurs in this respect are the mesosaurs and hupehsuchids. This may or may not be an indication of close relationship between them.

(122) Upper temporal fenestra absent (0) present (1).

A second ichthyosaur autapomorphy is the presence of an upper temporal fenestra of uniquely ichthyosaurian type. Whether or not it is derived from a primarily diapsid condition is irrelevant in this context, as the topology of the surrounding bones at any rate distinguishes it from the fenestrae supratemporales encountered in other groups. The ichthyosaurian temporal fenestra is primitively surrounded by the postfrontal, postorbital, parietal and to an unusually large extent the supratemporal, whereas the squamosal never contributes to its margin (Maisch 1997a, 1998b contra Motani et al. 1998). Both the exclusion of the squamosal and the large extent to which the supratemporal takes part in the border of the fenestra are characteristic features of ichthyosaurs not encountered in any other group of tetrapod and therefore constitute a valid autapomorphy of the group.

(123) Ectopterygoid present (0) absent (1).

A third feature that can be cited is the loss of the ectopterygoid. This is, however, shared with a number of other rather basal amniotes or parareptiles, namely the mesosaurs, captorhinids and testudines, as well as with derived synapsids (including mammals). As it is a simple reductional character it should not be viewed as indicative of close relationship to any of these groups. The presence of an ectopterygoid has been tentatively admitted by Merriam (1908) in the Middle Triassic *Cymbospondylus petrinus*. As pers. obs. of the UCMP specimens at Berekely has shown, this is, however, not correct. In *Utatsusaurus* and *Chaohusaurus* there is no trace of a separately ossified ectopterygoid.

(124) External naris subterminal (0) posteriorly displaced (1).

A fourth feature is the position of the external naris, which is not at or close to the anterior end of the snout (that is in a terminal or subterminal position) in ichthyosaurs, but instead displaced far posteriorly, rather close to the anterior orbital margin, although this feature is not as strongly expressed in basal than it is in derived ichthyosaurs. This posterior displacement of the external nares is, among basal amniotes, only shared by the mesosaurs and hupehsuchids. It also occurs in some derived groups, e. g. the phytosaurs and, to a much lesser extent, the pliosaurid sauropterygians. In both ichthyosaurs and mesosaurs one could argue that the posterior displacement of the external naris is to some extent corellated to the anterior prolongation of the premaxilla into a pronounced rostrum, but at least in primitive ichthyosaurs it is obvious that the naris is not only relatively, but in fact absolutely further posterior than in other basal amniotes.

(125) Hyperphalangy of manus and pes absent (0) present (1).

A fifth and very obvious autapomorphy is the hyperphalangy in the fore- and hindlimbs which needs no further discussion, except that, of course, it also exists in a variety of other secondarily aquatic tetrapods (sauropterygians, cetaceans etc.) and is therefore a feature which must be regarded with caution when used for establishing large-scale phylogenetic analyses.

(126) Thoracal ribs articulate with neural arch and centrum (0) with centrum only (1).

A sixth feature, which is unique among tetrapods, is the exclusively central articulation of the thoracal ribs, which is already displayed by the most basal ichthyosaurs known.

(127) Posterolateral process of postfrontal absent (0) present (1) (MOTANI 1999b, character 9).

(128) Postfrontal participation in upper temporal fenestra absent (0) present (1) (MOTANI 1999b, character 10).

MOTANI also cited the postfrontal contribution to the temporal fenestra and the postfrontal posterolateral process as typical ichthyosaur features (MOTANI 1999b). These might not be primitive for Ichthyosauria, however, as both features are not found in *Thaisaurus chonglakmanii* (MAZIN et al. 1991), which appears as the most basal ichthyosaur currently known in the phylogeny proposed here. MOTANI (1999b) did not include *Thaisaurus* in his analysis. As the genus is little known, it might change its current phylogenetic position as soon as more data on its osteology become available and the postfrontal relationships might turn out to be autapomorphic rather than plesiomorphic. For the time being, the character states displayed by *Thaisaurus* have to be regarded as primitive, however, and the two postfrontal features can thus not be confidently regarded as ichthyosaur autapomorphies.

CALDWELL (1996) cited a number of ichthyosaurian autapomorphies; these are, however, only of value if ichthyosaurs are a priori regarded to be derived diapsids, and many of them (as the frontal contribution to the temporal fenestra or the contact of lacrimal and external naris) are simply wrong. We therefore see no reason for further discussion of CALDWELL's preliminary study.

5. The Genera of Ichthyosaurs

Almost 40 allegedly valid genera of ichthyosaurs are currently recognized. Below, we provide a rigorous survey of the Triassic and post-Triassic ichthyosaurs. It will be shown that recently there has been an artificial increase in the number of Upper Jurassic to Cretaceous ichthyosaur genera, and that all the known forms can most probably be accomodated in only 5 genera. Many of the "shastasaurs" are based on undiagnostic or inadequately known material and must therefore be rejected as nomina dubia. We only recognize 35 clearly valid genera of ichthyosaurs (of which 3 are newly erected) with 69 species (of which one is new). Of these 22 genera and 28 species are Triassic, 12 genera (with 32 species) are Jurassic and 1 genus (with 9 species) is Cretaceous. The obvious trend through the geological ages is that ichthyosaur generic diversity decreased, whereas specific diversity of individual genera increased. Most of the post-Triassic genera are well known, so that 11 out of 13 could be included in the phylogenetic analysis. Many of the Triassic taxa are incompletely known or insufficiently described, but nevertheless 21 of 22 showed enough characters to be included. The only missing genera are *Chacaicosaurus*, *Nannopterygius* and *Rotundopteryx*. The status of *Isfjordosaurus* as an ichthyosaur is not totally certain (see discussion below) and it was therefore also excluded, as well as with regard to the fact that it is certainly the ichthyosaur genus based on the most incomplete material (a single humerus).

Of very few Triassic ichthyosaurs is the osteology completely known and none is completely described, whereas most of the Jurassic genera are known from virtually complete skeletons. The only known Cretaceous genus (*Platypterygius*) is known from comparatively good material but descriptions are again insufficient in some respects and we had no opportunity so far to study much of the relevant original material.

Some of the genera currently accepted in the literature invariably showed to be the sister groups of other genera when introduced in the phylogeny, and the same was the case with certain genera and species currently referred to different genera. These are: *Toretocnemus* MERRIAM, 1903/*Merriamia* BOULENGER, 1904 (synonymized already by MOTANI 1999b), *Eurhinosaurus* ABEL, 1909/ *Excalibosaurus* MCGOWAN, 1986, *Brachypterygius* VON HUENE, 1922/ *Otschevia* EFIMOV, 1998, *Ophthalmosaurus* SEELEY, 1874/*Paraophthalmosaurus* ARKHANGELSKY, 1997 and *Platypterygius* VON HUENE, 1922/ *Plutoniosaurus* EFIMOV, 1997. We have chosen in all these cases to formally synonymize these forms, as the potentially synonymous genera never showed such distinct autapomorphies that it was regarded as appropriate to retain them separately. In the data matrix the data from the earlier described genera are, of course, where possible and necessary, supplemented by those from the junior subjective synonyms.

Three new genera and one new species are introduced below. These are *Callawayia* gen. nov. for "*Shastasaurus*" *neoscapularis* MCGOWAN, 1994a, *Phantomosaurus* gen. nov. for "*Shastasaurus*" *neubigi* SANDER, 1997 and *Rotundopteryx hulklei* gen. et sp. nov. for undoubted ichthyosaur postcrania previously referred to the omphalosaurid *Pessopteryx nisseri* WIMAN, 1910.

Diagnoses are provided for all valid ichthyosaur genera and species. The taxa not included in the phylogeny, the cases where we have proposed taxonomic changes and taxa currently still used in the literature but regarded here as invalid are discussed in somewhat more detail. This taxonomic discussion is necessary, as it is the only way to make the alphataxonomic basis for our phylogenetic analysis transparent and definitely clear.

5.1. The valid genera of ichthyosaurs

1. Genus: *Thaisaurus* Mazin, Suteethorn, Buffetaut, Jaeger & Helmcke-Ingavat, 1991

Type species: *Thaisaurus chonglakmanii* Mazin, Suteethorn, Buffetaut, Jaeger & Helmcke-Ingavat, 1991 (Figs. 24, 30, 33).
Distribution: ? Lower Triassic (the age is uncertain, horizon unspecified) of Khao Tong near Phattalung, Southern Thailand. Holotype and two additional specimens.

Diagnosis. – Small ichthyosaur with delicate snout, conical, pointed teeth with smooth crowns, postfrontal excluded from the temporal fenestra, postorbital with long posterior lamina, foramen parietale between frontal and parietal, humerus, femur and zeugopodial elements extremely elongate and slender, humerus lacks lamina anterior.

2. Genus: *Utatsusaurus* Shikama, Kamei & Murata, 1978

Type species: *Utatsusaurus hataii* Shikama, Kamei & Murata, 1978 (Figs. 1, 10, 24, 30)
Distribution: Lower Triassic (Spathian), Upper Osawa Formation, of Tatezaki (Type locality), Osawa, Okatsu, Hazawa and Onagawa, Miyagi, Japan (Shikama et al. 1978; Motani et al. 1998), the genus has also been described from the Lower Triassic (Vega Phroso member of Sulphur Mountain Formation, Spathian) of Ganoid Range near Wapiti Lake, British Columbia (Nicholls & Brinkman 1993).

Diagnosis. – Small ichthyosaur with moderately slender snout, teeth isodontous, conical, mesiodistally flattened, prefrontal with anterolateral lamina reaching into orbit, prefrontal and postfrontal separate, interclavicle with heart-shaped anterior end and long posterior stylus, two well-developed sacral ribs retained, ilium strongly expanded distally.

3. Genus: *Chaohusaurus* Young & Dong, 1972

Synonyms: *Chensaurus* Mazin, Suteethorn, Buffetaut, Jaeger & Helmcke-Ingavat, 1991.
Anhuisaurus Chen, 1985 nom. praeocc.
Type species: *Chaohusaurus geishanensis* Young & Dong, 1972 (Figs. 1, 14, 17, 24, 30, 33).
Distribution: Lower Triassic (Spathian), Chin Long limestone, Gei Shan, Chao County, Anhui, China (holotype) (Young & Dong 1972); Majiashan Formation, Chao County, Anhui, numerous additional specimens (Chen 1985; Maisch in press b).

Diagnosis. – Small ichthyosaur with very delicate and slender snout, dentition heterodontous, maxillary teeth blunt, posterior dentary teeth rounded and blunt, several maxillary tooth rows, radius with marked anteroproximal prominence, neural spines of caudal vertebrae rather short.

4. Genus: *Grippia* Wiman, 1929

Type species: *Grippia longirostris* Wiman, 1929 (Figs. 1, 10, 14, 17, 20, 24, 30).
Distribution: Lower Triassic (Spathian), *Grippia*-niveau of the Sticky Keep Formation (Wiman 1933; Mazin 1981b), Agardh Range, Sassendalen, Spitsbergen (holotype, lost, and additional specimens), Mt. Milne-Edwards (several specimens), Mount Ibsen, Sassendalen, Spitsbergen (Wiman 1928, 1933; Mazin 1981b), possibly from the Vega Phroso member of the Sulphur Mountain Formation (Spathian) of Ganoid Range near Wapiti Lake, British Columbia (Brinkman et al. 1992, but see Motani 1998a).

Diagnosis. – Very similar to *Chaohusaurus*, but with posterodorsal flange on surangular, posterior thoracal vertebrae elongate, radius with small anteroproximal and anterodistal prominence, distalmost phalanges of forefin rounded.

5. Genus: *Parvinatator* NICHOLLS & BRINKMAN, 1995

Type species: *Parvinatator wapitiensis* NICHOLLS & BRINKMAN, 1995 (Figs. 1, 24).
Distribution: Sulphur Mountain Formation (horizon unknown, probably Lower Triassic), Wapiti Lake, British Columbia, Canada (holotype and isolated forefin, NICHOLLS & BRINKMAN 1995; BRINKMAN et al. 1992; MOTANI 1999b).

Diagnosis. – Very small ichthyosaur with isodontous, conical teeth, lower jaw very high with long processus retroarticularis, very deep jugal-quadratojugal notch, very long and slender processus quadratus of quadratojugal, processus postorbitalis of jugal very long, small neomorphous element distal to pisiform.

6. Genus: *Wimanius* MAISCH & MATZKE, 1998

Type species: *Wimanius odontopalatus* MAISCH & MATZKE, 1998 (Figs. 2, 14).
Distribution: Grenzbitumenzone of Besano Formation (Anisian/Ladinian boundary) of Monte San Giorgio, Tessin, Switzerland (holotype only).

Diagnosis. – Moderately small ichthyosaur (skull length ca. 25 cm), palatine with row of pointed teeth, jugal with suborbital and postorbital processes equal in size, pterygoid with totally straight medial margin.

7. Genus: *Mixosaurus* BAUR, 1887

Synonym: *Sangiorgiosaurus* BRINKMANN, 1998.

Diagnosis. – Small mixosaurids not exceeding 25 cm skull length and 1,5 m total length, tooth implantation subthecodontous to aulacodontous, no plicidentine, orbit very large, postorbital skull segment only about one quarter of anteroposterior orbital diameter in length, sagittal crest low, not protruding far above dorsal skull outline, postaxial sixth finger of forefin rudimentary.

Type species: *Mixosaurus cornalianus* (BASSANI, 1886) (Figs. 2, 17, 20, 24, 33).
Distribution: Grenzbitumenzone of Besano Formation (Anisian/Ladinian boundary) of Besano, Lombardia, Italy (holotype, lost, and neotype, numerous additional specimens, BASSANI 1886; REPOSSI 1902; WIMAN 1912; PINNA 1967) and Monte San Giorgio, Tessin, Switzerland (numerous specimens, VON HUENE 1935, 1939; MAISCH & MATZKE 1997b, 1998c; BRINKMANN 1998b).
Diagnosis. – Posterior maxillary and dentary teeth slender and pointed, widely spaced.

Additional valid species. – *Mixosaurus kuhnschnyderi* (BRINKMANN, 1998a) BRINKMANN, 1998b.
Distribution: Grenzbitumenzone of Besano Formation (Anisian/Ladinian boundary) of Monte San Giorgio, Tessin, Switzerland (BRINKMANN 1998a, b, two specimens).
Diagnosis. – Posterior maxillary teeth robust and blunt, posterior dentary teeth very blunt and rounded, closely spaced.

8. Genus: *Phalarodon* MERRIAM, 1910

Diagnosis. – Small to medium-sized mixosaurids, reaching a skull length of more than 30 cm at maximum, tooth implantation thecodontous, posterior maxillary and dentary tooth crowns always blunt and with a certain amount of mesiodistal elongation, teeth labyrinthodont, orbit of moderate size, postorbital skull segment about one third of anteroposterior orbital diameter, sagittal crest very high, distinctly protruding above dorsal skull outline, well developed sixth postaxial finger (known in *Phalarodon nordenskioeldii* only).

Type species: *Phalarodon nordenskioeldii* (HULKE, 1873) (Figs. 2, 14, 17, 20, 25, 30, 33).
Distribution: Middle Triassic (Ladinian), Tschermakfjellet Formation of Saurie Hook, Isfjord, Spitsbergen (Type locality, HULKE, 1873; WIMAN 1910) as well as Mount Kongress, Dickson Land, Spitsbergen (MAZIN 1984), Middle Triassic (Anisian), Prida Formation, West Humboldt Range, Nevada (MERRIAM 1908, 1910; SANDER & BUCHER 1990), Middle Triassic (Anisian), Llama and Whistler members of the Sulphur Mountain Formation, Wapiti Lake, British Columbia (CALLAWAY & BRINKMAN 1989; NICHOLLS et al. 1999), Grenzbitumenzone of Besano Formation (Anisian/Ladinian boundary) of Monte San Giorgio, Tessin, Switzerland (BRINKMANN 1998a, b).
Diagnosis. – Small species of the genus, skull length not exceeding 30 cm, posterior dome-shaped teeth very large and outnumbering conical teeth in adults.

Additional valid species. – *Phalarodon major* (VON HUENE, 1916) MAISCH & MATZKE in press b.
Distribution: Lower Muschelkalk (Lower Anisian), Aach near Freudenstadt, Baden-Württemberg, Germany (lectotype only).
Diagnosis. – Very large species, skull length considerably exceeding 30 cm, posterior dome-shaped teeth small and extremely compressed laterally, probably few in number.

9. Genus: *Contectopalatus* MAISCH & MATZKE, 1998

Type species: *Contectopalatus atavus* (QUENSTEDT, 1851–52) MAISCH & MATZKE, 1998 (Figs. 2, 10, 17).
Distribution: Lower Muschelkalk (Lower Anisian) of Calw-Althengstett, Baden-Württemberg, Germany (type locality, QUENSTEDT 1851–52; VON HUENE 1916; MAISCH & MATZKE 1998b), Simmozheim, Dietersweiler near Freudenstadt, Palmberg near Glatten, Rohrdorf, Bödigheim, Baden-Württemberg (VON HUENE 1916; MAISCH & MATZKE 1998b, 2000a, in press a) and Upper Muschelkalk (Upper Anisian) of Rüdersdorf near Berlin (EDINGER 1935; MAISCH & MATZKE 1998b, 2000a, in press b), Germany.

Diagnosis. – Moderately heterodontous dentition, all teeth conical with bluntly pointed tips, adult skull size exceeds 50 cm, sagittal crest extremely high in adult (as high as the entire rest of the skull), only 9–10 maxillary teeth arranged in a single row, posterior dentary and maxillary teeth with cross-section of the root in the shape of the number 8, surangular covered by posterior laminae of dentary both medially and laterally, quadrate with extensive fan-shaped ascending flange.

10. Genus: *Toretocnemus* MERRIAM, 1903

Synonyms: *Leptocheirus* MERRIAM, 1903 nom. praeocc., *Merriamia* BOULENGER, 1904.

Diagnosis. – Small ichthyosaur, probably less than 2 m in entire length, skull with large orbit, jugal slender, angular small, forefin with three primary digits, humerus slender with incipient trochanter dorsalis, notches in leading and trailing edges of digits in fore- and hindfin, hindfin not much smaller than forefin, femur with very slender shaft, much expanded distally, fibula not posterodistally inclined, thoracal vertebrae, as far as known, with double rib articulations, neural spines and haemapophyses of tail very long and slender.

Type species: *Toretocnemus californicus* MERRIAM, 1903 (Figs. 18a, 30, 33).
Distribution: Upper Triassic (Carnian), Hosselkus Limestone Formation, Bear Cove, Shasta County, California (holotype only).

Diagnosis. – Thoracal vertebrae much shorter than high.

Additional valid species. – *Toretocnemus zitteli* (MERRIAM, 1903) MOTANI, 1999b (Figs. 18b, 25).
Distribution: Upper Triassic (Carnian), Hosselkus Limestone Formation, Smith's Cove, Shasta County, California (holotype only).
Diagnosis. – Thoracal vertebrae relatively elongate, about as long as high.

11. *Qianichthyosaurus* LI, 1999

Type species: *Qianichthyosaurus zhoui* LI, 1999
Distribution: Wayao member of Falang Formation (Carnian), Huangtutang, Guanling County, Guizhou Province, southwestern China (holotype and paratype only, LI 1999).

Diagnosis. – Small ichthyosaur, less than 2 m entire length, snout very short, orbit very large, forefins with three primary and well developed fourth postaxial digits, neural spines elongate in trunk and anterior tail, haemapophyses very long and slender, as in *Toretocnemus*.

12. Genus: *Cymbospondylus* LEIDY, 1868

Diagnosis. – Very large ichthyosaur, more than 10 m adult length, skull low, with long and very robust snout, dentition thecodontous, premaxilla with long processus supranarialis, nasal reaches posterior to contact postfrontals, big anterior terrace of temporal fenestra, sagittal crest, formed by supratemporal and parietal, frontal reaches anterior margin of temporal fenestra, pterygoid with strong transverse processes, occipital condyle strongly concave, well ossified unpaired interparietal present, angular relatively high posteriorly, dorsomedial portion of scapula elongated into blade-like structure, anterodorsal margin concave, coracoid with reduced anterior extension, medial flange of clavicle very wide, neck region elongate, more than 55 presacral vertebrae, thoracal rib articulations truncate anterior margin of centrum.

Type species: *Cymbospondylus piscosus* LEIDY, 1868.
Distribution: Middle Triassic (Anisian), Prida Formation, New Pass, Toiyabe Range, near Austin, Nevada (LEIDY 1868; MERRIAM 1902, 1908; holotype only).
Diagnosis. – Dorsal vertebral centra more than half as long than high.

Additional valid species. – *Cymbospondylus petrinus* LEIDY, 1868 (Figs. 3, 10, 13, 15, 17, 18c-m, 20, 25, 30, 33).
Distribution: Middle Triassic (Anisian), Prida Formation, Star Canyon, Humboldt County, Nevada (Type locality, LEIDY 1868; MERRIAM 1902), West Humboldt Range, Nevada (MERRIAM 1902, 1908).
Diagnosis. – Postorbital skull segment very long, longer than orbit, postfrontal extends far beyond orbit, excluded from orbital margin by postorbital, humerus long and slender, ulna with posterior notch, more than 65 presacral vertebrae, dorsal vertebral centra more than twice as high as long.

Cymbospondylus buchseri SANDER, 1989 (Fig. 25).
Distribution: Grenzbitumenzone of Besano Formation (Anisian/Ladinian bondary) of Monte San Giorgio, Tessin, Switzerland (SANDER 1989).
Diagnosis. – Postorbital skull segment rather short, postfrontal does not extend far beyond orbit, humerus rather short and wide, ulna convex posteriorly, dorsomedial process of scapula wide, dorsal vertebrae similar to *C. piscosus* (possibly the two species are synonymous, but as *C. buchseri* is based on very good material it is probably best to keep the two separate at the moment).

The genus is also known from the Muschelkalk (Ansisian) of Germany (VON HUENE 1916) and Lunéville, France (CORROY 1928; BARDET & CUNY 1993) and the Tschermakfjellet Formation (Anisian/Ladinian) of Spitsbergen (SANDER 1992).

13. Genus: *Phantomosaurus* gen. nov.

Type-species: *Shastasaurus neubigi* SANDER, 1997 (Figs. 15, 34).
Distribution: Upper Muschelkalk, *pulcher/robustus*-Zone (Late Anisian), Karlstadt/Main, Bavaria, Germany.
Derivatio nominis: Named after the protagonist of the famous novel "Phantom of the opera" (1911) by GASTON LOUIS ALFRED LEROUX (1868–1927), who had to hide his disgraced face behind a mask. The reason is the horrible and disgraceful damage to the original bones of the skull of the holotype caused by inappropriate acid preparation.

Diagnosis. – Large ichthyosaur, skull length exceeds 50 cm, basioccipital condyle saddle shaped, opisthotic tightly sutured to basioccipital, supernumary paired ossifications dorsal to supraoccipital, articular exposed on outside of lower jaw posterior to surangular, anterior vertebral centra extremely amphicoelous, with ventrolateral keels, zygapophyses very extensive and totally horizontal, hindfin with very long and slender femur, tibia and fibula.

Discussion. – This particular ichthyosaur is known exclusively from a single incomplete, badly preserved and strongly disarticulated skeleton from the Upper Muschelkalk of Southern Germany. It does not belong to the genus *Shastasaurus*, as shown by the retention of many plesiomorphic features (see also MAISCH 2000). It has an opisthotic which is most similar to that of *Mixosaurus cornalianus* among ichthyosaurs where it is known but, in contrast to the latter, is tightly sutured to the basioccipital which is a unique feature. The carotid foramina are paired and situated in the centre of the basal plate of the parasphenoid, the articular is tightly sutured to the surangular and is well visible in lateral view of the lower jaw both along the dorsal and – uniquely – the posterior margin of the retroarticular process. The zygapophyses of the cervical and anterior thoracal neural arches are extensive and totally horizontal, strong lateroventral keels are found on the corresponding vertebral centra (not found in any other ichthyosaur). The femur is close to that of *Cymbospondylus petrinus* (MERRIAM 1908) and the posterior zeugopodium is very elongated with the tibia and fibula retaining long diaphyses and enclosing a large spatium interosseum. These, as well as many other peculiarities serve to distinguish it not only from North American *Shastasaurus* but actually all other known ichthyosaurs. The taxon is currently under re-study by us and a detailed re-description, correcting the original account of SANDER (1997), will appear elsewhere.

From the structure of the skull and the hindlimb, *Phantomosaurus* is closest to *Cymbospondylus*, but slightly more advanced by possessing a saddle-shaped instead of a deeply concave occipital condyle. It forms the sister taxon of *Cymbospondylus* in the phylogeny proposed here and is consequently referred to the family Cymbospondylidae VON HUENE, 1948.

14. Genus *Rotundopteryx* gen. nov.

Derivatio nominis: Lat. rotundus = round, pteryx = wing or fin. Chosen because of the rounded shape of the humerus and most of the referred fin elements of this ichthyosaur.

Type species: *Rotundopteryx hulkei* sp. nov.

Holotype: The complete humerus, figured by WIMAN (1910, pl. 8, fig. 1), Palaeontological Museum of the University of Upsala. (Fig. 36)

Locus typicus: Middelhook, Isfjord, Spitsbergen.

Stratum typicum: Lower Saurian Niveau (Spathian).

Derivatio nominis: In honour of JOHN WHITTAKER HULKE, renowned British palaeoherpetologist of the 19th century, who was the first to describe Triassic ichthyosaurs from Spitsbergen.

Diagnosis. – A medium-sized ichthyosaur with a humerus without distinct caput humeri, a large anterior flange which is not notched but retains a convex anterior outline, radial facet marginally larger than ulnar facet, articulatory ends of limb bones very little ossified and probably capped with large amounts of cartilage in life which leads to a characteristic surface structure of rugosities and pits.

Referred material: elements figured by WIMAN 1910, Palaeontological Museum of the University of Upsala:
Pl. 8, figs. 2, 3, 4 humeri.
Pl. 8, figs. 5–10, zeugopodials.
Pl. 8, figs. 20–33, podials.
Pl. 9, figs. 1–4, femora.
Pl. 9, figs. 6–11(? fibulae and tibiae).

Of the material described by MAZIN (1983b), the following is referrable to *Rotundopteryx*: SVT 219 (humerus), SVT 239, 245, 247 (zeugopodials), SVT 236, 253, 257 (podials) , SVT 230 (femur) SVT 222, 223 (tibia ?).

Additional material may pertain to this taxon, but evidence is scanty at best and referral should await the discovery of additional, articulated specimens.

Discussion. – The new genus must be discussed in relation to *Pessopteryx*. The genus *Pessopteryx* WIMAN, 1910, usually regarded as a junior subjective synonym of *Omphalosaurus* (e. g. MAZIN 1983b), was recently resurrected by MOTANI (1999b). Reasons for this are unclear, however. A holotype of *Pessopteryx nisseri* was not designated by WIMAN (1910) and MAZIN (1983b), who revised the material, did not designate a lectotype. Holotypes were equally not designated by WIMAN for any of the other three species of *Pessopteryx*, *P. minor* (the type of MOTANI's genus *Isfjordosaurus*), *P. arctica* and *P. pinguis*, all erected in 1910 on the basis of isolated humeri from the Lower Saurian Niveau of Spitsbergen. All these taxa were treated as junior subjective synonyms of *P. nisseri* by MAZIN (1983b) and – in the case of *P. arctica* and *P. pinguis* – as nomina dubia by MOTANI (1999b), a decision with which we agree.

Pessopteryx nisseri is based on a scattered assemblage of cranial (jaw) and postcranial fragments. The cranial fragments with their typical dentition show great similarity to the enigmatic ichthyosaur-like reptile *Omphalosaurus nevadanus* MERRIAM, 1906 from the Anisian Prida Formation of Nevada. This was first pointed out by MERRIAM (1911) who referred to the species as *Omphalosaurus* (?) *nisseri*. WIMAN (1916) acknowledged the great similarity of the jaw fragments of *P. nisseri* to *O. nevadanus*, and intended to separate them from *P. nisseri*, but this was never done in an explicit way. Therefore there are no two named species "*Omphalosaurus nisseri*" and "*Pessopteryx nisseri*", as incorrectly stated by MOTANI (1999b). MAZIN (1983b) believed that all of WIMAN's *Pessopteryx* material belonged to a single species and treated it as a particular species of *Omphalosaurus*, a decision followed by all subsequent authors up to MOTANI (1999b).

The problem now of course is: What is to be regarded as the type-material of *P.*

nisseri, what means, is it an omphalosaur or an ichthyosaur? WIMAN's and MAZIN's papers are of no help in this question. As, particularly since MAZIN's work, it has been generally acknowledged that *P. nisseri* is an omphalosaur, it appears to us of little use to refer to this species, restricted to the postcranial material, as an ichthyosaur, as done by MOTANI (1999b).

We regard *Pessopteryx* WIMAN, 1910 as a junior subjective synonym of *Omphalosaurus* and the jaw fragments specified and figured by WIMAN (1910: 140, pl. 9, figs. 23–30) as the syntypic series of *Pessopteryx nisseri*. The question remains how to treat the undoubted ichthyosaur remains which occur together with the *P. nisseri* teeth taxonomically. MOTANI (1999b) correctly pointed out that the humerus of "*Pessopteryx*" resembles that of "shastasaurs", but differs from all other known taxa by its convex and unnotched anterior margin (which is, in fact, a plesiomorphic trait). As at least the humeri originally referred to *P. nisseri* are diagnostic at the generic and specific level, there is a valid ichthyosaur taxon in the Lower Saurian Niveau of Spitsbergen among WIMAN's material.

We propose the new generic and specific name *Rotundopteryx hulkei* for this particular ichthyosaur. Because so little of its skeletal anatomy is known, it is difficult to place *Rotundopteryx* phylogenetically. It is, however, clear that it is more highly derived than the mixosaurs from the shape of the humerus, which corresponds most closely to such taxa as *Mikadocephalus*, *Besanosaurus* and *Shastasaurus* among known ichthyosaurs. The interesting fact is, that *Rotundopteryx* is much older than any of these taxa, being Spathian in age.

15. Genus: *Californosaurus* KUHN, 1934

Synonym: *Delphinosaurus* MERRIAM, 1905 nom. praeocc.

Type species: *Californosaurus perrini* (MERRIAM, 1902) KUHN, 1934 (Figs. 18 q-r, 21, 26, 31, 34).

Distribution: Upper Triassic (Carnian), Hosselkus Limestone Formation of The Cove, Shasta County, California (MERRIAM 1902, 1908).

Diagnosis. – Medium-sized ichthyosaur, about 3 m in length, forefin tridactyl, humerus short but with extensive posterior shaft and deep, wide anterior notch, radius and ulna moderately elongate, scapula and coracoid with reduced anterior extensions, glenoid and contact facets enlarged, ilium with posterior process, pubis with very wide obturator notch, slightly smaller than ischium, thoracal vertebral centra rather elongate, more than two thirds as long as high, thoracal neural arches short and wide.

16. Genus: *Shastasaurus* MERRIAM, 1895

Diagnosis. – A large ichthyosaur, total length of adults exceeding 7 meters. Isodontous dentition, teeth with mesial and distal carinae, premaxilla with long processus supranarialis forming entire dorsal margin of external naris, posterior portion of both maxilla and dentary edentulous, large, anteroposteriorly elongate orbit, relatively short postorbital skull segment (shorter than anteroposterior orbital diameter), anterior terrace of temporal fenestra very small, frontal forms part of it but does not contribute to anterior margin of temporal fenestra proper, lacrimal with a plethora of small nutritive foramina instead of big, large vascular foramen, jugal very robust and thick, supratemporal with high, short ramus anterior, postorbital forms most of the lateral margin of the temporal fenestra internally and probably a short segment externally, so that postfrontal and supratemporal are (very probably) not in contact, temporal fenestra large, ramus occipitalis of parietal massive with rectangular cross section, expanded rugose parietal platform behind foramen parietale, palate with very small fenestra interpterygoidea, parasphenoid without obvious carotid entrance, artery probably entering between parasphenoid and basioccipital, basioccipital condyle convex or possibly saddle-shaped, probably more than 50 presacral and more than 10 cervical vertebrae, atlas centrum convex anteriorly with small concavity, cervical ribs dicephalous, thoracal, sacral and caudal ribs unicephalous, neural arches with high and robust processus spinosi in cervical and trunk region, rounded in cross section, often with strong anterior and posterior and weaker lateral ridges, scapula with reduced anterior but rather large posterior extension of blade, coracoid with anterior extension smaller than posterior one, humerus of subrectangular shape with small anterodorsally oriented caput and little development of crista deltopectoralis, humerus and radius anteriorly notched, radius and ulna very short, rectangular, with small spatium interosseum, intermedium apparently very small, pelvic girdle with pubis and ischium of similar size, pubis with posteriorly open obturator notch, ilium distally expanded, big spatium interosseum retained between tibia and fibula.

Type species: *Shastasaurus pacificus* MERRIAM, 1895.

Distribution: Upper Triassic (Carnian), Hosselkus Limestone Formation, Shasta County, California.

Diagnosis. – Pubis with almost closed obturator notch in posterior margin, proximal margin of pubis as wide as distal margin, posterior thoracal vertebral centra more than half as long as they are high.

Additional valid species. – *Shastasaurus alexandrae* MERRIAM, 1902 (Figs. 3, 10, 15, 18 n-p, 21, 25, 34).

Distribution: Upper Triassic (Carnian), Hosselkus Limestone Formation, The Cove, Shasta County, California (MERRIAM 1902, 1908), Upper Triassic (Carnian), El Antimonio District, Sonora, Mexico (CALLAWAY & MASSARE 1989; MAISCH 2000).

Diagnosis. – Pubis with obturator notch more widely open and proximal margin narrower than distal margin, posterior thoracal vertebral centra more than twice as high as they are long. Otherwise as for genus.

17. Genus: *Besanosaurus* DAL SASSO & PINNA, 1996

Type species: *Besanosaurus leptorhynchus* DAL SASSO & PINNA, 1996 (Figs. 3, 20, 25, 31, 34).

Distribution: Grenzbitumenzone of Besano Formation (Anisian/Ladinian boundary), Besano, Lombardy, Italy (DAL SASSO & PINNA 1996, type locality) and Monte San Giorgio, Tessin, Switzerland.

Diagnosis. – Very large ichthyosaur (entire length exceeds 5 m), teeth isodontous, very small, snout very gracile and slender, frontal unpaired and anteriorly extended over nasals, no foramen parietale, very small processus postnarialis of maxilla, ratio skull length-entire length about 1:10, humerus longer than wide, with anterior notch and conspicuous posterior shaft, radius elongate (compared to *Mikadocephalus*).

18. Genus: *Mikadocephalus* MAISCH & MATZKE, 1997

Type species: *Mikadocephalus gracilirostris* MAISCH & MATZKE, 1997 (Figs. 3, 15, 21, 25, 31, 34, 36 a-f).

Distribution: Grenzbitumenzone of Besano Formation (Anisian/Ladinian boundary), Monte San Giorgio, Tessin, Switzerland (holotype and several additional specimens), Tschermakfjellet Formation (Ladinian) of Middelhook, Isfjord, Spitsbergen (WIMAN 1910).

Diagnosis. – Medium-sized ichthyosaur, skull length exceeds 50 cm, total length about 3 m, snout extremely gracile and slender, orbit moderately large, teeth isodontous, pointed, thecodont to aulacodont, pterygoid with concave medial margin, big interpterygoid vacuity developed, quadrate with triangular medioventral process, ratio skull length – entire length about 1:5, humerus short and wide, with rounded margins, posterior shaft almost entirely reduced.

19. Genus: *Shonisaurus* CAMP, 1976

Type species: *Shonisaurus popularis* CAMP, 1976 (Figs. 21, 25, 31, 34).

Distribution: Luning Formation (Upper Carnian), West Union Canyon, Shoshone Mountains, Nevada (CAMP 1976, 1980).

Diagnosis. – Very large ichthyosaur, adult length exceeds 12 m, very long but robust snout, foramen parietale between frontal and parietal, coronoid very large, basioccipital with strongly convex condyle, fore- and hindfins essentially tridactyl, ulna very small in relation to radius, intermedium probably lost, scapula rather long and slender with reduced anterior and posterior extensions, thoracal and caudal vertebral centra very high, thoracals more than three times as high as long.

20. Genus: *Callawayia* gen. nov.

Type-species: *Shastasaurus neoscapularis* MCGOWAN, 1994a (Figs. 21, 26).

Distribution: Upper Triassic (Norian), Pardonet Formation, Peace Reach, Williston Lake, British Columbia, Canada (MCGOWAN 1994a).

Derivatio nominis: After the late Dr. R. M. CALLAWAY, who made a lot of important contributions to the knowledge of Triassic ichthyosaurs, particularly from North America.

Diagnosis. – Small ichthyosaur, total length probably around 2 m, parasphenoid reduced in size, basisphenoid enlarged, carotid foramen paired in basisphenoid, interpterygoid vacuities well developed, scapula with elongated dorsomedial blade and anterior and posterior extensions completely reduced, coracoids with clear medial symphysis, clavicle very slender, humerus short, forefin tridactyl, ulna small, intermedium possibly absent.

Discussion. – This taxon, described by MCGOWAN in 1994 as a new species of *Shastasaurus*, *Shastasaurus neoscapularis*, is one of the most interesting derived Triassic ichthyosaurs known. Additional specimens have been found by E. L. NICHOLLS (pers. comm.) and colleagues and are currently under study.

It has already been stated elsewhere (MAISCH 2000) that this species is not referrable to *Shastasaurus* but represents another genus. Its closest affinities evidently lie with the post-Triassic ichthyosaurs. Most important of all – and this was clearly recognized by MCGOWAN 1994 and his reason for choice of the specific name – it shares with them the shape of the scapula, with its elongated blade-like medial portion, reduced anterior and posterior extensions and superficial resemblance to the scapula of a terrestrial tetrapod. This character alone is clearly sufficient to exclude

Shastasaurus neoscapularis from the genus *Shastasaurus*, which has a more plesiomorphic scapula than even *Mikadocephalus* or *Californosaurus*. There are some similarities between *Shastasaurus neoscapularis* and *Shonisaurus popularis* in the shape of the coracoid, which is not so much similar to that of *Shastasaurus alexandrae* (McGowan 1994a) but to that of *Shonisaurus*. The coracoids of *Shastasaurus neoscapularis* also have an essentially straight medial margin, along which they meet to form a well-defined symphysis (McGowan 1994a, fig. 6). In the specimens of *Shastasaurus alexandrae*, where the coracoids are known (Merriam 1902, 1908) the medial margin of the bone is essentially rounded and no real symphysis is formed.

Little is known about the skull of *Shastasaurus neoscapularis*, but the angular is seen to form a considerable part of the external mandibular surface and the dentition consists of small, pointed teeth. The orbits are large and the snout is of moderate length. The latter two features might in part be correlated with the very probably juvenile status of the specimen (McGowan 1994a). The structure of the base of the skull is very interesting. The basisphenoid appears to form most of the basis cranii, whereas the parasphenoid forms the processus cultriformis and a posterior extension which separates the foramina for the carotis interna. As noted earlier (Maisch & Matzke 1997a) this is most reminiscent of the situation in *Temnodontosaurus*, and, if Camp's description is correct, similar to the situation in *Shonisaurus* as well.

The forefin of *Shastasaurus neoscapularis* is essentially tridactyl. Most of the third finger was certainly lost during excavation in the holotype specimen, as its presence is indicated by some bone fragments along the trailing edge of the fin (compare McGowan 1994a, 1997a). This is definitely shown by the newly discovered specimens (E. L. Nicholls pers. comm.). The humerus is similar to that of both *Shastasaurus* (Merriam 1902, 1908) and *Shonisaurus* (Camp 1980). In the fin, the radius is unnotched, as in *Shonisaurus* (Camp 1980) but in contrast to *Shastasaurus* (Merriam 1902), whereas the radial and all the more distal elements are notched in both *Shonisaurus* and *Shastasaurus neoscapularis* (Camp 1980; McGowan 1994a, 1997a), but the radial is unnotched in *Shastasaurus alexandrae* (Merriam 1902, 1908).

Although these latter differences are probably of minor importance, it is in summa clear, that *Shastasaurus neoscapularis* has more in common with *Shonisaurus popularis* on one and the post-Triassic ichthyosaurs on the other hand than with any of the described species of *Shastasaurus*. The small size of the animal, with a skull length of only 45 cm and a probable entire lenth of only 250 cm at maximum renders it likely that it could be a juvenile. It is, however, interesting in this context to compare *Shastasaurus neoscapularis* to the juvenile of *Temnodontosaurus* (probably *T. trigonodon*) (Maisch 1998a) formerly identified as *Leptopterygius integer* mut. *dissidens* by von Huene (1931a). This specimen has a presacral length (excluding the skull) of 55 cm, an orbital diameter of 12 cm, a postnarial skull length of 20 cm and a forefin 23,5 cm long. These measurements come close to those in the type of *Shastasaurus neoscapularis*, particularly the small size of the forefin as compared to the skull. Nevertheless, the juvenile *Temnodontosaurus* is certainly more immature, as it lacks notches in the first digit of the forefin and the coracoids are rounded and lack an anterior notch or well defined symphysis (von Huene 1931a; Maisch 1998a). It therefore appears likely, that the type of *Shastasaurus neoscapularis* is a juvenile of a larger-growing ichthyosaur, but that it did probably not exceed a length of 5 or 6 meters when fully grown. It is thus distinctly smaller than *Shonisaurus popularis* or *Temnodontosaurus*.

21. Genus: *Hudsonelpidia* McGowan, 1995

Type species: *Hudsonelpidia brevirostris* McGowan, 1995 (Figs. 26, 31).
Distribution: Upper Triassic (Norian), Pardonet Formation, Peace Reach, Williston Lake, British Columbia, Canada (McGowan 1995).

Diagnosis. – Small ichthyosaur, less than 2 m in length, snout short, orbits large, anterior neural spines very elongated, haemapophyses still ossified, spatium interosseum in forelimb reduced to foramen, fore- and hindfins at least tetradactyl, ischium and pubis elongate and slender, pubic foramen and notch entirely lost, tibia remains elongate.

22. Genus: *Macgowania* Motani, 1999b

Type species: *Ichthyosaurus janiceps* McGowan, 1996a (Figs. 4, 21, 26).
Distribution: Upper Triassic (Norian), Pardonet Formation, Peace Reach, Williston Lake, British Columbia, Canada (McGowan 1996a, type locality, holotype and isolated forefin, McGowan 1991, see Motani 1999b).

Diagnosis. – Medium-sized ichthyosaur, probably reaching 3 m in length, orbit large, naris very large, jugal-quadratojugal notch very deep, humerus with almost completely reduced anterior flange, zeugo- to autopodial elements form polygonal mosaic pattern, zeugopodials very short, enclose very small spatium interosseum, radius and most following anterior fin elements notched, three primary, one accessory postaxial digit.

23. Genus: *Temnodontosaurus* Lydekker, 1889

Synonym: ?*Proteosaurus* Home, 1814.

Diagnosis. – Very large ichthyosaurs, exceeding 12 m in length, skull large with robust snout, maxilla long anterior to naris, postorbital skull segment long, carotid foramina paired in basisphenoid, separated by parasphenoid, processus cultriformis with strong ventral keel, forefins with three primary and one postaxial accessory digit, proximal elements form mosaic, more distal elements rather rounded, at least two notches in forefin, hindfin more than two thirds the length of forefin, tailbend not very strong (less than 35°).

Type species: *Temnodontosaurus platyodon* (Conybeare, 1822) Lydekker, 1889 (Figs. 4, 19a, 22, 26, 34).
Distribution: Lower Jurassic (Upper Hettangian-Lower Sinemurian), Lyme Regis, Dorset, England (Conybeare 1822; Hawkins 1840; Owen 1881; von Huene 1922; McGowan 1974a), Lower Sinemurian (Bucklandi Zone), Herlikofen near Schwäbisch Gmünd and (Turneri Zone) Dusslingen, Baden Württemberg, Germany (Berckhemer 1938; Maisch 1999), Arlon, Lorraine, Belgium (Godefroit 1993b).
Diagnosis. – Maxilla low, with straight suture to premaxilla, jugal and premaxilla not in contact, angular and surangular make up more than half of lateral mandibular surface, quadratojugal very high, contacts postfrontal, snout very long and slightly dorsally curved, teeth with mesial and distal carinae in adults, few notches in forefin.

Additional valid species. – *Temnodontosaurus trigonodon* (von Theodori, 1843) Lydekker, 1889 (Figs. 4, 13, 16, 17, 26, 31).
Distribution: Lower Jurassic (Lower Toarcian), Unnersdorf near Banz (von Theodori 1843, type locality), Ansbach, Bavaria, Holzmaden, Ohmden, Schömberg, Dotternhausen, Schlierbach near Göppingen, Frittlingen, Reichenbach near Aalen, Baden-Württemberg, Germany (Fraas 1891; von Huene 1922, 1931a; Maisch 1998c), Lower Toarcian of Saint

Colombe, Yonne, France (Gaudry 1892), Upper Toarcian, Aalen, Baden-Württemberg, Germany (pers. obs. of SMNS material).

Diagnosis. – Maxilla low, with straight suture to premaxilla, jugal and premaxilla in contact, vomer short, angular and surangular of normal proportions, quadratojugal moderately high, does not reach postfrontal, snout very long and straight or slightly ventrally curved, teeth with two to four carinae in adults, most elements of first digit notched.

Temnodontosaurus acutirostris (Owen, 1840) Maisch, 1997 (Fig. 11)

Distribution: Lower Jurassic (Lower Toarcian), Whitby, Yorkshire, England (Owen 1840, 1881; Seeley 1880).

Diagnosis. – Maxilla low, with straight suture to premaxilla, orbit relatively large, jugal contacts premaxilla, snout rather gracile and slender, ending in a pointed tip.

Temnodontosaurus nuertingensis (von Huene, 1931) Maisch & Hungerbühler, 1997

Distribution: Lower Jurassic (Lower Pliensbachian), Nürtingen, Baden-Württemberg, Germany (von Huene 1931a; Maisch & Hungerbühler 1997a, holotype only).

Diagnosis. – Maxilla high, with serrated suture to premaxilla, vomer very long, teeth without carinae, snout long and straight.

Temnodontosaurus eurycephalus McGowan, 1974 (Fig. 4)

Distribution: Lower Jurassic (Lower Sinemurian, Bucklandi Zone) of Lyme Regis, Dorset, England (holotype only, Owen 1881; McGowan 1974a).

Diagnosis. – Snout and lower jaw very short and high, jaws with few but very large teeth, orbit very small.

24. Genus: *Leptonectes* McGowan, 1996b

Synonym: *Leptopterygius* von Huene, 1922, nom. praeocc.

Diagnosis. – Skull with long and exceedingly slender snout but no distinct overbite, orbits very large but directed largely laterally and only slightly anteriorly, forefins without notches except in radius, with few usually rounded and rather widely spaced phalanges, hindfins less than two thirds of the length of the forefins.

Type species: *Leptonectes tenuirostris* (Conybeare, 1822) McGowan, 1996b (Figs. 5, 11, 17, 27, 32, 34).

Distribution: Uppermost Triassic (Rhaetian), Street, Somerset, England (neotype locality, McGowan 1974b) to Lower Jurassic (Hettangian-Sinemurian) of Lyme Regis, Dorset, England, Lower Sinemurian (Turneri Zone) of Dusslingen, Baden-Württemberg, Germany (von Huene 1922; Maisch 1999).

Diagnosis. – Small species never exceeding 4 m in length, snout very long.

Additional valid species. – *Leptonectes solei* (McGowan, 1993) McGowan, 1996b.

Distribution: Lower Jurassic (Upper Sinemurian, Obtusum Zone), Charmouth, Dorset, England (type-locality, McGowan 1993), Lower Sinemurian (Semicostatum Zone), Lyme-Regis, England (McGowan 1993).

Diagnosis. – Large species, exceeding 5 m in length, snout very long.

Leptonectes moorei McGowan & Milner, 1999.

Distribution: Lower Jurassic (Lower Pliensbachian), Seatown, Dorset, England (holotype only, McGowan & Milner 1999).

Diagnosis. – Small species, not exceeding 3 m in length, snout short.

The genus is also indicated in the Pliensbachian of Lorraine, Belgium (Godefroit 1992).

25. Genus: *Eurhinosaurus* ABEL, 1909

Synonym: *Excalibosaurus* MCGOWAN, 1986

Diagnosis. – Large ichthyosaur, reaching > 6 m adult size, upper jaw extremely elongate and slender, lower jaw slender and weak, but much shorter, distinct overbite, orbits directed anterolaterally, temporal fenestrae extremely small, supratemporal very large and wide in dorsal view, reaches orbital margin, frontals covered by nasals in dorsal view, prefrontal very small, postfrontal large, postorbital skull region very narrow, postorbital lacks lamina posterior, quadratojugal with long posteromedial processus quadratus and pierced by foramen of unknown significance, palate with small interpterygoid vacuities, pterygoid short and wide, parasphenoid ends anterolateral to unpaired carotid foramen, lower jaw with long processus retroarticularis, fore- and hindfins long and slender, with three primary digits each, notches in leading edge present in variable number, hindfins more than two thirds the length of forefins, dorsal ribs not clearly double-headed, tailbend slight, no lunate tailfin, caudal vertebrae with cartilaginous chevrons.

Type species: *Eurhinosaurus longirostris* (VON JAEGER, 1856) ABEL, 1909 (Figs. 5, 11, 16, 17, 22, 27, 32, 35).

Distribution: Lower Jurassic (Lower Toarcian), Holzmaden, Ohmden, Bad Boll, Aalen, Dotternhausen, Schömberg, Baden-Württemberg, Germany (VON JAEGER 1856; VON HUENE 1922, 1928, 1931b, 1951), Banz, Bavaria, Germany (VON THEODORI 1854; VON HUENE 1922); Whitby, Yorkshire, England (MANTELL 1851; MCGOWAN 1994b), Dudelange, Luxembourg (GODEFROIT 1994), Pic-Saint-Loup, Montagne Noire (LAMAUD 1979) and Noirefontaine, Franche Comté (PHARISAT et al. 1993), France.

Diagnosis. – Overbite very strong, mandible less than 60 % of skull lenth, forefin extremely long and slender.

Additional valid species. – *Eurhinosaurus costini* (MCGOWAN, 1986) comb. nov.

Distribution: Lower Jurassic (Lower Sinemurian, Bucklandi Zone), Lilstock, Somerset, England (MCGOWAN 1986, holotype only).

Diagnosis. – Overbite moderate, mandible exceeding 60 % of skull length, forefin moderately long and slender.

26. Genus: *Suevoleviathan* MAISCH, 1998

Diagnosis. – Large ichthyosaurs, adult size more than 4 m, skull low, orbit medium-sized, premaxilla and dentary with well developed grooves extending in alternating fashion from fossa praemaxillaris and fossa dentalis, maxilla short anteriorly, jugal robust and short, squamosal large, forming most of posterior margin of cheek and reaching down to ventral margin of skull, processus quadratus of quadratojugal thus apparently separated from the main body of the bone, pre- and postfrontal subequal in size, teeth robust and crenulated in typical fashion, only 42–44 presacral vertebrae, postflexural segment of tail very long and flexible, neural arches of posterior thoracal region very low with expanded processus spinosi, rib articulation of thorax unicipital posteriorly, interclavicle unossified, forefin with three primary digits, third digit subdivided into three secondary rays, no notches in leading edge of forefin, digits of forefin fanning out distally, most autopodial elements rounded and widely spaced, pelvis tripartite, pubis slender and curved, ischium broad and subrectangular, hindfin tridactyl, most elements of first digit notched.

Type species: *Suevoleviathan disinteger* (VON HUENE, 1926a) MAISCH, 1998 (Figs. 5, 27, 32, 35).

Distribution: Lower Jurassic (Lower Toarcian), Holzmaden, Baden-Württemberg, Germany (VON HUENE 1926a; MAISCH 1998a, in press a).
Diagnosis. – Maxilla forms largest part of ventral narial margin and takes part in anteroventral orbital margin, posterior maxillary and dentary teeth reduced, processus ventralis posterior of lacrimal short, jugal very robust, secondary premaxillary and dentary fossae very clear and regular, angular high posteriorly, dorsal contour of skull very flat, 44 presacrals, 88 preflexurals, anterior thoracal and cervical processus spinosi rather high and slender, coracoid with minimal craniolateral incision, ilium with wing-shaped anterior process.

Additional valid species. – *Suevoleviathan integer* (BRONN, 1844) MAISCH, 1998 (Fig. 5).
Distribution: Lower Jurassic (Lower Toarcian), Holzmaden, Baden-Württemberg, Germany (VON HUENE 1926a; MAISCH 1998a, in press a).
Diagnosis. – Maxilla low, reaches neither naris nor orbit, posterior maxillary and dentary teeth not reduced, lacrimal with long processus ventralis posterior, jugal slender, secondary premaxillary and dentary fossae irregular and not very well developed, angular very low posteriorly, dorsal countour of skull moderately vaulted, 42 presacrals, (?) less than 88 preflexurals, anterior thoracal and cervical processus spinosi rather short, coracoid rounded, ilium without anterior process.

27. Genus: *Ichthyosaurus* DE LA BECHE & CONYBEARE, 1821

Synonyms: *Eurypterygius* JAEKEL, 1904
Protoichthyosaurus APPLEBY, 1979

Diagnosis. – Moderately large to large ichthyosaurs, skull length between 30 and 60 cm, quadratojugal with long processus quadratus, humerus robust and short, forefin with four primary digits and postaxial accessories, fin elements form a completely closed polygonal mosaic pattern in the fore- and hinfin, except the distal tips, coracoid with anterior and posterior notches, about 44 presacral vertebrae, neural spines of thoracal vertebral column long.

Type species: *Ichthyosaurus communis* CONYBEARE, 1822 (Figs. 6, 11, 13, 16, 22, 27, 32).
Distribution: Lower Jurassic (Hettangian – Lower Sinemurian) of Lyme Regis, Dorset and Street, Somerset, England (MCGOWAN 1974b), Upper Sinemurium, Lorraine, Belgium (GODEFROIT 1996).
Diagnosis. – Large species, skull reaching more than 60 cm in length, snout robust and moderately long, orbit moderately large, less than 20 maxillary teeth, teeth robust and curved, with blunt tips, roots never abruptly expanding, lacrimal with enormous anterior extension below premaxilla, jugal with rounded cross-section, quadratojugal moderately short dorsoventrally, quadrate ascending plate robust.

Additional valid species. – *Ichthyosaurus intermedius* CONYBEARE, 1822 (Figs. 6, 17, 35).
Distribution: Lower Jurassic (Hettangian or Sinemurian), Lyme Regis (CONYBEARE 1822, type, lost), Street near Somerset (OWEN 1881; APPLEBY 1979), ?Lower Jurassic, ?Whitby, Yorkshire, England (MAISCH 1997b).
Diagnosis. – Small species, skull less than 40 cm in length, skull proportions similar to *I. communis*, number of maxillary teeth much larger than 20, teeth heavily striated, crowns very long and slender, roots often expanding rather abruptly, posterior maxillary teeth situated below orbit and distinctly recurved, jugal with dorsoventrally compressed suborbital ramus with lateral ridge, quadratojugal very short dorsoventrally, ascending plate of quadrate very delicate.

Ichthyosaurus breviceps OWEN, 1881 (Fig. 6).
Distribution: Lower Jurassic (Lower Sinemurian, Bucklandi Zone), Lyme Regis, Dorset, England (type, MCGOWAN 1974b), Upper Hettangian – Lower Sinemurian, Lyme Regis (additional specimens).
Diagnosis. – Orbit very large, snout extremely short, less than 20 maxillary teeth, teeth

robust and large, maxilla with small processus postnarialis, premaxilla with long processus supranarialis reaching prefrontal.

Ichthyosaurus conybeari LYDEKKER, 1888 (Fig. 6).
Distribution: Lower Jurassic (Hettangian – Lower Sinemurian), Lyme Regis, Dorset, England (McGOWAN 1974b).
Diagnosis. – Orbit large, skull and particularly snout exceedingly delicate and fragile, skull extremely high-crowned, less than 20 maxillary teeth, teeth slender and very pointed.

The genus has also been announced from the Lower Jurassic Nordegg Formation of Alberta (McGOWAN 1978) and the Lower Sinemurian of the Langenbrückener Senke, Baden-Württemberg, Germany (REIFF 1935; MAISCH 1999).

28. Genus: *Stenopterygius* JAEKEL, 1904 emend. VON HUENE, 1922

Diagnosis. – Moderately sized longipinnate, maximum length around 4 m, postorbital skull region very short, fenestra temporalis large, maxilla short, excavatio internasalis not very clear, quadratojugal short, with short, posteromedially directed processus quadratus, parabasisphenoid with unpaired carotid foramen posterior to which there is a depression subdivided by a ridge, basioccipital with well developed cuneiform process, no clear stapedial facets, palatine small, pterygoid with processus postpalatinalis, forefins with four primary and fifth postaxial finger, at least two elements notched, humerus slender, pelvis bipartite, hindfins with three primary digits, a postaxial fourth accessory, 44–46 presacral vertebrae, thoracal ribs clearly bicipital, postflexural tail segment always shorter than preflexural segment, no haemapophyseal facets in caudal vertebrae.

Type species: *Stenopterygius quadriscissus* (QUENSTEDT, 1856) JAEKEL, 1904 (Figs. 7, 22, 27, 32, 35).
Distribution: Lower Jurassic (Lower Toarcian), Holzmaden, Ohmden, Frittlingen, Zell, Bad Boll, Baden-Württemberg, Germany (QUENSTEDT 1856; FRAAS 1891; VON HUENE 1922, 1931b; GODEFROIT 1994; HUNGERBÜHLER 1994; MAISCH 1998c), Dudelange, Bettembourg, Scouweiler, Luxembourg (GODEFROIT 1994).
Diagnosis. – Juveniles with numerous small teeth, adults lack dentition largely or entirely, snout long and robust, always longer than 2/3 skull length, often longer than 2/3 lower jaw length, orbit moderately large, high-crowned skull profile, maxilla does not reach naris, postfrontal and frontal in contact, head smaller than 1/3 preflexural length, forefins moderately large, mostly about 2/3 lower jaw length, body in adults stout with very long ribs.

Additional valid species. – *Stenopterygius longifrons* (OWEN, 1881) VON HUENE, 1939 (Figs. 7, 12, 16).
Distribution: Lower Jurassic (Lower Toarcian), Curcy, Normandie, France (type locality, OWEN 1881), La Caîne, Normandy (EUDES-DESLONGCHAMPS 1877; MAZIN 1988), Holzmaden, Schömberg, Baden-Württemberg, Banz, Altdorf, Bavaria, Germany (VON HUENE 1922, 1931b; GODEFROIT 1994; MAISCH 1998c); Bettembourg, Dudelange, Bascharage, Esch-sur-Alzette, Luxembourg (GODEFROIT 1993a, 1994), Teysachaux, Fribourg, Switzerland (VON HUENE 1939), Whitby, Yorkshire, England (OWEN 1881; GODEFROIT 1994; pers. obs.).
Diagnosis. – Orbit moderately large, snout very long, always longer than 2/3 lower jaw length, very delicate and slender, dentition in adult animals retained but consisting of very small teeth, maxilla high, reaches naris, frontals very reduced and narrow, parietal reaches nasal, high-crowned skull, forefins small and rounded, about 2/3 lower jaw length or somewhat less, skull much less than 1/3 preflexural length, body slender, ribs short.

Stenopterygius hauffianus VON HUENE, 1922 (Fig. 7).
Distribution: Lower Jurassic (Lower Toarcian), Holzmaden, Ohmden (VON HUENE 1922; 1931b; GODEFROIT 1994; MAISCH 1998c); Dudelange, Bascharage, Luxembourg (GODEFROIT 1994), Ilminster, Somerset, England (McGOWAN 1978).

Diagnosis. – Orbit very large, snout short, 2/3 skull length at maximum, mostly much less, maxilla high, frontal and postfrontal in contact, nasals short, maxillary dentition strong, moderately large teeth in posterior dentary and premaxilla, very small anterior teeth, only half the size of the maxillary teeth, highly vaulted orbital skull segment, head always shorter than 1/3 preflexural length, small, rounded forefins, body slender, ribs short.

Stenopterygius megalorhinus VON HUENE, 1922 (Fig. 7).

Distribution: Lower Jurassic (Lower Toarcian), Holzmaden, Bad Boll, Baden-Württemberg, Germany (VON HUENE 1922; MAISCH 1998c).

Diagnosis. – Orbit moderately large, dentition strong, teeth large to very large, never – even in very large, old adults – even remotely reduced, snout long, always longer than 2/3 skull length, usually about 2/3 lower jaw length, high and robust, maxilla usually high but never reaches naris, low-crowned skull, postfrontal and frontal in contact, skull has about 1/3 preflexural length, forefins long and slender, always longer than 2/3 lower jaw length.

The genus has also been described from the Upper Toarcian (Aalensis Zone) of Aveyron, Southern France (SANDER & BUCHER 1993) and the Lower or Middle Lias of Mickleton, Gloucester, England (MCGOWAN 1978). Undescribed material from the Lower Aalenian of Heiningen near Göppingen, Baden-Württemberg, Germany may also belong to *Stenopterygius* (pers. obs. of SMNS and GPIT material).

29. Genus: *Chacaicosaurus* FERNÁNDEZ, 1994

Type species: *Chacaicosaurus cayi* FERNÁNDEZ, 1994.

Distribution: Middle Jurassic (Early Bajocian), Los Molles Formation, Chacaico Sur, Neuquen, Argentina (holotype only).

Diagnosis. – Skull with large orbit and very long snout, lateral ridges on premaxillary rostrum, dentition lost in adults, forefin with three primary and accessory postaxial digit, most elements of leading edge notched, phalanges of rectangular-polygonal rather than rounded shape.

Discussion. – This genus was described from an incomplete skeleton, including a much mutilated skull and almost complete forefin, from the Early Bajocian Los Molles Formation of Chacaico Sur, Neuquen, Argentina (FERNÁNDEZ 1994). It is only known from this, the holotype specimen (MOZ 5803) so far. It was not assigned to a particular family by FERNÁNDEZ (1994). The cranial measurements given in that publication have been found by us to agree almost perfectly with those of *Ophthalmosaurus icenicus* (based on an articulated three-dimensional skull in the GPIT), the only difference is, that the orbit is slightly smaller and the snout slightly longer in *Chacaicosaurus*, but these differences could only account for a specific distinction between the two (skull length in both the holotype of *Chacaicosaurus* and the GPIT *Ophthalmosaurus* is 98 cm, prenarial length is 64 cm in both, snout length is 76 cm in *Ophthalmosaurus*, 79 cm in *Chacaicosaurus*, orbital diameter is 13 cm in *Chacaicosaurus* and 15 cm in *Ophthalmosaurus*). The snout is considerably longer and the orbit considerably larger than in any of the Lower Jurassic species of the genus *Stenopterygius*.

The forefin, however, is principally similar to that of *Stenopterygius* and if found in the Posidonia Shale of Southern Germany would probably have been assigned to this genus. As in *Stenopterygius* there are 4 digits which articulate with the proximal carpals and the fin is of the “longipinnate” type, that is, only one digit is fully articulated to the intermedium. Most of the autopodial elements are rectangular rather than rounded in shape and form a relatively tightly fitting mosaic pattern. There is one postaxial accessory digit which does not articulate with the proximal carpal row. There is no preaxial accessory digit and only the radius and ulna establish contact to the humerus proximally. Most elements of the first digit are notched.

In all these characters, *Chacaicosaurus* agrees very well with *Stenopterygius* but is markedly distinguished from *Ophthalmosaurus*. It appears as if *Chacaicosaurus cayi* is one of the rare forms which are true structural intermediates. It combines a typical ophthalmosaur skull with very long snout and reduced dentition with a typically stenopterygian forefin. The discovery of this taxon in strata intermediate in age between those from which *Stenopterygius* (?Pliensbachian, Toarcian, ?Aalenian) and those from which *Ophthalmosaurus* are known (Bajocian-Tithonian) makes its interpretation as a relatively advanced stenopterygiid/basal ophthalmosaurid even more plausible.

Unfortunately the type material does not allow to assess important characters distinctive of this clade, such as the fused ischiopubic plate or the processus postpalatinalis of the pterygoid. Nevertheless, there is nothing in the known parts of the skeleton which precludes an identification of *Chacaicosaurus* as a stenopterygiid, and it is therefore tentatively referred to that family. The presence of lateral ridges on the premaxillaries (FERNÁNDEZ 1994) is a character unique to *Chacaicosaurus*. Before there is more material available, the genus should therefore be allowed to stand, although it could almost equally well be referred to *Stenopterygius* as a particularly derived species.

30. Genus *Aegirosaurus* BARDET & FERNÁNDEZ, 2000

Type species: *Aegirosaurus leptospondylus* (WAGNER, 1853)
Distribution: Upper Jurassic (Lower Tithonian), Solnhofen Limestone Formation, Langenaltheim, Apfeltal, Solnhofen, Bavaria, Germany.

Diagnosis. – Medium-sized ichthyosaur (known specimens are probably all juveniles) less than 2 m long, snout gently merging into skull roof, external naris bilobate, postorbital skull segment very short, squamosal reduced and delicate, dentition not reduced, tooth crowns smooth, humerus with distal articulation facet for intermedium (neotype only), anterior preaxial accessory finger present which does not contact humerus, 5 primary digits in forefin, hindfin with three primary digits and one postaxial accessory, ischiopubic plate present.

Discussion. – The genus *Aegirosaurus* was introduced by BARDET & FERNÁNDEZ (2000) as a valid generic designation for the Solnhofen ichthyosaurs generally referred to as "*Macropterygius*" (a genus which is a nomen dubium). As the type material of *Ichthyosaurus leptospondylus* WAGNER, 1873, the only previously described Solnhofen species based on diagnostic material, was destroyed in World War II they selected a complete skeleton in the SCHWEGLER private collection as the neotype for this species (in our opinion this decision is somewhat problematic, as type specimens should be kept in public collections). A second specimen in the Munich collection was referred to the same taxon. Differences between the two specimens were explained as ontogenetic variation.

In our opinion it is doubtful, however, whether these two specimens are conspecific. They differ in several important characters, particularly of the skull and forefin. As we had no opportunity to study the neotype in detail our codings of *Aegirosaurus* are based exclusively on the Munich specimen and a yet undescribed specimen in the SMNS collection. The possibility of taxonomic differences between these specimens, which are certainly conspecific, and the neotype of *Aegirosaurus* should be kept in mind in this context. A clarification of this matter is, however, beyond the scope of the present paper.

31. Genus: *Ophthalmosaurus* SEELEY, 1874

Synonyms: *Sauranodon* MARSH, 1879 nom. praeocc.
Baptanodon MARSH, 1880
Apatodontosaurus MEHL, 1927
Ancanamunia RUSCONI, 1942
Paraophthalmosaurus ARKHANGELSKY 1997
Yasykovia EFIMOV, 1999
Undorosaurus EFIMOV, 1999
Mollesaurus FERNÁNDEZ, 1999

Diagnosis. – Large ichthyosaur, between 3 and 6 m in length, skull with long snout and very large orbit, postorbital skull segment very short, dentition reduced in adults, maxilla takes part in external naris, thoracal vertebrae very short and high, scapula widened proximally, forefin with well developed preaxial accessory finger which contacts humerus in additional facet, no notches in leading edge of forefin, most autopodial elements rounded and very thick, pelvis bipartite, hindfins very small.

The numerous described species differ only marginally and definite diagnoses have to await a thorough revision. The following are provisionally accepted as valid, but largely for geographic and stratigraphic reasons only.

Type species: *Ophthalmosaurus icenicus* SEELEY, 1874, Middle Jurassic, England, France (Figs. 8, 12, 13, 19 c-f, 23, 28, 32).

Additional species provisionally regarded as valid: *Ophthalmosaurus natans* (MARSH, 1879), Upper Jurassic, Wyoming (Figs. 8, 12, 13, 16, 19 g-k, 23, 28, 35).
Ophthalmosaurus saveljeviensis (ARKHANGELSKY, 1997) comb. nov., Upper Jurassic, Russia (Figs. 23, 28).
Ophthalmosaurus yasykovi (EFIMOV, 1999) comb. nov., Upper Jurassic, Russia (Figs. 23, 28, 32).
Ophthalmosaurus gorodischensis (EFIMOV, 1999) comb. nov., Upper Jurassic, Russia (Figs. 23, 28).
Ophthalmosaurus periallus (FERNÁNDEZ, 1999) comb. nov., Middle Jurassic, Argentina.

32. Genus *Caypullisaurus* FERNÁNDEZ, 1997

Type species: *Caypullisaurus bonapartei* FERNÁNDEZ, 1997 (Figs. 23, 28, 35).
Distribution: Upper Jurassic (Lower Tithonian), Vaca Muerta Formation, Cerro Lotena, Neuquen, Argentina.

Diagnosis. – Large ichthyosaur, exceeding 3 m in length, skull with very large orbit and short postorbital skull segment, dentition reduced in adults, forefin with elements forming closely fitting mosaic pattern, more than one well developed preaxial finger the posteriormost of which contacts humerus in additional facet, up to 8 fingers in total, ulna much smaller than radius.

Discussion. – This ichthyosaur genus was described on the basis of two incomplete skeletons from the Lower Tithonian Vaca Muerta Formation of Cerro Lotena, Neuquen, Argentina (FERNÁNDEZ 1997) and additional material, including a good skull, was recently described by FERNÁNDEZ (1998), making this one of the better known Upper Jurassic ichthyosaurs.

It clearly is a valid genus, although it shares certain features with both *Ophthalmosaurus* and *Platypterygius*, and it is evidently a highly derived ichthyosaur. The forefins are characterized by being much larger than the hindfins, a humerus with well-developed trochanter dorsalis and three articulatory facets, well developed pre- and postaxial accessory fingers and a rather tightly fitting pattern of the fin elements. The latter feature reminds of *Platypterygius*, whereas the three articulatory facets also recall *Ophthalmosaurus* (KIRTON 1983 in MCGOWAN 1997b). The skull, however, shows closest resemblance to *Ophthalmosaurus*, the maxilla is, apparently, very short and does not even extend anterior to the external naris (FERNÁNDEZ 1997) and the dentition is almost completely reduced in adults (FERNÁNDEZ 1997, 1998).

When *Caypullisaurus* is introduced into the phylogenetic analysis, it forms a clade with *Ophthalmosaurus*, the two together forming the sister-group to *Brachypterygius* and *Platypterygius*.

33. Genus: *Brachypterygius* VON HUENE, 1922

Synonyms: *Grendelius* MCGOWAN, 1976
Otschevia EFIMOV, 1998

Diagnosis. – Large ichthyosaur, exceeding 5 m in total length, skull with moderately large orbit, large, well developed dentition retained in adults, maxilla very long anterior to external naris, from which it is separated, forefin with well developed pre- and postaxial accessory fingers, intermedium contacts humerus and forms third medial facet.

Type species: *Brachypterygius extremus* (BOULENGER, 1904) VON HUENE, 1922 (Fig. 29).
Distribution: Upper Jurassic (Kimmeridgian), Kimmeridge Clay, area of Bath, England (holotype only).
Diagnosis. – Forefin very short and wide, humerus rather short.

Additional valid species. – *Brachypterygius mordax* (MCGOWAN, 1976) MCGOWAN, 1997 (Figs. 9, 29).
Distribution: Upper Jurassic (Kimmeridgian), Kimmeridge Clay, Norfolk (holotype), Kimmeridge Bay, Dorset, England (MCGOWAN 1976, 1997b).
Diagnosis. – Forefin very short and wide, humerus even shorter and stouter than in *B. extremus*.

Brachypterygius pseudoscythius (EFIMOV, 1998) comb. nov. (Figs. 23, 29).
Diagnosis. – Upper Jurassic (Upper Tithonian, Pseudoscythia Zone), Ulyanovsk, Volga region, Russia (holotype, EFIMOV 1998), Saratov, Russia (ARKHANGELSKY 1998a).
Diagnosis. – Forefin elongate, humerus slender.

Discussion. – The type species of the genus is currently only known from the holotype, an isolated forefin (BMNH R3177), allegedly from the Kimmeridge Clay of England. Of *B. mordax* there is a skull with some attached postcrania (the holotype of *Grendelius mordax*, decribed by MCGOWAN 1976, SMC J 68516) and an incomplete skeleton (BRSMG Ce 16696), both equally from the English Kimmeridge Clay. Recently, two new ichthyosaur species have been described from the Russian Upper Jurassic, *Brachypterygius zhuravlevi* (ARKANGELSKY, 1998a) and *Otschevia pseudoscythia* (EFIMOV, 1998). They are clearly conspecific and referrable to the genus *Brachypterygius*, as correctly recognized by ARKHANGELSKY (1998a). Although very similar to the English species, differences in the detailed structure of the fin suggest that it is a third valid species of *Brachypterygius*. It is known from an incomplete skeleton from the Tithonian of Ulyanovsk, Russia (the holotype of *Otschevia pseudoscythia*), including parts of the skull and dentition, much of the vertebral column, a complete shoulder girdle and almost complete forelimbs, and an incomplete paddle (the holotype of *Brachypterygius zhuravlevi*) from the Tithonian of Saratov, Russia.

Brachypterygius is obviously one of the rarest and least well known post-Triassic ichthyosaurs and much about its osteology remains to be learned. The basis cranii is fortunately known (McGowan 1976) and it is well advanced, with the parasphenoid ending anterior to the unpaired carotid foramen. The skull shows some distinctive features. The postorbital skull region is short and the quadratojugal appears to be a small and largely covered component of it (McGowan 1976). The teeth are large and numerous and, as in *Platypterygius*, show no tendency of reduction, as they do in *Stenopterygius quadriscissus*, *Ophthalmosaurus*, *Caypullisaurus* and *Chacaicosaurus*. They are best described by Efimov (1998) in *B. pseudoscythius*, where they show close similarity to the teeth of *Platypterygius*, including a subrectangular cross section of the root. In general, the skull is otherwise much like that of a *Stenopterygius* or *Ichthyosaurus*, except for the very long, splint-like anterior extension of the maxilla. This is certainly not a primitive feature but appears to be a reversion which is equally found in *Platypterygius* (where it was incorrectly interpreted as plesiomorphic by Maisch 1998b). The palate is, unfortunately, unknown, but the build of the basis cranii suggests that it was very similar to that of other post-Triassic ichthyosaurs, with large interpterygoid vacuities and the basis cranii uncovered by the pterygoids, and *Brachypterygius* was coded accordingly for the derived state with respect to these characters. Whether there was a processus postpalatinalis of the pterygoid, as in *Stenopterygius* or *Ophthalmosaurus* remains, however, unknown. The pelvic girdle is equally unknown in *Brachypterygius* so it cannot be told whether it possessed a bipartite pelvis, as *Stenopterygius*, *Ophthalmosaurus*, *Aegirosaurus* and *Platypterygius* (Nace 1939). The forefins of *Brachypterygius* are the most diagnostic portion of the skeleton known. It shows a unique middle facet for the intermedium on the humerus (Boulenger 1904; von Huene 1922; McGowan 1997b; Arkhangelsky 1998a; Efimov 1998) and therefore certainly merits the status of a separate genus. Such a middle intermedium facet of the humerus is also found in the neotype of *Aegirosaurus leptospondylus*, which raises the question of a close relationship between this genus and *Brachypterygius* (see also Bardet & Fernández 2000).

The forefin is further characterized by its "latipinnate" configuration and the presence of a well-developed preaxial accessory digit. The latter feature is uniquely shared with *Aegirosaurus*, *Ophthalmosaurus*, *Platypterygius* and *Caypullisaurus* (in the latter two there may be even more than one preaxial accessory) and indicates a quite close relationship between all these taxa. The typical mosaic pattern of the meta- and autopodial elements found in *Platypterygius* and *Caypullisaurus* is lacking in *Brachypterygius extremus* and *B. mordax* but closely approached by *B. pseudoscythius* from Russia (Efimov 1998, fig. 4). In *B. extremus* the digital elements are more widely spaced and with rather rounded margins, and in this respect the fin resembles *Ophthalmosaurus* more closely. The most probable phylogenetic position of *Brachypterygius* is that it forms a clade with *Platypterygius* and (*Caypullisaurus* +

Ophthalmosaurus). To which of these it is most closely related remains, however, a matter of some debate and final clarification must await more information on its osteology. In our analysis it accordingly forms a trichotomy with *Platypterygius* and the *Caypullisaurus*/*Ophthalmosaurus* clade.

34. Genus: *Nannopterygius* VON HUENE, 1922

Type species: *Nannopterygius enthekiodon* (HULKE, 1871) VON HUENE, 1922
Distribution: Upper Jurassic (Kimmeridgian), Kimmeridge Bay, Dorset, England (HULKE 1871); probably also from the Lower Tithonian, Solnhofen Limestone Formation, Daiting, Bavaria (FRICKHINGER 1994).

Diagnosis. – Moderately large ichthyosaur, snout long and very slender, dentition well developed, fore- and hindfins extremely reduced, forefin less than half mandibular length, neural spines elongated.

Discussion. – *Nannopterygius enthekiodon* was described by HULKE (1871) on the basis of a poorly preserved but largely complete skeleton from the Kimmeridge Clay of Dorset. The genus is, without doubt, valid, as is shown by the extreme size reduction of the fore- and hindfins, which is reflected in the generic name. The anterior caudal spinal processes are, judging from HULKE's (1871) figure, unusually long for a post-Triassic ichthyosaur and, together with the tiny fins, suggest an unusual form of locomotion in this peculiar animal. A second skeleton of *Nannopterygius* was figured by FRICKHINGER (1994) from the Lower Tithonian Solnhofener Plattenkalk of South Germany. The specimen, the main slab of which is preserved in the Jura Museum Eichstätt, whereas the counterslab – which shows a distinct tailbend – is in the Staatliches Museum für Naturkunde Karlsruhe (E. FREY, pers. comm.), remains undescribed at present. Very little can be said concerning the phylogenetic position of the genus at present, except that the lack of haemapophyses and the short postorbital skull region, as well as the lack of a preaxial accessory digit suggest that it is a relatively primitive "*Stenopterygius*-grade" ichthyosaur.

35. Genus: *Platypterygius* VON HUENE, 1922

Synonyms: *Myopterygius* VON HUENE, 1922
Myobradypterygius VON HUENE, 1926b
Simbirskiasaurus OCHEV & EFIMOV, 1985
Plutoniosaurus EFIMOV, 1997
Longirostria ARKHANGELSKY, 1998
Tenuirostria ARKHANGELSKY, 1998
Pervushovisaurus ARKHANGELSKY, 1998

Diagnosis. – Large ichthyosaur, adult size up to 9 m, skull low-crowned, long snout, small orbit, long postorbital region, maxilla extremely long anteriorly, strong dentition, roots of teeth quadrangular in cross-section, external naris subdivided, septomaxilla well ossified, squamosal lost, condylus occipitalis semihemispherical, area extracondylaris extremely reduced, atlas-axis co-ossified with third cervical vertebra, intercentra not differentiated, humerus with very strong trochanter dorsalis, two or three distal facets, anterior and posterior accessory digits well developed, all podial elements very thick, forming close-fitting polygonal mosaic pattern as in *Ichthyosaurus*, pelvis and hindfin little known but apparently extremely reduced, caudal peduncle short.

As in *Ophthalmosaurus* numerous species have been described, and the validity of most is far from well established. Usually for geographical and stratigraphical reasons, we provisionally accept the species listed below as valid, pending a thorough revision of the genus.

Type species: *Platypterygius platydactylus* (BROILI, 1907) VON HUENE, 1922, Lower Cretaceous, Germany (Figs. 19 b, 29).

Additional species provisionally regarded as valid: *Platypterygius hauthali* (VON HUENE, 1926b) MCGOWAN, 1972, Lower Cretaceous, Argentina.
Platypterygius americanus (NACE, 1939) ROMER, 1968, Lower Cretaceous, Wyoming (Fig. 9).
Platypterygius hercynicus KUHN, 1946, Lower Cretaceous, Germany (Fig. 29).
Platypterygius kiprijanoffi ROMER, 1968, Lower Cretaceous, Russia.
Platypterygius birjukovi (OTSCHEV & EFIMOV 1985) comb. nov., Lower Cretaceous, Russia.
Platypterygius longmani WADE, 1990, Lower Cretaceous, Queensland (Figs. 9, 13).
Platypterygius bedengensis (EFIMOV, 1998) comb. nov., Lower Cretaceous, Russia (Figs. 23, 29).
Platypterygius bannovkensis ARKHANGELSKY, 1998, Upper Cretaceous, Russia (Fig. 9).

Discussion. – The genus *Platypterygius* is the only currently recognized genus of Cretaceous ichthyosaurs and the majority, if not all specimens known from that period and described from all around the world belong to it (MCGOWAN 1972a; WADE 1984, 1990; ARKHANGELSKY 1998b). The best-known species are *Platypterygius longmani* WADE, 1990 from the Aptian of Queensland (MCGOWAN 1972a; WADE 1984, 1990) and *Platypterygius americanus* from the Lower Cretaceous of Wyoming (NACE 1939, 1941; ROMER 1968; MCGOWAN 1972a). The type-species, *P. platydactylus* was originally known from a fairly complete skeleton (BROILI 1907), but it was destroyed as part of the Hamburg collection in World War II and there is currently no specifically diagnostic additional material known which can be referred to it.

ARKHANGELSKY (1998b) recently proposed a subdivision of the genus into four subgenera, but this is abandoned here. ARKHANGELSKY's diagnoses are insufficient. The characters on which the subgenera are based are largely related to skull proportions or minute differences in fin morphology. Although these are sufficient to recognize different species, the same could be applied, e.g. to *Ichthyosaurus* and *Stenopterygius*, where almost any of the known species would necessitate a subgenus of its own (*Stenopterygius hauffianus* and *S. longifrons* are, e. g. much more different in skull proportions than any of the species of *Platypterygius*, cf. GODEFROIT 1994; MAISCH 1998c). We therefore regard it as premature to establish a division of the genus *Platypterygius*, although, considering the unusually high number of species, this appears to be necessary when more information is available and more thorough comparative work has been done. It has to be based, however, on proper phylogenetic argumentation. At any rate, if a subdivision should become necessary, *Myopterygius* VON HUENE, 1922 is the oldest available name and should be used instead of creating an unnecessary plethora of "new taxa".

Platypterygius is obviously a very advanced ichthyosaur. MAISCH (1998a) suggested that it was rather plesiomorphic, because of the long anterior extension of the maxilla and the rather long postorbital skull region, features which are generally absent in the more derived post-Triassic ichthyosaurs. Whereas the long anterior extension of the maxilla is a valid character, the length of the postorbital skull region is probably overexaggerated in *P. americanus* due to dorsoventral compression and deformation (ROMER 1968) or could be in part specifically autapomorphic. In *P. longmani* (MCGOWAN 1972a; WADE 1984, 1990) the postorbital skull segment is not remarkably longer than in, e. g. *Ichthyosaurus communis*. The long anterior extension of the maxilla is also found in *Brachypterygius mordax* (McGowan 1976, 1997b), another obviously highly derived and late (Upper Jurassic) ichthyosaur, and, as suggested above, might be the result of a reversal rather than a retained plesiomorphy. The extent of the maxilla shows undoubtedly a general trend of reduction in the phylogeny of ichthyosaurs, but is probably not a very reliable character for large-scale phylogenetic analyses, particularly if it is regarded almost in isolation.

Maisch (1998b) also noted, that the forefins of *Platypterygius* are of the longipinnate type and could be derived from those of *Temnodontosaurus* by the addition of pre- and postaxial accessories. This is certainly true, and McGowan (1972a) spoke of *Platypterygius* as a "longipinnate in latipinnate clothing". The feature clearly distinguishes *Platypterygius* from *Ophthalmosaurus* and *Brachypterygius*, which are typical latipinnates, on a generic level. It can, however, also not be looked at in isolation. Nace (1939) described the pelvic girdle of *P. americanus* and found only two bones, a slender illium and an exceedingly reduced ischiopubis, even lacking a foramen oblongum. This is, certainly, a highly derived character in which *Platypterygius* is even more advanced than *Ophthalmosaurus* or *Stenopterygius*. The basis cranii of *Platypterygius* shows a reduced parasphenoid and unpaired carotid foramen (Bardet 1989; Wade 1990), the tailbend of *Platypterygius* is very well developed, the tail is short in relation to the body. There are, certainly autapomorphously, 54 presacral centra in *P. platydactylus* and the trunk is very elongated in this ichthyosaur (Broili 1907). In *P. longmani*, only 46 presacrals are recorded (Wade 1990), and as this number is similar to the presacral counts of all other post-Triassic genera it is taken as representing the grundplan condition of *Platypterygius*, which was therefore coded as possessing less than 50 presacrals in the analysis.

The hindfins, as far as it is known, are much smaller than the forefins. The rib articulations of the presacral vertebrae are universally bicipital, there are no haemapophyses or haemapophyseal facets, the quadratojugal is largely covered by adjacent elements and the squamosal appears to be vestigial or even entirely lost (Romer 1968; Wade 1990; Maisch 1998b). In all these features, *Platypterygius* is at least as highly derived as *Stenopterygius* and set widely apart from *Temnodontosaurus*. It furthermore shares the unique condition of well-developed preaxial accessory digits with *Aegirosaurus*, *Brachypterygius*, *Ophthalmosaurus* and *Caypullisaurus*, and, at least in some species (*P. americanus*, *P. longmani*), there is even an additional preaxial facet on the humerus as in *Ophthalmosaurus* and *Caypullisaurus* (McGowan 1972a). There can be no doubt that *Platypterygius* is one of the most highly derived ichthyosaurs known, which is well in accordance with the late stratigraphic occurence of the genus, and its placement as a very plesiomorphic form by Maisch (1998b) was certainly in error, resulting from the too restricted set of characters chosen to establish phylogenetic relationships among post-Triassic ichthyosaurs. The Russian genera *Simbirskiasaurus* Ochev & Efimov, 1985 and *Plutoniosaurus*, recently erected by Efimov (1998), are referrable to *Platypterygius* for reasons discussed below.

5.2. Invalid ichthyosaur genera currently still in use

Pessopteryx WIMAN, 1910

Omphalosaurid, non-ichthyosaurian (see discussion on *Rotundopteryx* gen. nov. in chapter 5. 1.)
Type-species: *Pessopteryx nisseri* WIMAN, 1910.

Isfjordosaurus MOTANI, 1999b

Probably ichthyosaurian.
Type-species: *Pessopteryx minor* WIMAN, 1910 (Fig. 36).

Discussion. – This genus, based as it is on the very slight evidence of an isolated humerus, may or may not be ichthyosaurian. We agree with MOTANI (1999b) that it represents a valid taxon. A single feature – the proximal end of the humerus being distinctly wider than the distal end – distinguishes it from all known ichthyosaur taxa. It is, however, reminiscent of the humerus of *Hupehsuchus* as illustrated by CARROLL & DONG (1991, figs. 4, 5, 11). A typical ichthyosaurian feature of *Isfjordosaurus* is the possession of an extensive anterior flange of the humeral shaft. This character is, however, also shared by *Hupehsuchus* (CARROLL & DONG 1991). We therefore regard it as a possibility, albeit a rather slight one, that the humerus of *Isfjordosaurus* is hupehsuchian and not ichthyosaurian. Should *Hupehsuchus* and related genera prove to fall within the Ichthyosauria by further research, this discussion will become redundant and *Isfjordosaurus* can be treated as another valid ichthyosaur genus.

Pachygonosaurus VON HUENE, 1916

Nomen dubium
Type-species: *Pachygonosaurus robustus* MAISCH & MATZKE, 1997

Discussion. – This genus was based on some isolated vertebrae from the Polish Muschelkalk. The type material, said to be in the Museum für Naturkunde, Berlin (Humboldt University) could not be relocated by us. As the material is so scanty, anyway, and the type is lost, it is probably best to regard the genus and species as nomina dubia.

Himalayasaurus YOUNG & DONG, 1972

Nomen dubium
Type species: *Himalayasaurus tibetensis* YOUNG & DONG, 1972

Discussion. – This genus and species was erected by YOUNG & DONG (1972) on the basis of jaw fragments and some probably associated postcranial material from the Upper Triassic of Tibet. It belongs to a very large ichthyosaur, but little more can be said with the currently available information. The existing descriptions and figures are insufficient to establish its generic validity, and we therefore regard it as a nomen dubium at present. The available material might be diagnostic, but this has to await a thorough reinvestigation (currently carried out by R. MOTANI, Berkeley and Z.-M. DONG, Beijing).

Tibetosaurus DONG in YOUNG et al., 1982

Nomen dubium
Type species: *Tibetosaurus tingjiensis* DONG in YOUNG et al., 1982

Discussion. – This is another Upper Triassic shastasaur-grade ichthyosaur from Tibet. The most diagnostic material known are the teeth, which resemble both *Cymbospondylus buchseri* and *Shastasaurus alexandrae* (CALLAWAY & MASSARE 1989), but also the Lower Jurassic *Temnodontosaurus* by the possession of mesial and distal carinae. Again existing descriptions and illustrations are insufficient to establish its generic validity, and it must be regarded as a nomen dubium.

Pessosaurus WIMAN, 1910

Nomen dubium
Type species: *Pessosaurus polaris* (HULKE, 1873) WIMAN, 1910

Discussion. – The genus *Pessosaurus* was most recently discussed by SANDER & FABER (1998) and regarded as a nomen dubium by these authors. We think their argumentation to be convincing and follow their conclusions here, with an exception noted below. The German Muschelkalk material known under the binomen *Pessosaurus suevicus* VON HUENE, 1916 could possibly also belong to *Besanosaurus* or a similar form, the vertebrae of which are quite indistinguishable from the *Pessosaurus* material (DAL SASSO & PINNA 1996) and this species is therefore also a nomen dubium (contra MAISCH & MATZKE 1997a).

As SANDER & FABER (1998) correctly pointed out, the material described as *Pessosaurus* from the Middle Triassic of Spitsbergen is largely undiagnostic. However, there remains one exception, namely the associated coracoid, humerus, radius and ulna described and figured by WIMAN (1910, 1916) (PMU R176). This taxon is different from that represented by the humerus SVT 293 described and figured by MAZIN (1984) which differs in details and is not considered further here.

As comparison with other known Triassic ichthyosaurs shows, the humerus and associated elements are almost unique. The humerus practically lacks a posterior shaft, as pointed out by MOTANI (1999a). The anterior flange is extensive and unnotched, with a convex anterior margin, which resembles *Rotundopteryx* gen. nov. (see below), which has, however, a more elongate humerus with a conspicuous posterior shaft.

The radius and ulna are extremely short and enclose a spatium interosseum which is practically reduced to a foramen. The coracoid is quite similar to that of *Shastasaurus alexandrae*, but the anterior extension is more considerable, reminiscent of *Besanosaurus leptorhynchus* (DAL SASSO & PINNA 1996).

Besanosaurus also differs from the Spitsbergen taxon in that the anterior margin of the humerus is notched and the radius and ulna are more elongate. In *Shastasaurus* the spatium interosseum is reduced and the humerus is equally elongate and has a marked posterior shaft. In *Mikadocephalus*, however, the humerus, radius and ulna have quite comparable proportions (Fig. 36). The humerus, which has no distinct anterior notch or emargination and a very reduced posterior shaft is indistinguishable from that of the Spitsbergen taxon. There is, however, no real spatium interosseum formed between radius and ulna, but this might be due to incomplete ossification in the articulated skeleton of *Mikadocephalus* in Zürich. Otherwise the radii are quite similar, except that the Spitsbergen taxon has an even shorter radius than the Monte

San Giorgio form. The coracoids are also very similar (Fig. 36), except that, again, that of *Mikadocephalus* appears more "rounded" and unfinished, but proportions are fundamentally the same. The single podial element associated with the coracoid and stylo- and zeugopodium of the Spitsbergen ichthyosaur (interpreted as an intermedium by WIMAN 1916) is totally rounded, as are most of the *Mikadocephalus* podials.

In view of the considerable similarities of the known skeletal elements of the Spitsbergen taxon and *Mikadocephalus*, we refer the specimen PMU R 176 to the genus *Mikadocephalus* MAISCH & MATZKE, 1997.

The differences in the shapes of the coracoids and radius, particularly with regard to the practically complete identity of the humeri, maybe attributable to the ontogenetic stage, as the Spitsbergen specimen is about one third larger than the Zürich specimen. With regard to the incompleteness of the Spitsbergen material, we tentatively identify it as *Mikadocephalus* cf. *gracilirostris* MAISCH & MATZKE, 1997, but a definite assessment whether it belongs to the same or another species must await the discovery of further material from the Spitsbergen Triassic. From the palaeobiogeographical viewpoint it is interesting to note that after *Cymbospondylus*, *Mixosaurus* and *Phalarodon* a fourth of the six Monte San Giorgio ichthyosaur genera is known now from the Teschermakfjellet Formation of Spitsbergen. This underlines that the ichthyosaur faunas of the Western Tethys and the Arctic Region were extremely similar in Anisian/Ladinian times.

Excalibosaurus MCGOWAN, 1986

Junior subjective synonym of *Eurhinosaurus*
Type species: *Excalibosaurus costini* MCGOWAN, 1986

Discussion. – The genus *Excalibosaurus* was erected by MCGOWAN on the basis of a well preserved skull with parts of the postcranial skeleton, including much of the forefin from the Sinemurian of Somerset, England (MCGOWAN 1986). As demonstrated by MCGOWAN (1986, 1989a) the species is very similar to both *Leptonectes tenuirostris* and *Eurhinosaurus longirostris*, and it in fact shares all the unique derived traits of the Leptonectidae as defined by MAISCH (1998a) and in this study (pers. obs.). It furthermore shares the unique feature of an extensive overbite of more than 30 % of the snout length with *E. longirostris*. The two species were therefore found to share a sister-group relationship when both were included in our phylogenetic analysis. We therefore think it unnecessary to retain *E. costini* in a separate genus, but rather suggest to refer it to *Eurhinosaurus* as a second valid species, *Eurhinosaurus costini* (MCGOWAN, 1986) comb. nov., because apart from the differences in the extent of the overbite there are no fundamental distinguishing features between the two forms known, which could justify a generic separation.

Protoichthyosaurus APPLEBY, 1979

Junior subjective synonym of *Ichthyosaurus*
Type species: *Protoichthyosaurus postaxalis* APPLEBY, 1979

Discussion. – It was already suggested by MAISCH & HUNGERBÜHLER (1997a) that *Protoichthyosaurus* should best be regarded as a junior subjective synonym of *Ichthyosaurus*. The specimens described by APPLEBY (1979) and referred to two species of the genus *Protoichthyosaurus*, *P. postaxalis* and *P. porostealis* are evidently very similar to other species of the genus *Ichthyosaurus*, although they show unusual features of the forefin which support the notion that the latipinnate *Ichthyosaurus* can be derived from a longipinnate ancestor (APPLEBY 1979). As the forefins of *Ichthyosaurus* are known to display an unusual amount of individual variation (see, e. g. MCGOWAN 1974b) we think, nevertheless, that this is not enough evidence to justify a separation of the species decribed by APPLEBY on the generic level. The features by which *Protoichthyosaurus* is diagnosed are, furthermore, all plesiomorphic with respect to typical members of the genus *Ichthyosaurus*. As long as there are no demonstrable unique derived characters uniting the two species of *Protoichthyosaurus* and as long as there are no demonstrable differences to other species of the genus known in other parts of the skeleton than the forefin we think it inappropriate to retain *Protoichthyosaurus* as a separate genus and suggest to regard it as a junior subjective synonym of the genus *Ichthyosaurus*. Wether the two species erected by APPLEBY (1979) can be allowed to stand remains an open question, pending a thorough reinvestigation of their entire skeletal anatomy.

Macropterygius VON HUENE, 1922

Nomen dubium
Type species: *Macropterygius trigonus* (OWEN, 1840) VON HUENE, 1922

Discussion. – The genus *Macropterygius* was introduced by VON HUENE (1922) for an assemblage of little known Upper Jurassic ichthyosaurs from Western Europe. Its type species, *M. trigonus* (OWEN, 1840), is based on inadequate material (an isolated vertebral centrum, see MCGOWAN 1976 and BARDET & FERNÁNDEZ 2000 for discussion) and therefore a nomen dubium. The best material usually ascribed to the genus are several more or less complete skeletons from the lithographic limestone of Solnhofen, Bavaria (Figs. 8, 32). As *Macropterygius* is an invalid genus, these have been recently referred to a new genus, *Aegirosaurus* BARDET & FERNÁNDEZ, 2000 which is discussed in chapter 5. 1.

The specimen described by GASPARINI (1988, Fig. 8, 22, 27) as *Ophthalmosaurus monocharactus* APPLEBY, 1956 from the Tithonian of Neuquen, Argentina is, in our opinion, congeneric with at least some of the Solnhofen specimens. It shows close resemblances in cranial and postcranial structure, particularly in the forefin, which differs considerably from any known species of *Ophthalmosaurus*, but agrees closely with the specimen BSP 1954 I 508 from the lithographic limestones of Solnhofen (pers. obs.). GASPARINI (1988) already noted this similarity between the Argentinan specimen and the Munich *Aegirosaurus*, and she only refrained from assigning them to the same taxon because the Munich specimen was at that time undescribed. We concur with this suggestion of GASPARINI and regard the two as congeneric, but generically distinct from *Ophthalmosaurus*.

Otschevia EFIMOV, 1998

Junior subjective synonym of *Brachypterygius*
Type species: *Otschevia pseudoscythia* EFIMOV, 1998

Discussion. – As discussed above (see *Brachypterygius*) this is another Russian “new genus” consistent with one of the already well-known European Upper Jurassic genera. The holotype specimen preserves almost complete forefins, and these clearly show the presence of a middle facet for the intermedium on the humerus, the diagnostic autapomorphy of *Brachypterygius*. The holotype differs from *B. extremus*, the type species, in its more closely spaced, polygonal rather than rounded fin elements and in the considerably greater length of the forefin, as well as in the rather elongate humerus (EFIMOV 1998). A generic distinction is unwarranted, however, as similar differences in forefin morphology are, e. g. encountered in the different species of *Ichthyosaurus* (MCGOWAN 1974b) or *Stenopterygius* (MCGOWAN 1979; GODEFROIT 1994; MAISCH 1998c). The new species *Brachypterygius zhuravlevi*, described by ARKHANGELSKY (1998a) in the same issue of the Palaeontological Journal, only some pages later (original edition), is identical in humerus morphology to *Otschevia* and therefore regarded as a junior subjective synonym. The only valid species is *Brachypterygius pseudoscythius* (EFIMOV, 1998) comb. nov.

Paraophthalmosaurus ARKHANGELSKY, 1997

Junior subjective synonym of *Ophthalmosaurus*
Type species: *Paraophthalmosaurus saveljeviensis* ARKHANGELSKY, 1997

Discussion. – The new genus *Paraophthalmosaurus* was introduced by ARKHANGELSKY for an incomplete ichthyosaur skeleton from the Tithonian of Ulyanovsk district, Russia. It apparently differed from *Ophthalmosaurus* in the possession of a third posterior facet on the humerus, whereas *Ophthalmosaurus* has an accessory facet on the preaxial margin of the humerus (KIRTON 1983, cited in MCGOWAN 1997b). As ARKHANGELSKY (1998a) demonstrated himself, this was a misinterpretation, the humerus of *Paraophthalmosaurus* being, in fact, identical to that of *Ophthalmosaurus* (ARKHANGELSKY interpreted the presence of an anterior accessory facet in *Paraophthalmosaurus* as a difference, probably because the new orientation of the *Ophthalmosaurus* paddle was not published at the time of his description, but it, in fact, demonstrates a high degree of similarity).

From the existing descriptions (ARKHANGELSKY 1997, 1998a) there appear to be no major differences between the Russian form and either *Ophthalmosaurus icenicus* or *O. natans* which could justify a separation on the generic level. ARKHANGELSKY (1997) states that the external naris is teardrop-shaped in *Paraopthalmosaurus*, whereas it is characteristically bilobate in *Ophthalmosaurus* (ANDREWS 1910; GILMORE 1905, 1906). However, the ventral margin of the external naris is shown to be incomplete in his figure (ARKHANGELSKY 1997, fig. 1) of the type of *Paraophthalmosaurus saveljeviensis* and what remains of the naris corresponds in position to the dorsal lobe of the naris in *Ophthalmosaurus*.

That the parietals are drawn up into a sharp crest rather than being flat could be a valid difference at least to *O. icenicus*; in *O. natans* there is, however, also some development of a crested intertemporal region (GILMORE 1905, 1906).

The single valid difference to other described species of *Ophthalmosaurus* therefore appears to be the shape of the coracoids, which, posterior to the sagittal symphysis, are drawn out into elongate triangular posterior projections in *P. saveljeviensis* (ARKHANGELSKY 1997, fig. 1, 2d). This is here considered as a valid specific difference to both *O. icenicus* and *O. natans*.

The second species of *Paraophthalmosaurus*, *P. saratoviensis*, was described by ARKHANGELSKY on the basis of a fragmentary skeleton lacking the skull from the Tithonian of Saratov. It was distinguished from the type species mainly because of its more robust humerus. Although this may constitute a valid difference, more material is needed to establish this with confidence, and the material should best be identified as *Ophthalmosaurus* sp. at present. The same holds true for the isolated forefin, already described by TRAUTSCHOLD (1879) and refigured by ARKHANGELSKY (1998a, fig. 1) from the Upper Jurassic of Mnevniki near Moscow. BOGOLJUBOV (1910) already identified it like that, and we see no reason to disagree with this assessment.

Yasykovia EFIMOV, 1999a

Junior subjective synonym of *Ophthalmosaurus*
Type-species: *Yasykovia yasykovi* EFIMOV, 1999a

Discussion. – The genus *Yasykovia* was erected (containing four species) for several incomplete ichthyosaur skeletons from the uppermost Jurassic (Tithonian) of European Russia. The genus was distinguished from other ichthyosaurs by a suite of features (EFIMOV 1999a: 92) of doubtful diagnostic value. The only remarkable feature is the alleged number of 55 presacral vertebrae. The evidence for this statement is, however, unclear. Although EFIMOV (1999a) states (p. 94) that one of the referred specimens of *Yasykovia yasykovi* preserves 55 vertebrae it is neither clear from the description nor from the figures whether these are all presacral, and we dare to doubt it before conclusive evidence is presented.

The fact that there is an anterior supplementary facet on the humerus for the most proximal element of a well-developed preaxial digit indicates close affinities to *Ophthalmosaurus* and *Caypullisaurus*. The pelvis is bipartite, as in *Ophthalmosaurus*, the skull has a large orbit, short postorbital segment and weak dentition, equally similar to *Ophthalmosaurus*, the shoulder-girdle with its proximally expanded scapula is equally *Ophthalmosaurus*-like, as are the short and high thoracic vertebrae.

It is remarkable, that in his comparison EFIMOV (1999a: 92–93) did not include the genus *Ophthalmosaurus*, which is obviously closest to *Yasykovia* in morphology. The differences between the four described species, *Y. yasykovi*, *Y. sumini*, *Y. mittai* and *Y. kabanovi* appear to be merely ontogenetic and the shoulder girdles of the four species figured by EFIMOV (1999a, fig. 4) are essentially alike, particularly with regard to their incomplete preservation. The "bony denticle of scapula", presumedly characteristic of *Y. mittai*, is, if anything, most likely to be a pathological feature, but it might also be an artifact of incomplete preservation, judging from the figures. If both scapulae of the type specimen were known and showed an identical anterior process, it would be acceptable that one is dealing with a valid osteological difference, but at the moment evidence for recognition of this species is too scanty. The enclosure of a foramen by the coracoid and scapula in *Y. kabanovi* is also not a unique feature, instead it is regularly found in large, well ossified individuals of other stenopterygiids and ophthalmosaurids, although rarely described. The peculiar medial coracoid symphysis of *Y. sumini* – again only known from one specimen – is a mere individual variation.

There is thus no evidence to recognize more than one species in the material described by EFIMOV (1999a), and it is questionable wether this taxon is really distinct from ARKHANGELSKY's "*Paraophthalmosaurus*". As the shape of the posterior portion of the coracoid of *Ophthalmosaurus* ("*Paraophthalmosaurus*") *saveljeviensis* is diagnostic and differs in detail from the "*Yasykovia*" specimens, it is considered best to keep the two taxa apart for the time being. There is no evidence whatsoever that

Yasykovia is a genus distinct from *Ophthalmosaurus*, instead it shows all features considered diagnostic of that genus by MOTANI (1999b) and ourselves. The genus *Yasykovia* is therefore a junior subjective synonym of *Ophthalmosaurus* and its single – provisionally valid – species is here referred to that genus as *Ophthalmosaurus yasykovi* (EFIMOV, 1999) comb. nov.

Undorosaurus EFIMOV, 1999b

Junior subjective synonym of *Ophthalmosaurus*
Type-species: *Undorosaurus gorodischensis* EFIMOV, 1999b

Discussion. – Yet again, EFIMOV (1999b) described another ophthalmosaurid "genus", in this case as the representative of a new family, from the Russian Volgian, which appears to have been a strange centre of ichthyosaur evolution when elsewhere in the world ichthyosaur diversity was on the low side.

Undorosaurus is said to be distinguished from *Ophthalmosaurus* by a number of features, and several at least appear to be remarkable. It is the lack of complete fusion of the ischiopubis, the slender scapula and the remarkably long hindfins (two thirds of the length of the forefins). However, a mounted complete skeleton of *Ophthalmosaurus icenicus* in the GPIT also lacks a complete fusion of ischium and pubis, so this might be a mere individual variation. The long hindfins and the slender scapula are apparently valid diagnostic characters. They are, however, not considered at present to indicate a generic distinction between *Undorosaurus* and *Ophthalmosaurus*. Particularly in the structure of the forefin, *Undorosaurus* agrees perfectly with *Ophthalmosaurus*, and this is also the case in the vertebral column with its high dorsal centra. It is totally unnecessary to erect a new family for this material, and it is considered unwarranted to refer it to a distinct genus, although we admit that when more information becomes available, particularly on the skull of "*Undorosaurus*", it could turn out to be generically distinct, but for the time being evidence is too scanty.

From the other Russian ophthalmosaur species, *Undorosaurus* is distinguished, apart from the larger size, by the shape of the coracoids with their widely rounded posterior margin. It is therefore out of question that the species *Undorosaurus gorodischensis* represents a valid taxon. The two other described species, *U. nessovi* and *U. khorlovensis*, are in no way distinguishable from *U. gorodischensis*, contrary to the statements of EFIMOV (1999b), except for trivial differences easily explicable by individual and ontogenetic variation. We consider *Undorosaurus* provisionally as a junior subjective synonym of *Ophthalmosaurus*, and the single valid species is referred to that genus as *Ophthalmosaurus gorodischensis* (EFIMOV, 1999b) comb. nov.

Khudiakovia ARKHANGELSKY, 1999

Junior subjective synonym of *Ophthalmosaurus*.
Type-species: *Khudiakovia calloviensis* ARKHANGELSKY, 1999

Discussion. – This genus and species is based on an isolated, incomplete forefin from the Callovian of Saratov. It is a typical *Ophthalmosaurus*, as demonstrated by ARKANGELSKY's (1999) description. It is too incompletely preserved to be specifically diagnostic, but shows great affinities to *Ophthalmosaurus icenicus* from the Callovian of England. The species *Khudiakovia calloviensis* is a nomen dubium. The specimen is here referred to *Ophthalmosaurus* sp.

Mollesaurus FERNÁNDEZ, 1999

Junior subjective synonym of *Ophthalmosaurus*
Type-species: *Mollesaurus periallus* FERNÁNDEZ, 1999

Discussion. – Recently, a typical *Ophthalmosaurus*, almost indistinguishable from the European type material, has been described from the Bajocian Los Molles Formation of Argentina as a new genus, *Mollesaurus*.

Mollesaurus is distinguishable from other species of *Ophthalmosaurus* merely by the somewhat longer postorbital skull segment. That the rostrum is "deep near the orbit" (FERNÁNDEZ 1999: 675) is a character of most other ichthyosaurs, as well, and *Mollesaurus* does not substantially differ from any other ophthalmosaur in this feature. That the orbit is large and the postorbital region narrow is a typical feature of *Ophthalmosaurus* (and several other genera). The reduced extracondylar area of the basioccipital is a character of all ophthalmosaurids. The "elongated areas" encountered there seem to be simply the true stapedial facets, as described and figured by APPLEBY (1956, 1961) in *Ophthalmosaurus icenicus*. The small size of the maxilla and reduction of the teeth are also typical *Ophthalmosaurus* features.

Apart from the Bajocian age, there are therefore no clear distinctive features of *Mollesaurus*. It is no wonder that it came out as the sister-group of *Ophthalmosaurus* in the small cladistic analysis of FERNÁNDEZ (1999), because it is simply an entirely typical member of that genus, at least as far as it is hitherto known. It cannot be excluded that further material of *Mollesaurus periallus* might reveal additional characters of other parts of the skeleton, which can serve to distinguish it on a generic level from *Ophthalmosaurus*. For the time being, such characters are not apparent and we therefore treat the genus as yet another junior subjective synonym of *Ophthalmosaurus* and refer the type species to that genus as *Ophthalmosaurus periallus* (FERNÁNDEZ, 1999) comb. nov.

Simbirskiasaurus OCHEV & EFIMOV, 1985

Junior subjective synonym of *Platypterygius*
Type species: *Simbirskiasaurus birjukovi* OCHEV & EFIMOV, 1985

Discussion. – This genus and species is based on an incomplete skull and part of the vertebral column from the Hauterivian of Ulyanovsk (Russia). It is a large ichthyosaur with an estimated skull length of 70 cm (OCHEV & EFIMOV 1985). It is distinctively different from most other ichthyosaurs by the possession of a large depression posterodorsal to the external naris in which two foramina are located. This depression is bordered anteriorly by the nasal and lacrimal, and a small foramen pierces the suture between the two bones, whereas a larger aperture is enclosed between them. The interpretation of this feature by OCHEV & EFIMOV (1985), namely that the external narial aperture has become subdivided, appears plausible. There are ventral processes of the nasals and dorsal ones of the lacrimal already in some Lower Jurassic ichthyosaurs, e. g. *Temnodontosaurus nuertingensis* (MAISCH & HUNGERBÜHLER 1997a). These can reach considerable sizes and give a bilobed appearance to the naris in *Ophthalmosaurus* (GILMORE 1905, 1906; ANDREWS 1910) and, apparently, some individuals of *Eurhinosaurus* (MCGOWAN 1979). This trend of narial subdivision has been carried to the extreme where the processus nariales of nasal and lacrimal meet in *Simbirskiasaurus*. The small foramen along the nasolacrimal suture and the large posterior opening are thus remnants of the posterior half of the external naris. Apart from this unusual feature, the skull of *Simbirskiasaurus* is that of a typical derived post-Triassic ichthyosaur. The anterior extension of the maxilla appears considerable, paralleling the situation in *Platypterygius* (ROMER 1968; MCGOWAN 1972a, b; WADE 1984, 1990) and *Brachypterygius* (MCGOWAN 1976, 1997b). What is preserved of the vertebral column is rather undiagnostic. The diapophyses and parapophyses of the presacrals are clearly divided and unite at the level of the sacrum, as in all post-Triassic ichthyosaurs. The posterior trunk ribs are still clearly bicipital, this feature is shared with *Ichthyosaurus*, *Stenopterygius*, *Ophthalmosaurus* and *Platypterygius* (cf. OCHEV & EFIMOV 1985, fig. 2b).

A somewhat different form of subdivision of the naris has recently been described by ARKHANGELSKY (1998b) from another Russian Cretaceous form, *Platypterygius* (*Pervushovisaurus*) *bannovkensis* (see *Platypterygius* for discussion). The apparent anterior "foramen for the ramus ophthalmicus of the trigeminal nerve" (ARKHANGELSKY 1998b, p. 613) is just the anteriormost extension of the naris, and the forked appearance of the posterior end of the premaxilla, which is simply divided into the processus subnarialis and supranarialis is not at all remarkable. It is nevertheless clear, that the naris in this form is subdivided and that the anterior foramen represents its reduced anterior half. The same phenomenon is well known in the Australian species *Platypterygius longmani* (WADE 1990). *P. bannovkensis* is thus clearly not identical to *Simbirskiasaurus*, but quite close to *Platypterygius longmani*. It is, nevertheless, evident, that the condition displayed by *Platypterygius bannovkensis* and *P. longmani* can be derived from that seen in *Simbirskiasaurus birjukovi*, which is consistent with the two former species' younger geological age (Albian-Cenomanian). In other species of *Platypterygius* no narial subdivision has yet been recorded, but this might be due to incomplete preservation or inadequate observation and requires reinvestigation. At present its apparent absence or presence in species of the genus is too little established to support the subgeneric subdivision proposed by ARKHANGELSKY (at any rate his subgenus *Longirostria* would be a junior objective synonym of *Myopterygius* VON HUENE, 1922). Concerning *Simbirskiasaurus* it is clear that it is an, apparently somewhat plesiomorphic, species of the genus *Platypterygius*, with at least two species of which it shares the otherwise unique character of narial subdivision.

Plutoniosaurus EFIMOV, 1997

Junior subjective synonym of *Platypterygius*
Type species: *Plutoniosaurus bedengensis* EFIMOV, 1997

Discussion. – This is another of the plethora of "new" Upper Jurassic to Cretaceous Russian genera created in the past few years by EFIMOV and ARKHANGELSKY, and yet again it proves to fall in the synonymy of a long known form at closer inspection. From EFIMOV's description there are no differences apparent to the genus *Platypterygius* as diagnosed by MCGOWAN (1972a) and WADE (1990). The description and figure of the skull are untrustworthy, as is obvious to anyone concerned with ichthyosaur cranial anatomy. The forefin, which is the most diagnostic part of the skeleton, shows a tightly fitting mosaic pattern of the individual elements, there is a preaxial accessory facet on the humerus and a development of both pre- and postaxial accessory fingers. The total digital count is no less than 7. The humerus has a large, well developed tochanter dorsalis. The roots of the teeth show a subrectangular cross section. All these are features encountered in *Platypterygius*. Efimov correctly points out the unusual shape of the coracoids, which lack an anterior notch. This appears to be a valid specific character, but does not merit distinction on the generic level.

6. Results of the phylogenetic analysis

The analyses of the data matrix based on the characters listed and discussed above yielded six most parsimonious trees with a consistency index of 0.69 and a retention index of 0.91.

The data matrix was processed with the computer program Paup 4.0b4a. A branch and bound search and a heuristic search with 10000 replicates was performed. The tree was rooted on an hypothetical all zero ancestor. All characters were assigned equal weight and they were all treated as unordered.

A strict consensus of the six most parsimonious trees is presented in Fig. 37. The results of the bootstrap analysis (heuristic search, 1000 replicates) are presented in Fig. 38.

The differences between the single most parsimoniuos trees are restricted to the position of *Macgowania* and *Hudsonelpidia* in relation to the post-Triassic ichthyosaurs and the position of *Platypterygius* and *Brachypterygius* and the clade *Ophthalmosaurus* + *Caypullisaurus*. These taxa are therefore engaged in the two trichotomies of the cladogram. Otherwise the phylogeny is fully resolved.

To translate the results of this phylogenetic analysis into a classification, we chose only to name those clades which showed numerous convincing synapomorphies. We also used the node-stem-triplet based phylogenetic taxonomy recently outlined by Sereno (1998) to define the suprageneric taxa of ichthyosaurs used or newly introduced below. This was thought advisable to arrive at a classification which is both reasonably stable and well-supported and can, hopefully, be used and extended in the near future.

The entire ingroup is the Ichthyosauria, introduced as an ordinal taxon by de Blainville in 1835, the often used designation Ichthyopterygia (also employed by Motani 1999b) is abandoned as a redundant term. The Ichthyosauria comprises all the taxa of the ingroup. There are a number of unequivocal autapomorphies of the Ichthyosauria which were also introduced into the analysis for reasons of completeness (see discussion above).

Order Ichthyosauria de Blainville, 1835

Definition. – The last common ancestor of *Thaisaurus chonglakmanii*, *Utatsusaurus hataii* and *Ophthalmosaurus icenicus* and all of its descendants.

Diagnosis. – Elongate premaxillary rostrum, naris displaced posteriorly, close to orbit, upper temporal fenestra of ichthyosaurian type (with very considerable contribution of supratemporal) present, ectopterygoid absent, thoracal ribs articulate exclusively with the centrum, hyperphalangy of manus and pes present, fibula immobile relative to femur.

The monophyly of all ichthyosaurs, except *Thaisaurus chonglakmanii*, is supported by three synapomorphies:

Character 76 (0→1): Humerus with well developed anterior flange.
Character 127 (0→1): Posterolateral process of postfrontal present.
Character 128 (0→1): Postfrontal participation in fenestra supratemporalis present.

The monophyly of all ichthyosaurs except *Thaisaurus chonglakmanii* and *Utatsusaurus hataii* is supported by six synapomorphies:

Character 37 (0→1): Pterygoid teeth absent.
Character 80 (0→1): Distal end of humerus enlarged with large radial facet.
Character 81 (0→1): Humerus and zeugopodium shorter than hand.
Character 97 (0→1): Metacarpal I semilunate or rounded (or lost).
Character 101 (0→1): Distal manual elements rounded.
Character 104 (0→1): Ilium narrow distally, articulates with one rib only.

MOTANI (1999b) used the ordinal name Grippidia WIMAN, 1929 for a monophylum comprised of *Grippia longirostris* and *Chaohusaurus geishanensis*. However, we see no reason to separate these typical basal ichthyosaurs from the rest of the group as a separate order. Instead we refer them to a family of their own, Grippiidae WIMAN, 1929 nom. transl. ex Grippidia WIMAN, 1929.

Definition. – The last common ancestor of *Grippia longirostris* and *Chaohusaurus geishanensis* and all of its descendants.

Diagnosis. – The monophyly of the Grippiidae WIMAN, 1929 is supported by three synapomorphies:

Character 6 (0→1): Posterior tooth crowns rounded.
Character 7 (0→1): Tooth size relative to skull width small (less than 0.05).
Character 8 (0→1): Maxillary tooth row multiple.

The monophyly of *Parvinatator wapitiensis* and Hueneosauria (see definition below) is supported by only one synapomorphy:

Character 92 (0→1): Manual phalangeal count seven or more.

The Hueneosauria taxon nov. is here introduced as a new taxon to comprise *Wimanius odontopalatus*, the Mixosauridae and the Longipinnati. It is named in honour of FRIEDRICH VON HUENE (1875–1969) of Tübingen University, who made the most extensive and important contributions to the knowldedge of Triassic and post-Triassic ichthyosaurs in the 20th century.

Definition. – The last common ancestor of *Mixosaurus cornalianus* and *Ophthalmosaurus icenicus* and all of its descendants.

Diagnosis. – The Hueneosauria is supported by 15 synapomorphies:

Character 13 (0→1): External naris placed largely laterally.
Character 23 (0→1): Anterior margin of orbit regularly rounded.
Character 32 (0→1): Ramus occipitalis of supratemporal well developed.
Character 36 (0→1): Processus transversus pterygoidei absent.
Character 56 (0→1): Posterior dorsal centra discoidal.
Character 58 (0→1): Sacral ribs indistinguishable.
Character 59 (0→1): Caudal vertebral centra short.
Character 67 (0→1): Interclavicle of triradiate shape.
Character 82 (0→1): Radius and ulna distinctly shortened.
Character 85 (0→1): Posterior margin of ulna convex or straight.

Character 87 (0→1): Proximal end of ulna about as wide as distal end.
Character 98 (0→1): Metacarpals II-IV shortened.
Character 100 (0→1): Metacarpal V smaller than distal carpal IV or absent.
Character 113 (0→1): Tibia and fibula shortened.
Character 118 (0→1): Metatarsals shortened.

The monophyly of *Wimanius odontopalatus* and the Mixosauridae is supported by only one synapomorphy:

Character 44 (0→1): Basis cranii completely covered by pterygoids.

Phalarodon, *Contectopalatus* and *Mixosaurus* form a monophylum, which was first recognized by BAUR (1887) and named Mixosauridae. The name "Mixosauria" introduced by MOTANI 1999b is redundant and has no taxonomic standing.

Definition. – The last common ancestor of *Mixosaurus cornalianus* and *Phalarodon nordenskioeldii* and all of its descendants.

Diagnosis. – The monophyly of the Mixosauridae is supported by 9 synapomorphies:

Character 10 (0→1): Processus supranarialis of premaxilla extremely small or absent.
Character 12 (0→1): Maxilla meets prefrontal.
Character 15 (0→1): Continuous high sagittal crest on nasal, frontal and parietal.
Character 22 (0→1): High supraorbital crest, formed by prefrontal and postfrontal.
Character 25 (0→1): Supratemporal with anterodorsal sheet overhanging fenestra supratemporalis.
Character 30 (0→1): Quadratojugal distinctly smaller than squamosal in external view.
Character 62 (0→1): Anterior dorsal neural spines high and straight.
Character 95 (0→1): Distal carpal I of similar size as metacarpal V or larger.
Character 111 (0→1): Hindfins less than two thirds the length of the forefins.

The monophyly of the two mixosaurid genera *Phalarodon* and *Contectopalatus* is supported by two synapomorphies:

Character 2 (0→1): Maxillary and posterior dentary teeth mesiodistally elongated.
Character 6 (0→1): Posterior tooth crowns rounded.

The rest of the Hueneosauria, comprising all the non-mixosaurid Middle Triassic to Upper Cretaceous taxa known (except the enigmatic *Wimanius*) could be designated by another new taxon name. As most, and probably all of these ichthyosaurs are characterized by the loss of the first digit in the forefin, which provides at least most of the early members of the group with slender and elongated fins, we chose to resurrect the old Longipinnati, formally erected by VON HUENE (1948) for this group.

Definition. – The Longipinnati are here re-defined as the last common ancestor of *Cymbospondylus petrinus* and *Ophthalmosaurus icenicus* and all of its descendants.

Diagnosis. – The Longipinnati are supported by 9 synapomorphies:

Character 74 (0→1): Coracoid with reduced anterior extension.
Character 75 (0→1): Humerus without well differentiated head.
Character 86 (0→1): Radius peripheral shaft reduced to notch or absent.
Character 88 (0→1): First digit of forefin lost.
Character 93 (0→1): Pisiform much smaller than ulnare or absent.

Character 96 (0→1): Distal carpals II-IV of similar size.
Character 99 (0→1): Metacarpal V with straight or concave posterior margin or absent.
Character 108 (0→1): Pubis and ischium with strongly convex medial margins, do not form symphysis.
Character 120 (0→1): Number of toes less than 5.

Qianichthyosaurus and *Toretocnemus* form a monophylum at the basis of the Longipinnati, for which the new name Toretocnemidae nov. fam. is introduced.

Definition. – The last common ancestor of *Toretocnemus californicus* and *Qianichthyosaurus zhoui* and all of its descendants.

Diagnosis. – The Toretocnemidae is supported by three synapomorphies.

Character 53 (0→1): Rib articulation in thoracal series mainly bicipital.
Character 89 (0→1): Forefin with accessory digit posterior to fourth finger.
Character 116 (0→1): Fibula at about the same level as femur.

All Longipinnati except the Toretocnemidae are united by five synapomorphies:

Character 14 (0→1): Nasal reaches distinctly over orbit.
Character 33 (0→1): Maximum skull length in adults more than 400 mm.
Character 42 (0→1): Carotid foramen paired in parasphenoid or basisphenoid.
Character 57 (0→1): Sacral ribs unicipital.
Character 61 (0→1): Processus spinosi in anterior and middle caudal region short and wide.

The remaining Longipinnati form two monophyla, the Cymbospondylidae von Huene, 1948 and the Merriamosauria Motani, 1999.

The Cymbospondylidae von Huene, 1948 is here defined as the last common ancestor of *Phantomosaurus neubigi* and *Cymbospondylus petrinus* and all of its descendants. It is at present only defined by strongly homoplastic characters and should be considered a metataxon, before uneqivocal synapomorphies become apparent.

The Merriamosauria was defined by Motani (1999b) as the last common ancestor of *Shastasaurus pacificus* and *Ichthyosaurus* and all of its descendants, but as *Shastasaurus pacificus* is very little known (Maisch 2000), we redefine it here as the last common ancestor of *Besanosaurus leptorhynchus* (the best known basal representative of the clade) and *Ichthyosaurus communis* and all of its descendants.

The Merriamosauria is diagnosed by 10 synapomorphies:

Character 60 (0→1): Middle caudal processus spinosi steep or inclined posteriorly.
Character 64 (0→1): Posterior gastralia absent.
Character 68 (0→1): Clavicle slender and narrow medially.
Character 69 (0→1): Scapular glenoid and coracoid facets enlarged.
Character 70 (0→1): Anterior scapular process reduced or absent.
Character 72 (0→1): Glenoid and scapular facets of coracoid enlarged.
Character 102 (0→1): Proximal phalanges of forefin largely rounded or rectangular.
Character 109 (0→1): Pubic foramen open posteriorly or absent.
Character 110 (0→1): Distance between obturator foramen/incisure and distal margin of pubis small.
Character 119 (0→1): Phalanges of hindfin largely rounded or rectangular.

All merriamosaurs except *Besanosaurus leptorhynchus* are united by 6 synapomorphies:

Character 9 (0→1): Processus subnarialis of premaxilla distinctive, reaches back more than one third of naris.
Character 18 (0→1): Frontal widest position at nasal suture.
Character 19 (0→1): Frontal contributes to foramen parietale.
Character 54 (0→1): Anterior dorsal rib facets not confluent with anterior central facets.
Character 84 (0→1): Spatium interosseum between radius and ulna reduced.
Character 107 (0→1): Pubis and ischium of similar size or ischium larger.

All merriamosaurs apart from *Besanosaurus leptorhynchus* and *Shastasaurus* are united by 4 synapomorphies:

Character 17 (0→1): Frontal distinctly smaller than parietal.
Character 27 (0→1): Posterior margin of skull roof moderately indented.
Character 47 (0→1): Articular transversely narrow.
Character 67 (1→2): Interclavicle T-shaped.

All merriamosaurs except *Besanosaurus*, *Shastasaurus* and *Shonisaurus popularis* are united by 5 synapomorphies:

Character 20 (0→1): Parietal ridge present.
Character 34 (0→1): Interpterygoid vacuities well developed.
Character 35 (0→1): Processus posteromedialis of pterygoid absent.
Character 45 (0→1): Coronoid ossification very narrow and small splint.
Character 79 (0→1): Ulnar and radial humeral facets of equal size.

There is no clear synapomorphy linking *Californosaurus* to the higher Merriamosauria at the moment.

The merriamosaurs above *Californosaurus perrini* are again united by five synapomorphies:

Character 41 (0→1): Basis cranii largely formed by basisphenoid.
Character 43 (0→1): Base of processus cultriformis narrow.
Character 71 (0→1): Posterior scapular process reduced.
Character 73 (0→1): Coracoid with straight medial symphysis.
Character 89 (0→1): Forefin with accessory digits posterior to fourth finger.

The Parvipelvia, defined by Motani (1999b) as the last common ancestor of *Hudsonelpidia*, *Macgowania*, *Ichthyosaurus* and all of its descendants is recognized here. It can be diagnosed by 7 synapomorphies:

Character 76 (1→2): Humerus anterior flange secondarily reduced.
Character 77 (0→1): Anterior margin of humerus markedly concave.
Character 105 (0→1): Ischium narrow.
Character 106 (0→1): Pubis narrow.
Character 112 (0→1): Femur tibial and fibular facets of equal size.
Character 116 (0→1): Fibula at same level as femur.
Character 117 (0→1): Tibia peripheral shaft notch or largely reduced.

All post-Triassic ichthyosaurs form a very distinct monophylum, for which the name Neoichthyosauria Sander, 2000 is available.

Definition. – The Neoichthyosauria is here defined as the last common ancestor of *Temnodontosaurus trigonodon* and *Ophthalmosaurus icenicus* and all of its descendants.

Diagnosis. – Monophyly of the Neoichthyosauria is based on 10 synapomorphies:

Character 1 (0→1): Teeth aulacodont.
Character 5 (0→1): Replacement teeth appear inside pulp cavity.
Character 11 (0→1): Processus postnarialis tiny or absent.
Character 16 (0→1): Excavatio internasalis present.
Character 26 (0→1): Anterior terrace of fenestra supratemporalis absent.
Character 50 (0→1): Atlas/axis co-ossified in adults.
Character 51 (0→1): Zygapophyses unpaired.
Character 63 (0→1): Ossified haemapophyses absent.
Character 78 (0→1): Humerus with big trochanter dorsalis.
Character 114 (0→1): Spatium interosseum between tibia and fibula absent.

All Neoichthyosaurs apart of *Temnodontosaurus* are united by a single synapomorphy:

Character 42 (1→2): Carotid foramen unpaired in basisphenoid.

The rest of the Neoichthyosauria consists of the Leptonectidae, *Suevoleviathan* and the Thunnosauria (Motani 1999b).

Eurhinosauria Motani, 1999b is a junior objective synonym of Leptonectidae Maisch, 1998 and therefore invalid. Monophyly of the Leptonectidae Maisch, 1998, which is defined here as the last common ancestor of *Leptonectes tenuirostris* and *Eurhinosaurus longirostris* and all of its descendants, is based on two synapomorphies:

Character 3 (0→1): Teeth smooth.
Character 28 (0→1): Quadratojugal in posterior position.

The monophyly of *Suevoleviathan* and the Thunnosauria is based on a single synapomorphy:

Character 66 (0→1): Well developed lunate tailfin.

All Neoichthyosauria which are more derived than *Suevoleviathan* form a well-defined monophylum, for which the name Thunnosauria Motani, 1999b has been proposed.

Definition. – The last common ancestor of *Ichthyosaurus communis* and *Stenopterygius quadriscissus* and all of its descendants.

Diagnosis. – Monophyly of the Thunnosauria is supported by five synapomorphies:

Character 30 (0→1): Quadratojugal small.
Character 31 (0→1): Squamosal small, delicate plate or absent
Character 53 (0→1): Rib articulation in thorax bicipital.
Character 65 (0→1): Tail short.
Character 111 (0→1): Hindfins much shorter than forefins.

All thunnosaurs apart of *Ichthyosaurus* are united by two synapomorphies:

Character 38 (0→1): Processus postpalatinalis present.
Character 103 (0→1): Pelvis bipartite with ischiopubic plate.

The Ophthalmosauridae Baur, 1887 is united by three synapomorphies:

Character 40 (0→1): Area extracondylaris very small.
Character 91 (0→1): Forefin with preaxial finger(s).
Character 94 (0→1): Propodial elements thick.

This clade has been called Ophthalmosauria by Motani (1999b), which is, however, a junior objective synonym of Ophthalmosauridae Baur, 1887 and taxonomically redundant.

Within the Ophthalmosauridae, a sister-group relationship of *Ophthalmosaurus* and *Caypullisaurus* is indicated by one synapomorphy:

Character 4 (0→1): Dentition reduced in adults.

The classification of ichthyosaurs proposed here can therefore be set out as follows:

Ichthyosauria de Blainville, 1835

- *Thaisaurus* Mazin et al., 1991
- *Utatsusaurus* Shikama, Kamei & Murata, 1978
- Grippiidae Wiman 1929 nom. transl. ex Grippidia
  - *Chaohusaurus* Young & Dong, 1972
  - *Grippia* Wiman, 1929
- inc. sed. *Parvinatator* Nicholls & Brinkman, 1995
- Hueneosauria taxon nov.
  - *Wimanius* Maisch & Matzke, 1998
  - Mixosauridae Baur, 1887
    - *Mixosaurus* Baur, 1887
    - *Phalarodon* Merriam, 1910
    - *Contectopalatus* Maisch & Matzke, 1998
  - *Rotundopteryx* gen. nov.
  - Longipinnati von Huene, 1948
    - Toretocnemidae fam. nov.
      - *Toretocnemus* Merriam, 1903
      - *Qianichthyosaurus* Li, 1999
    - Cymbospondylidae von Huene, 1948
      - *Phantomosaurus* gen. nov.
      - *Cymbospondylus* Leidy, 1868
    - Merriamosauria Motani, 1999
      - *Besanosaurus* Dal Sasso & Pinna, 1996
      - *Shastasaurus* Merriam, 1895
      - *Mikadocephalus* Maisch & Matzke, 1997
      - *Shonisaurus* Camp, 1976
      - *Californosaurus* Kuhn, 1934
      - *Callawayia* gen. nov.
      - Parvipelvia Motani, 1999
        - *Hudsonelpidia* McGowan, 1995
        - *Macgowania* Motani, 1999
        - Neoichthyosauria Sander, 2000
          - Temnodontosauridae McGowan, 1994
            - *Temnodontosaurus* Lydekker, 1889
          - Leptonectidae Maisch, 1998
            - *Leptonectes* McGowan, 1996
            - *Eurhinosaurus* Abel, 1909
          - Suevoleviathanidae Maisch, in press a

Suevoleviathan MAISCH, 1998
inc. sed. *Nannopterygius* VON HUENE, 1922
Thunnosauria MOTANI, 1999
  Ichthyosauridae BONAPARTE, 1841
    Ichthyosaurus DE LA BECHE & CONYBEARE, 1821
  Stenopterygiidae WOODWARD in ZITTEL, 1932
    Stenopterygius JAEKEL, 1904
    ? *Chacaicosaurus* FERNÁNDEZ, 1994
  Aegirosaurus BARDET & FERNÁNDEZ, 2000
  Ophthalmosauridae BAUR, 1887
    Ophthalmosaurus SEELEY, 1874
    Caypullisaurus FERNÁNDEZ, 1997
    Brachypterygius VON HUENE, 1922
    Platypterygius VON HUENE, 1922

If one compares the results of phylogenetic analysis to the fossil record, a good agreement is observed. The Lower Triassic taxa (*Thaisaurus*, *Parvinatator*, *Utatsusaurus*, *Chaohusaurus*, *Grippia*, the first two of somewhat uncertain age) are the most basal ones in the phylogeny. The mixosaurids, which are exclusively Middle Triassic, are the next highly derived group, but the most basal longipinnates, *Toretocnemus* and *Qianichthyosaurus*, are Upper Triassic (Carnian) which is certainly an anomaly. Further anomalies are encountered within the shastasaur-grade forms. *Shastasaurus* and *Shonisaurus* are of Carnian age, but hold a position less derived than the Middle Triassic (Anisian/Ladinian) *Mikadocephalus*. The Norian forms *Callawayia*, *Macgowania* and *Hudsonelpidia* are, however, the most-derived Triassic taxa which is in good agreement with the fossil record. *Temnodontosaurus* is the most basal post-Triassic ichthyosaur, and the next least derived are the leptonectids. As *Temnodontosaurus* already probably occurs in the Norian (MCGOWAN 1997a) and the leptonectids are already found in beds of presumably Rhaetic age (MCGOWAN 1974b; 1989; 1996b) this is, again, in good agreement with the fossil record. An anomalous position is occupied by *Suevoleviathan*, which is so far exclusively Lower Toarcian but apparently less derived than *Ichthyosaurus*, already known from the lowermost Jurassic. The phylogenetic position of *Suevoleviathan* seems rather well supported and a considerable ghost-lineage has therefore to be postulated for this genus, which goes back at least to the Triassic/Jurassic boundary. The phylogenetic arrangement of the more highly derived forms *Stenopterygius* to *Platypterygius* agrees generally very well with the fossil record and no long ghost lineages have to be postulated.

In summa the phylogenetic arrangement proposed here is in reasonably good agreement with the fossil record of ichthyosaurs. One has to be aware, with respect to the anomalies pointed out above, that our knowledge of the fossil record of ichthyosaurs is certainly severely biased towards only very few highly productive localities which have yielded material as complete as necessary to be diagnostic. Most other ichthyosaur occurrences are restricted to isolated or fragmentary material, which is usually not even determinable to family level, particularly in the Jurassic.

Of the 35 valid genera of ichthyosaurs, 6 occur in the Anisian/Ladinian of Monte San Giorgio, 4 in the Carnian of California, Nevada and Mexico, 3 in the Lower

Liassic of England or coeval beds in continental Western Europe, 4 in the Lower Toarcian Posidonienschiefer of Western Europe and 2 in the English Kimmeridge Clay. The other genera have been found outside these few localities, but most of these are also restricted to a few special fossillagerstätten. The fossil record of Upper Triassic ichthyosaurs outside North America and of Lower Jurassic ichthyosaurs outside Western Europe is, for example, close to non-existent, and the early Middle Jurassic record is extremely poor all around the globe. It is therefore expectable, that the correspondence between phylogeny and stratigraphic record will increase considerably in the future, both by discovery of additional records (as in the case of *Shastasaurus* or *Suevoleviathan*) and by better data sets for some little-known taxa, which might affect their phylogenetic position (as with *Shonisaurus*).

At any rate the present phylogenetic hypothesis supports the notion that the fossil record of ichthyosaurs, patchy as it might be, is at least complete enough to provide a clue for a good understanding of ichthyosaur history, to which the present paper has hopefully contributed.

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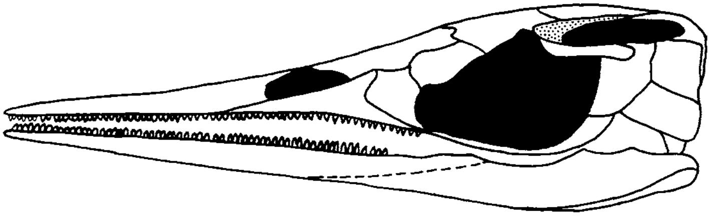
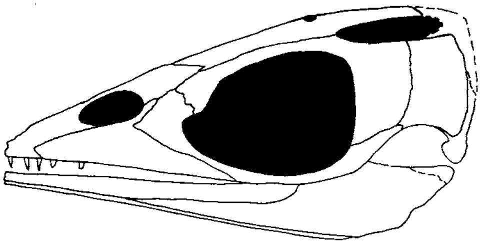
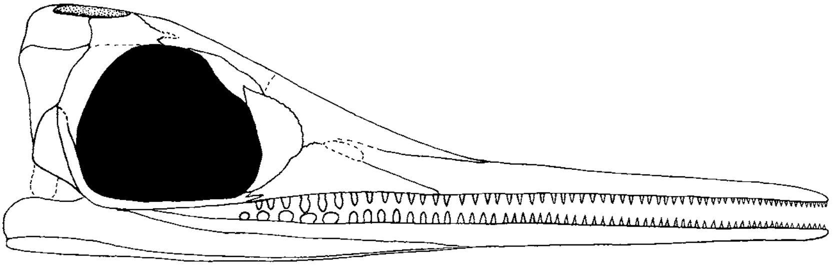


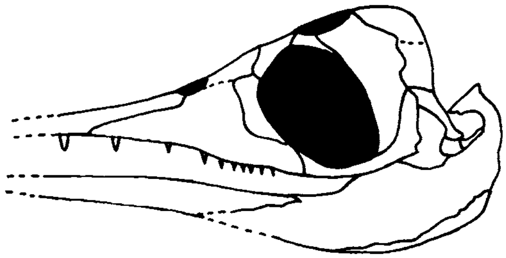
Utatsusaurus hataii



Grippia longirostris



Chaohusaurus geishanensis



Parvinatator wapitiensis

Fig. 1. Skull reconstructions of Lower Triassic ichthyosaurs in lateral view. *Utatsusaurus hataii* modified from Motani 1999b, *Grippia longirostris* modified from Wiman 1933 and von Huene 1943, *Chaohusaurus geishanensis* from Maisch in press b, *Parvinatator wapitiensis* modified from Nicholls & Brinkman 1996.

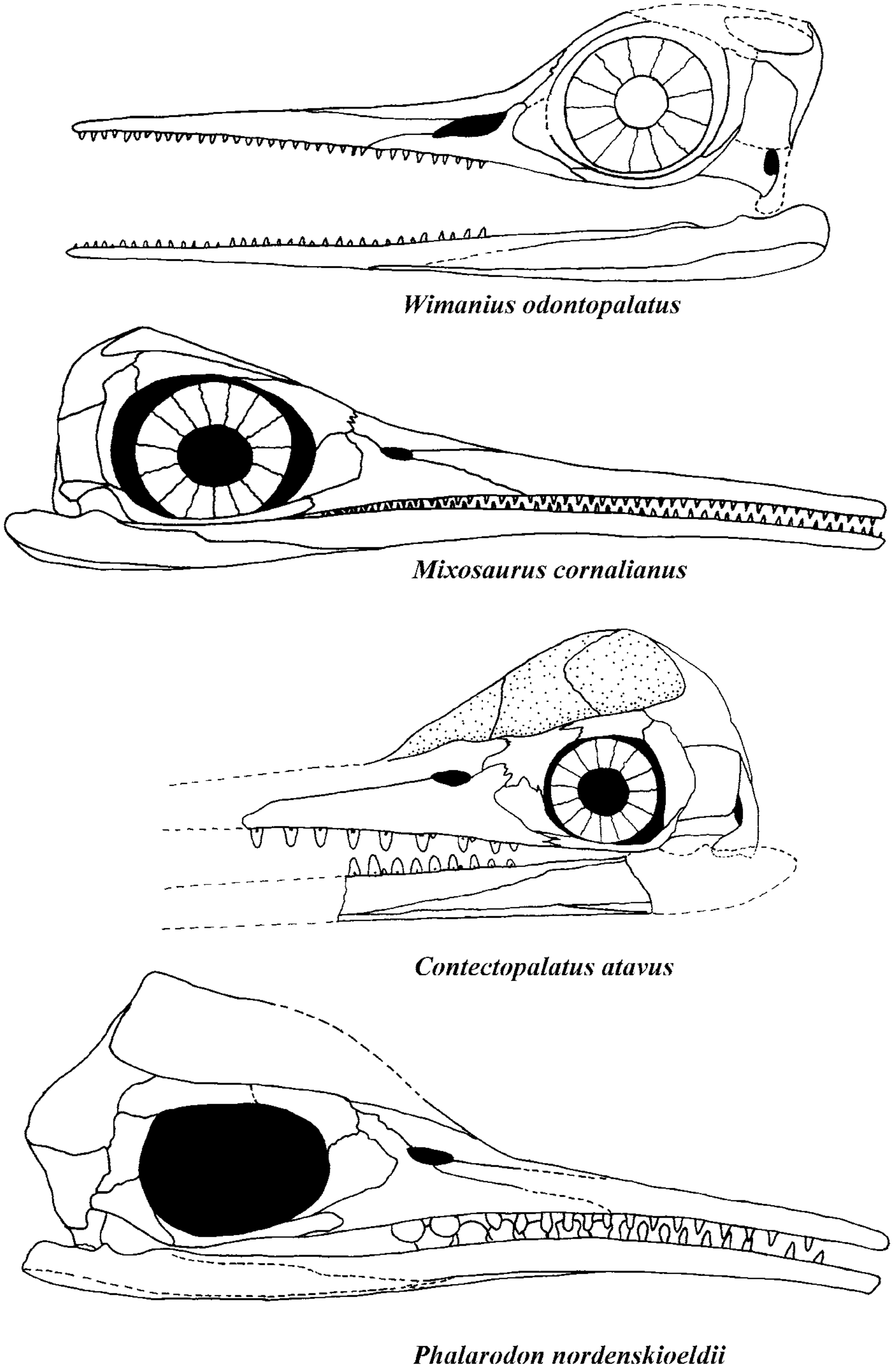
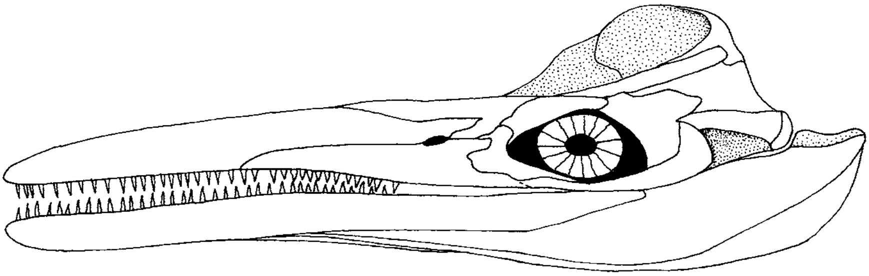
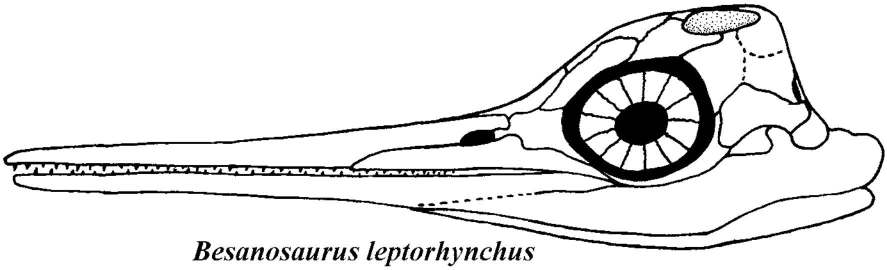


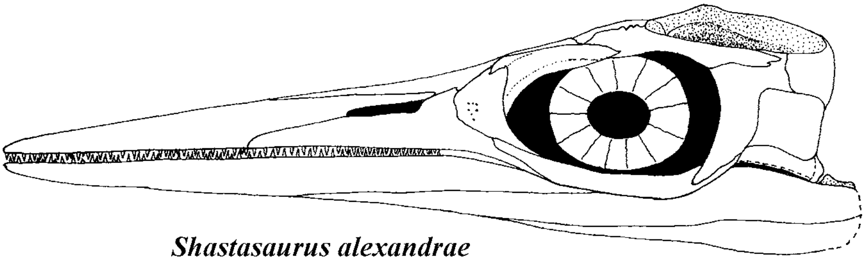
Fig. 2. Skull reconstructions of Middle Triassic ichthyosaurs in lateral view. *Wimanius odontopalatus* from Maisch & Matzke 1999, *Mixosaurus cornalianus* from Maisch & Matzke 1997 b, *Contectopalatus atavus* from Maisch & Matzke in press a, *Phalarodon nordenskioeldii* based on Nicholls et al. 1999 and pers. obs. (*Phalarodon fraasi*, Berkeley).



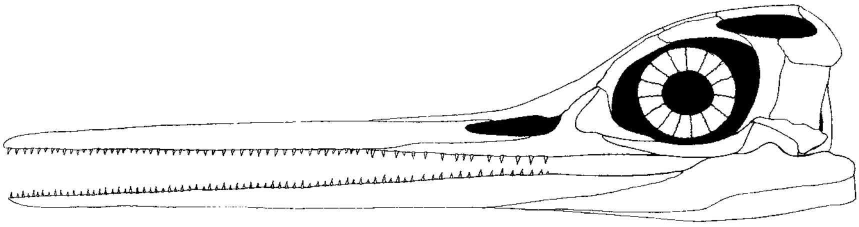
Cymbospondylus petrinus



Besanosaurus leptorhynchus



Shastasaurus alexandrae



Mikadocephalus gracilirostris

Fig. 3. Skull reconstructions of Middle to Upper Triassic ichthyosaurs in lateral view. *Cymbospondylus petrinus* from Maisch 2000, *Besanosaurus leptorhynchus* based on Dal Sasso & Pinna 1996 and pers. obs. (Zürich), *Shastasaurus alexandrae* from Maisch 2000, *Mikadocephalus gracilirostris* from Maisch & Matzke 1999.

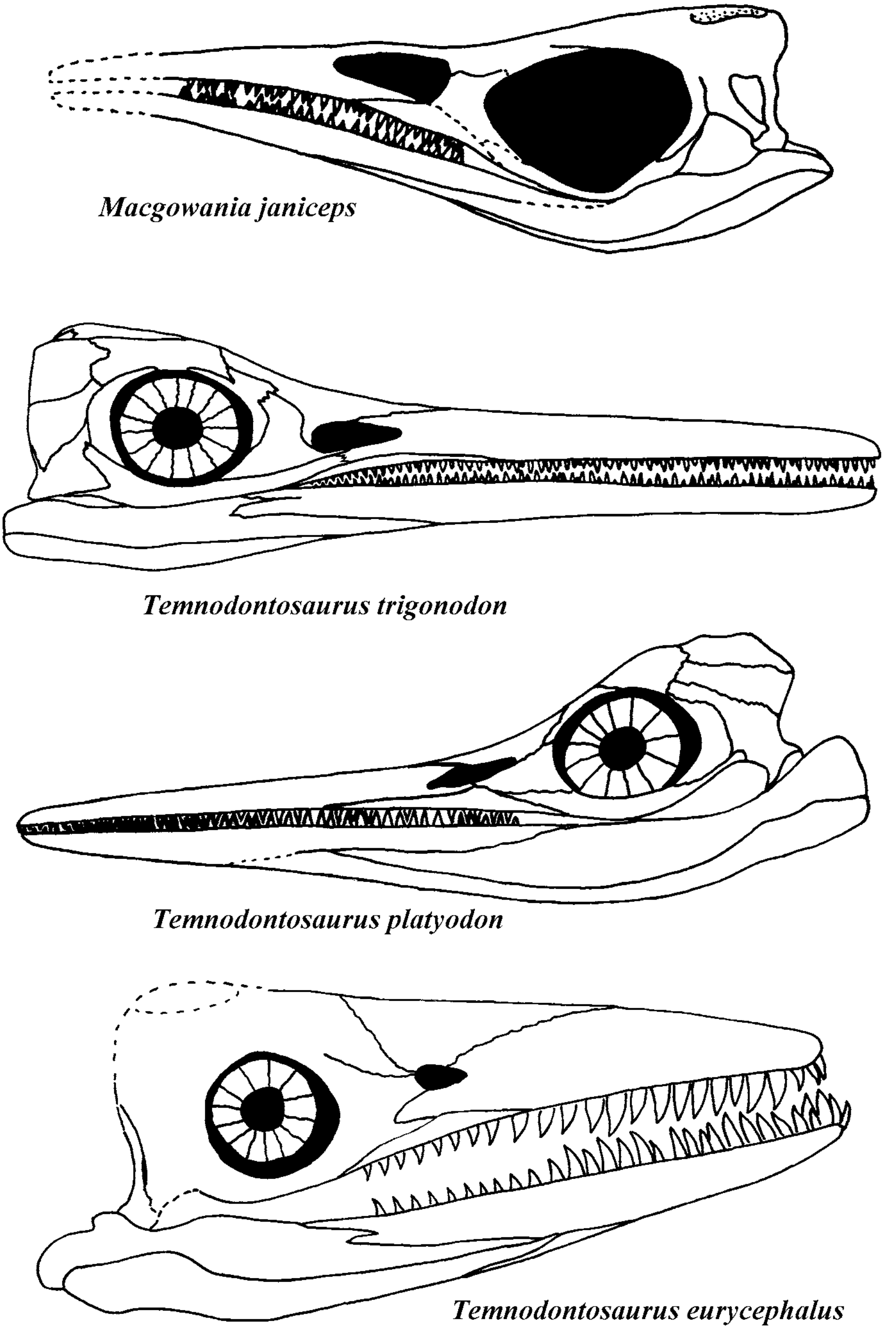
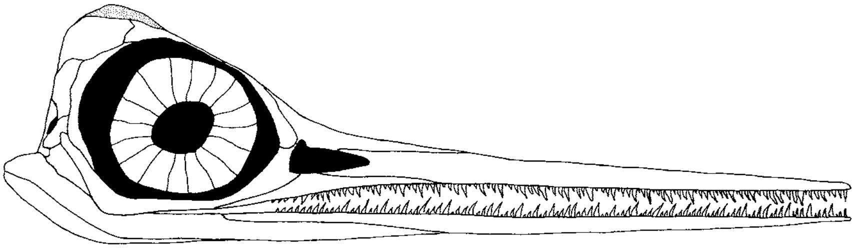
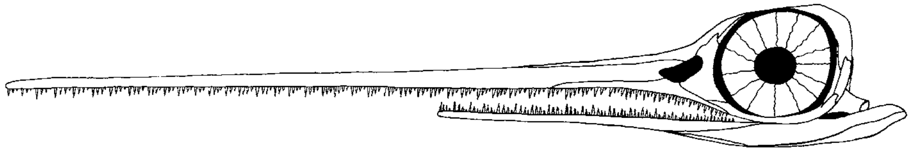


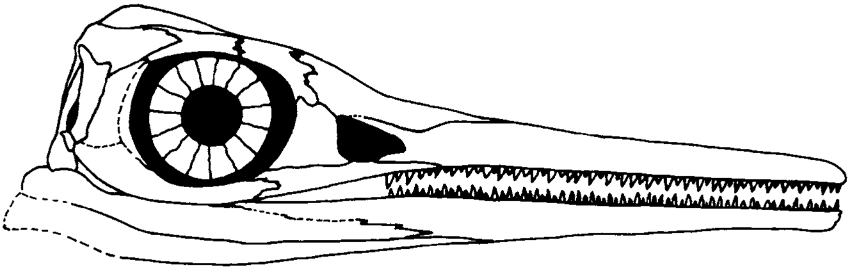
Fig. 4. Skull reconstructions of Upper Triassic to Lower Jurassic ichthyosaurs in lateral view. *Macgowania janiceps* modified from McGowan 1996a, *Temnodontosaurus trigonodon* from Maisch & Hungerbühler 1997b, *Temnodontosaurus platyodon* based on Owen 1881 and Maisch & Hungerbühler in press, *Temnodontosaurus eurycephalus* modified from Owen 1881.



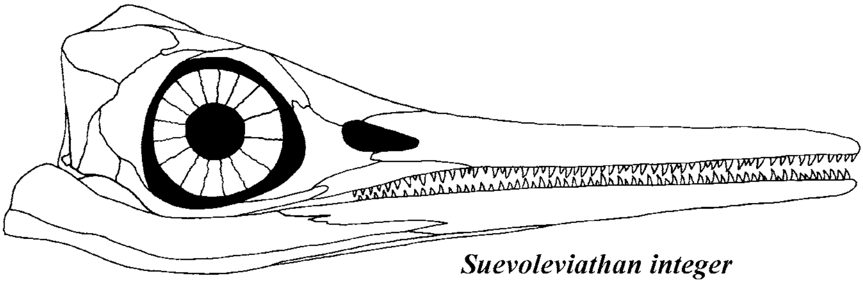
Leptonectes tenuirostris



Eurhinosaurus longirostris

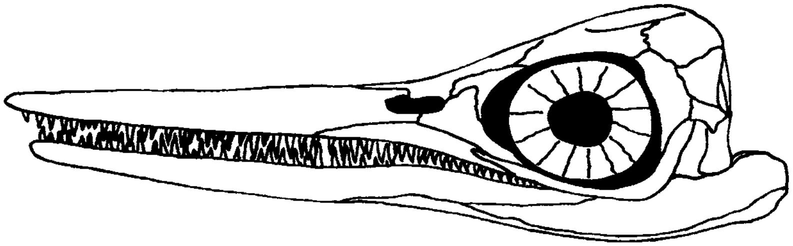


Suevoleviathan disinteger

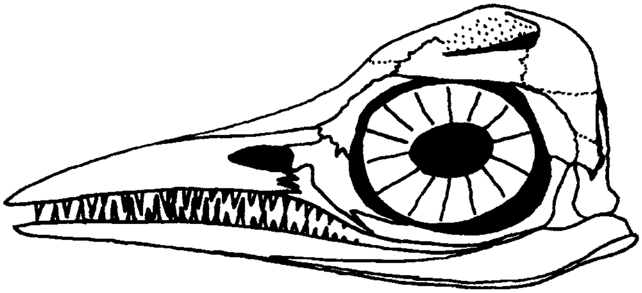


Suevoleviathan integer

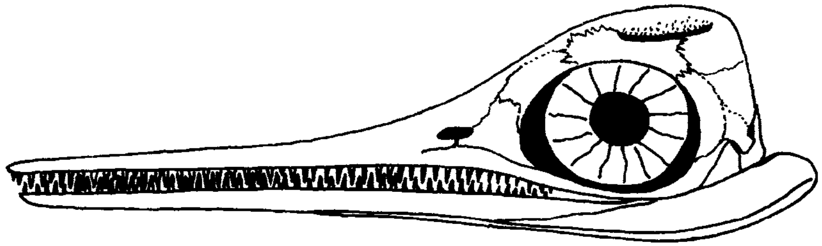
Fig. 5. Skull reconstructions of Lower Jurassic ichthyosaurs in lateral view. *Leptonectes tenuirostris* based on pers. obs. (Berlin), *Eurhinosaurus longirostris* based on pers. obs. (Stuttgart), *Suevoleviathan disinteger* from MAISCH in press a, *Suevoleviathan integer* from MAISCH in press a.



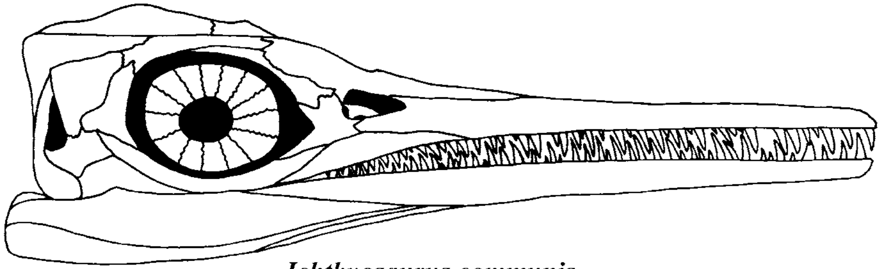
Ichthyosaurus intermedius



Ichthyosaurus breviceps

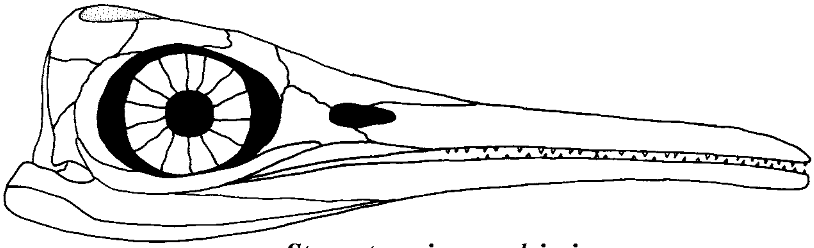


Ichthyosaurus conybeari

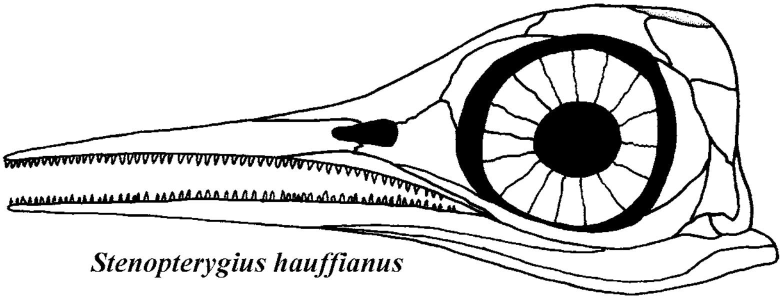


Ichthyosaurus communis

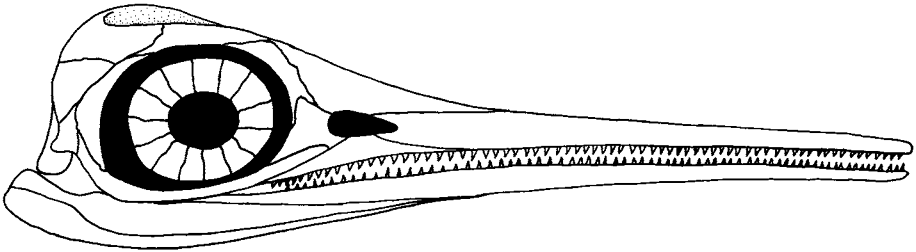
Fig. 6. Skull reconstructions of the species of *Ichthyosaurus* in lateral view, *Ichthyosaurus intermedius* modified from MAISCH 1997b, *Ichthyosaurus breviceps* based on McGOWAN 1974b and pers. obs. (Tübingen), *Ichthyosaurus conybeari* based on McGOWAN 1974b and pers. obs. (Coburg), *Ichthyosaurus communis* from MAISCH & MATZKE 2000b.



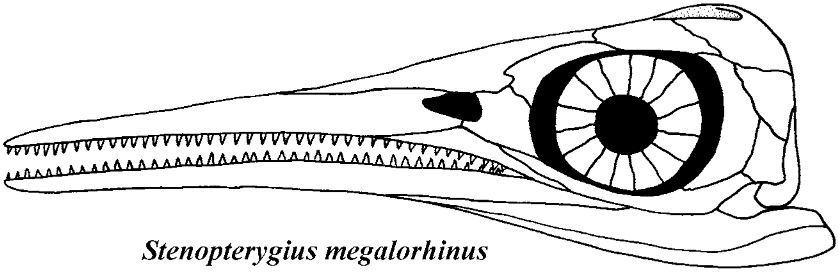
Stenopterygius quadriscissus



Stenopterygius hauffianus

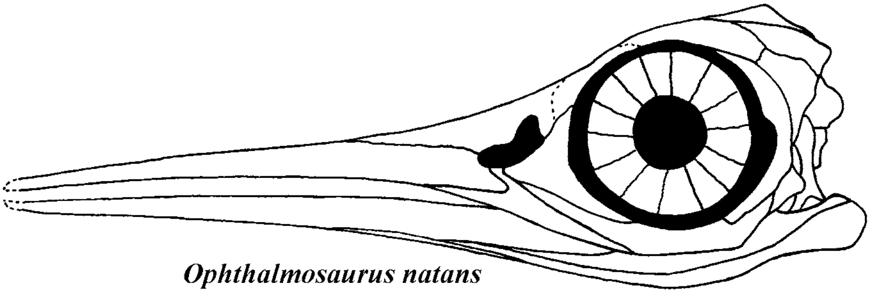


Stenopterygius longifrons

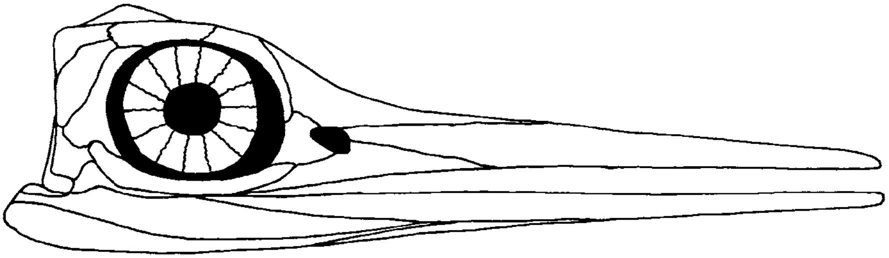


Stenopterygius megalorhinus

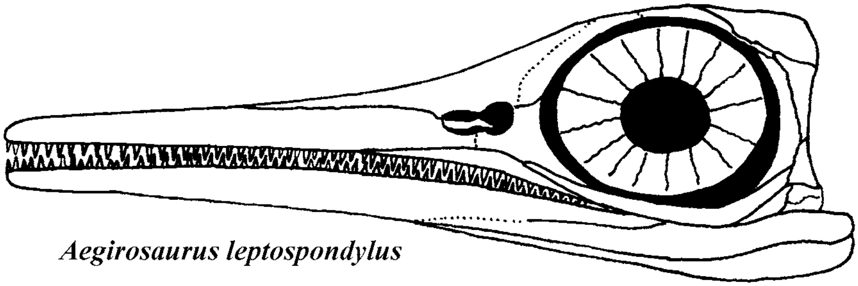
Fig. 7. Skull reconstructions of the species of *Stenopterygius* in lateral view. *Stenopterygius quadriscissus* pers. obs. (Tübingen, Stuttgart), *Stenopterygius hauffianus* pers. obs. (Tübingen, Stuttgart), *Stenopterygius longifrons* pers. obs. (Tübingen, Stuttgart), *Stenopterygius megalorhinus* pers. obs. (Tübingen, Stuttgart).



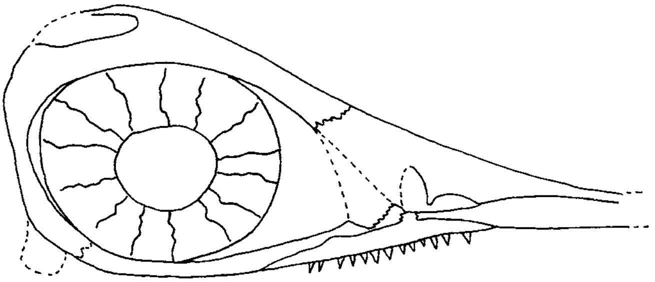
Ophthalmosaurus natans



Ophthalmosaurus icenicus

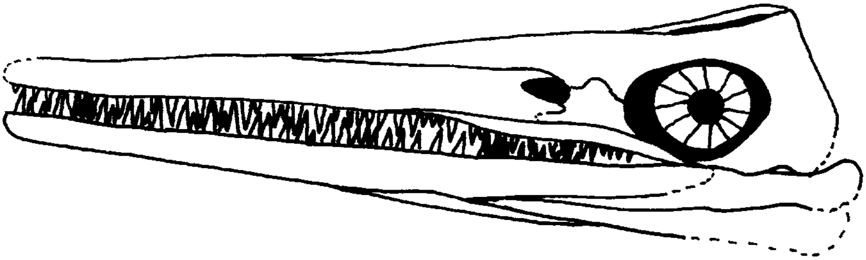


Aegirosaurus leptospondylus

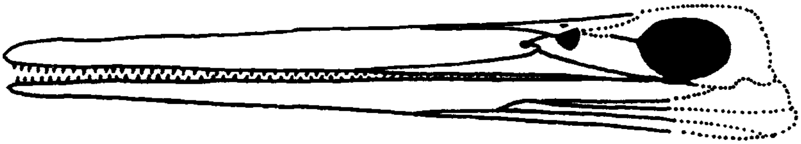


Aegirosaurus sp.

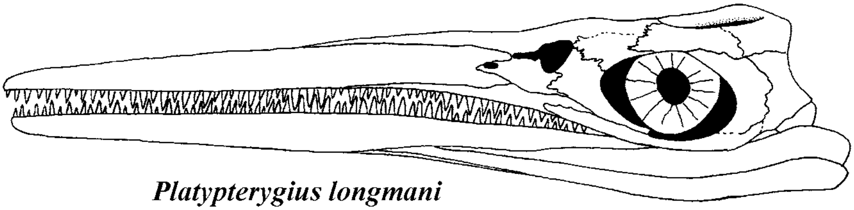
Fig. 8. Skull reconstructions of Middle to Upper Jurassic ichthyosaurs in lateral view. *Ophthalmosaurus natans* modified from GILMORE 1905, *Ophthalmosaurus icenicus* based on ANDREWS 1910, MAISCH 1998b, *Aegirosaurus leptospondylus* pers. obs. (München, Stuttgart), *Aegirosaurus* sp. modified from GASPARINI 1988.



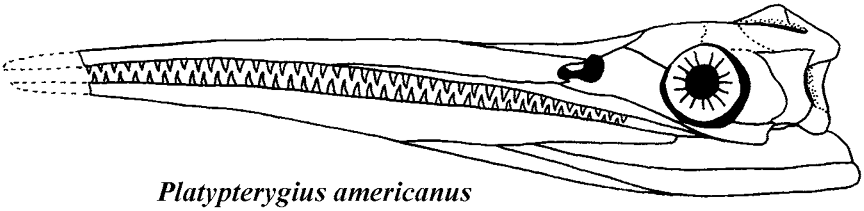
Brachypterygius mordax



Platypterygius bannovkensis

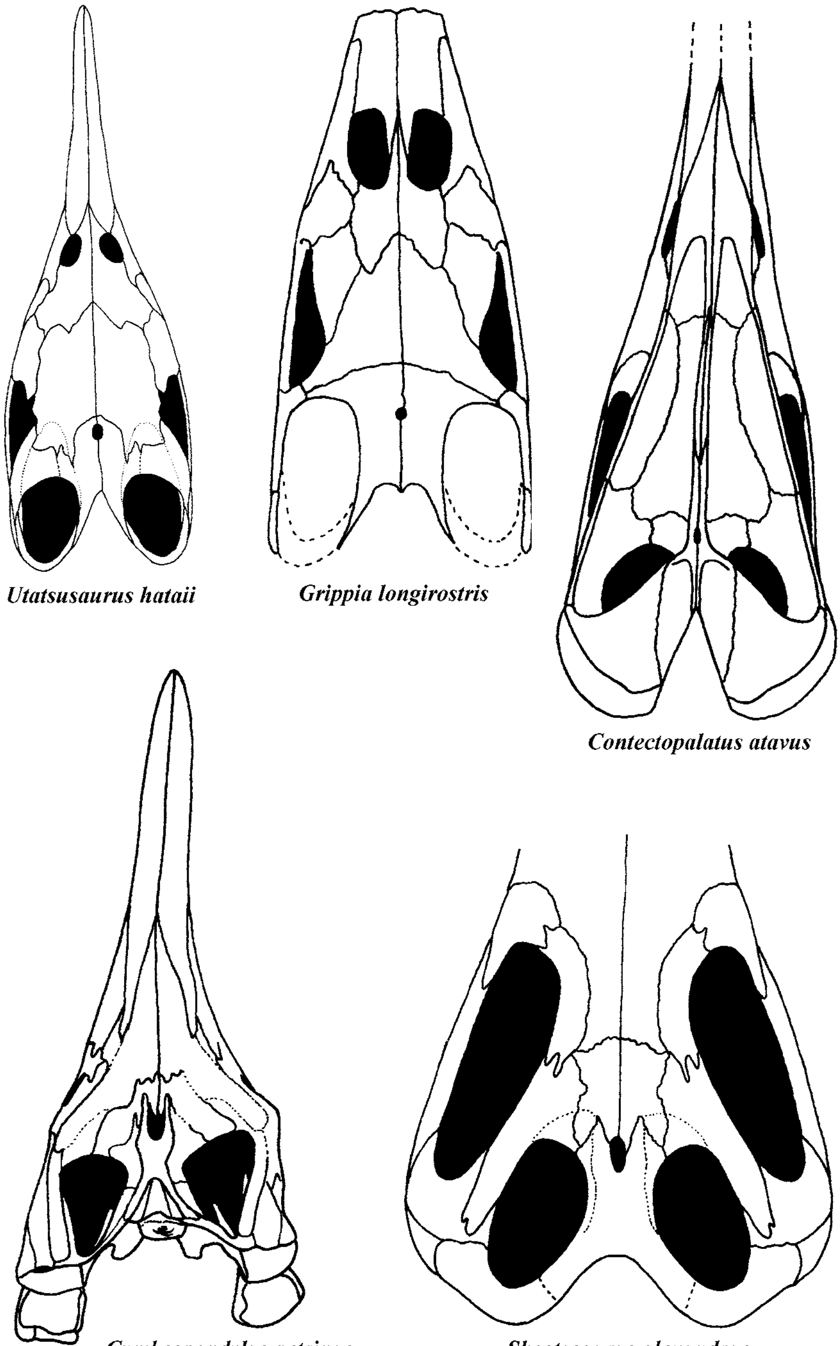


Platypterygius longmani



Platypterygius americanus

Fig. 9. Skull reconstructions of Upper Jurassic to Cretaceous ichthyosaurs in lateral view. *Brachypterygius mordax* modified from McGowan 1976, *Platypterygius bannovkensis* from Arkhangelsky 1998b, *Platypterygius longmani* modified from Wade 1984, 1990, *Platypterygius americanus* from Romer 1969.



Utatsusaurus hataii

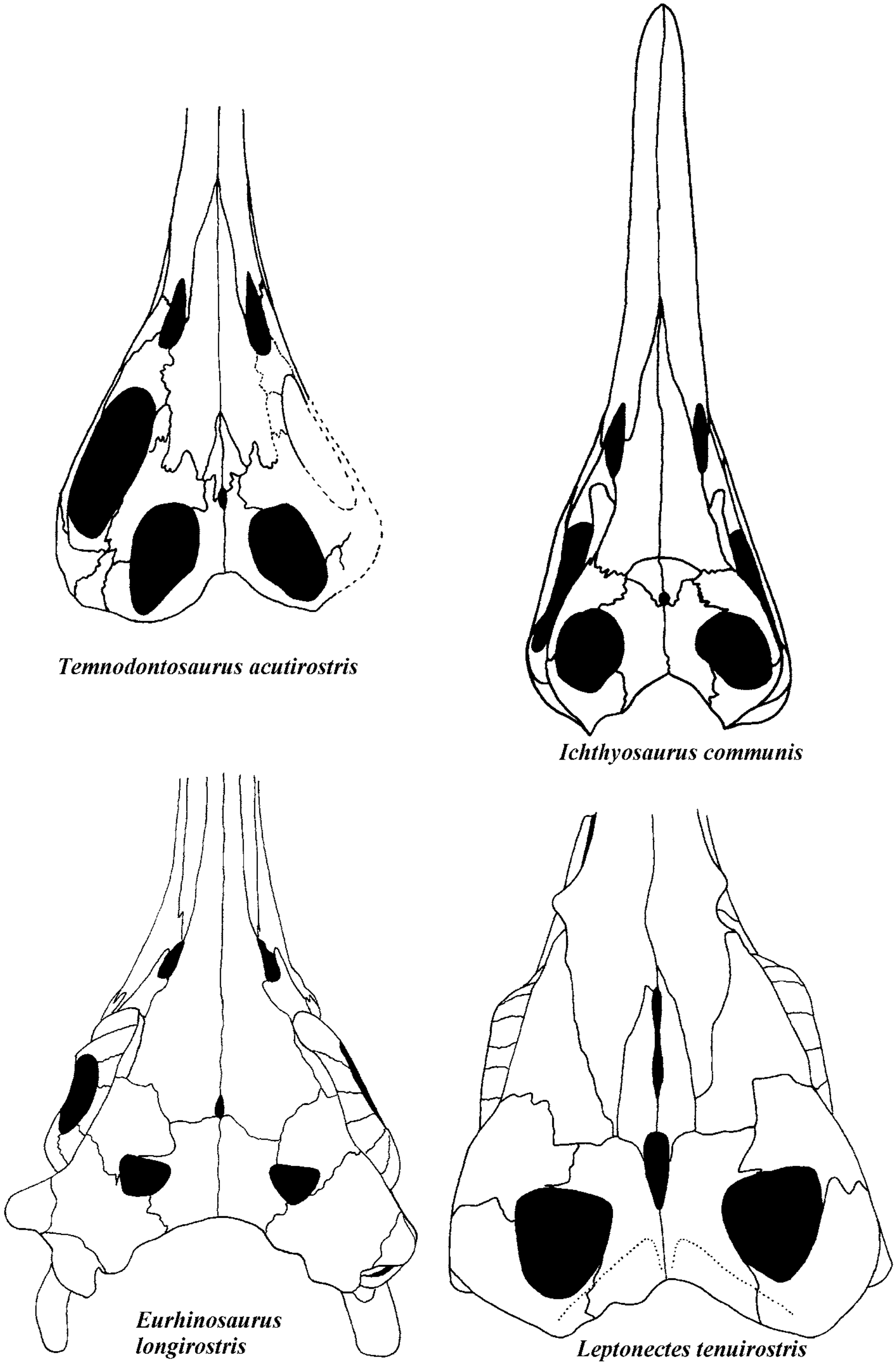
Grippia longirostris

Contectopalatus atavus

Cymbospondylus petrinus

Shastasaurus alexandrae

Fig. 10. Skull reconstructions of Triassic ichthyosaurs in dorsal view. *Utatsusaurus hataii* pers. obs. (MOTANI's specimens), *Grippia longirostris* modified from WIMAN 1933 and MOTANI 1998b, *Contectopalatus atavus* pers. obs. (Stuttgart, Berlin), *Cymbospondylus petrinus* based on MERRIAM 1908 and pers. obs. (Berkeley), *Shastasaurus alexandrae* pers. obs. (Berkeley).



Temnodontosaurus acutirostris

Ichthyosaurus communis

Eurhinosaurus longirostris

Leptonectes tenuirostris

Fig. 11. Skull reconstructions of Lower Jurassic ichthyosaurs in dorsal view. *Temnodontosaurus acutirostris* modified from SEELEY 1880, *Ichthyosaurus communis* modified from SOLLAS 1916, *Eurhinosaurus longirostris* pers. obs. (Stuttgart), *Leptonectes tenuirostris* pers. obs. (Berlin).

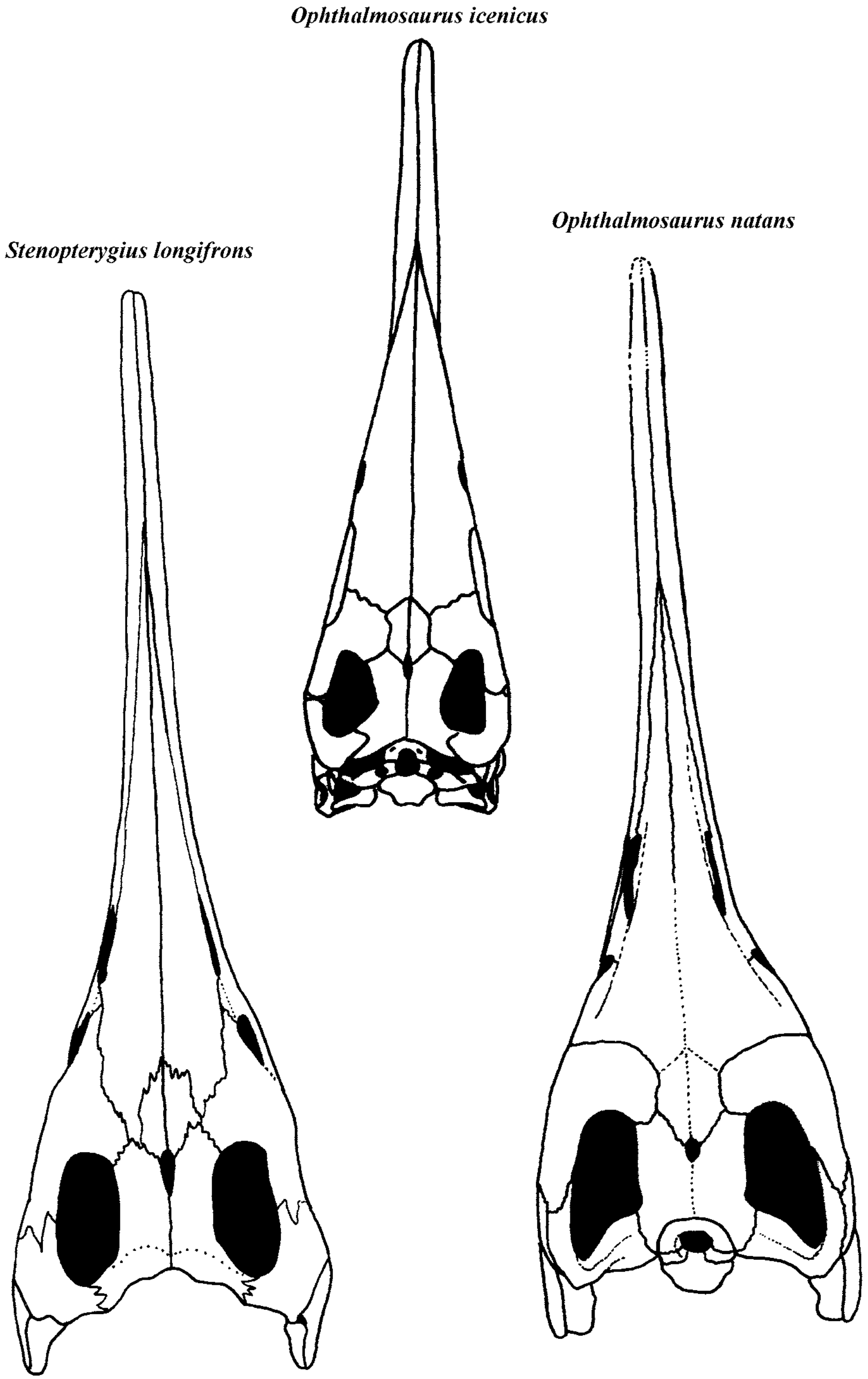
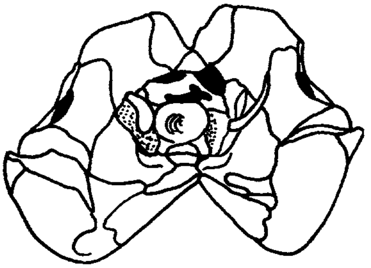
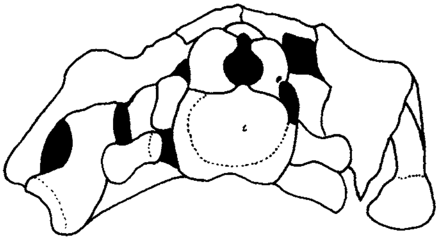


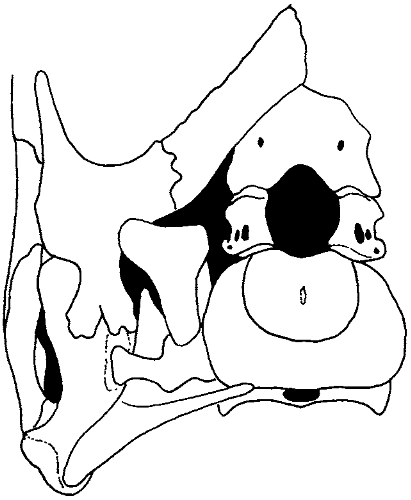
Fig. 12. Skull reconstructions of Lower to Upper Jurassic ichthyosaurs in dorsal view. *Stenopterygius longifrons* from Deslongchamps 1876, *Ophthalmosaurus icenicus* from Appleby 1956, *Ophthalmosaurus natans* modified from Gilmore 1905.



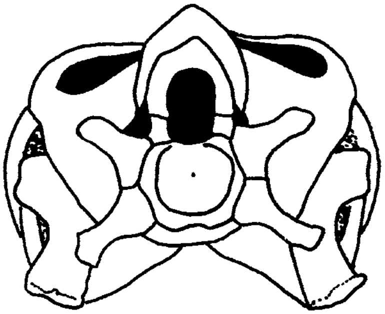
Cymbospondylus petrinus



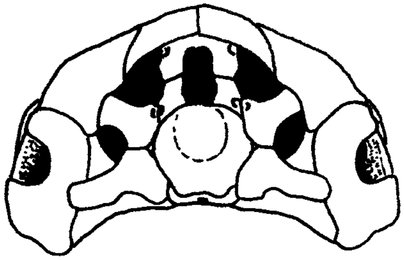
Temnodontosaurus trigonodon



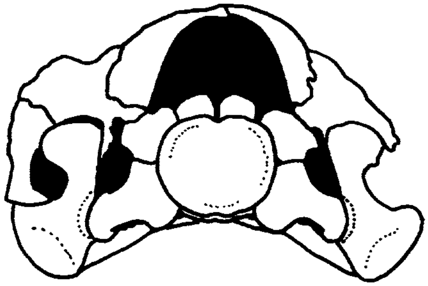
Ichthyosaurus communis



Ophthalmosaurus natans

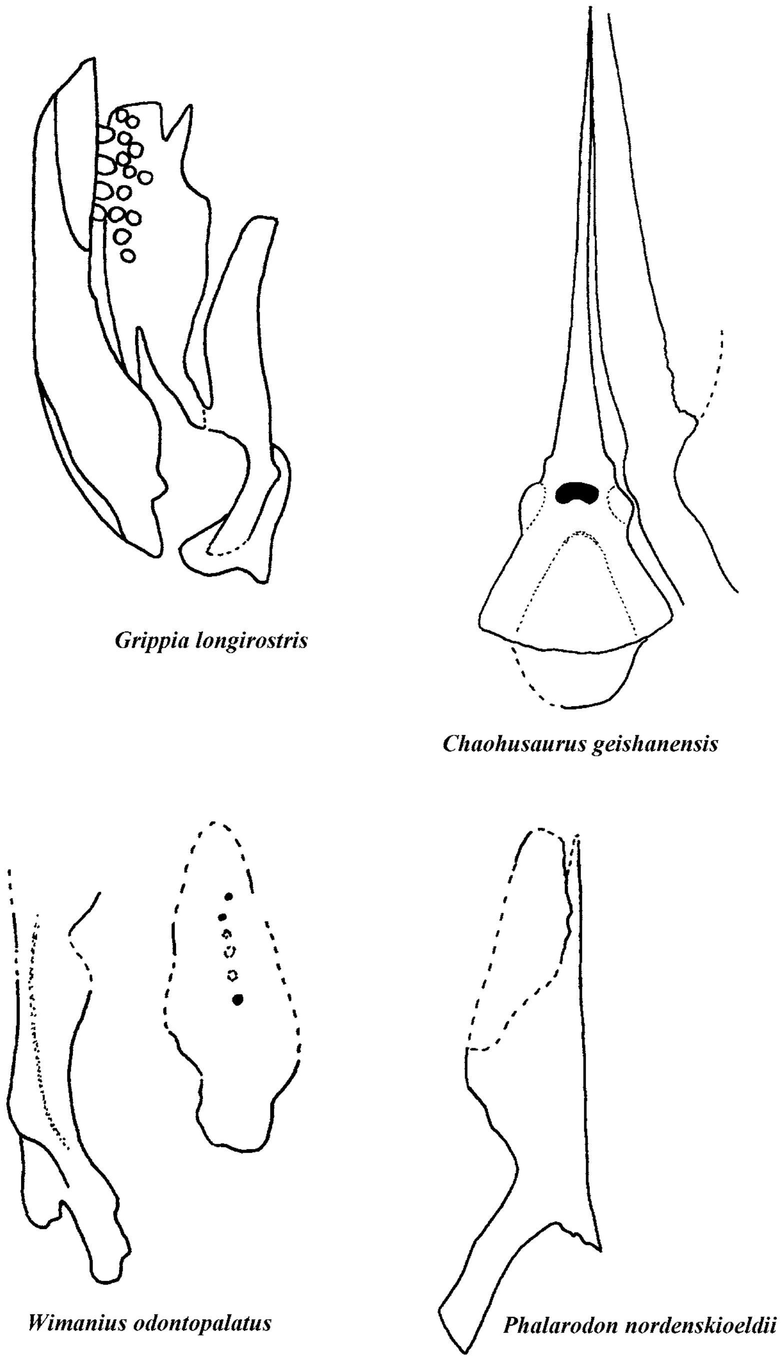


Ophthalmosaurus icenicus



Platypterygius longmani

Fig. 13. Reconstructions of ichthyosaur skulls in occipital view. *Cymbospondylus petrinus* from Merriam 1908, *Temnodontosaurus trigonodon* from Fraas 1913, *Ichthyosaurus communis* modified from McGowan 1973, *Ophthalmosaurus natans* from Gilmore 1905, *Ophthalmosaurus icenicus* from Appleby 1956, *Platypterygius longmani* from Wade 1990.



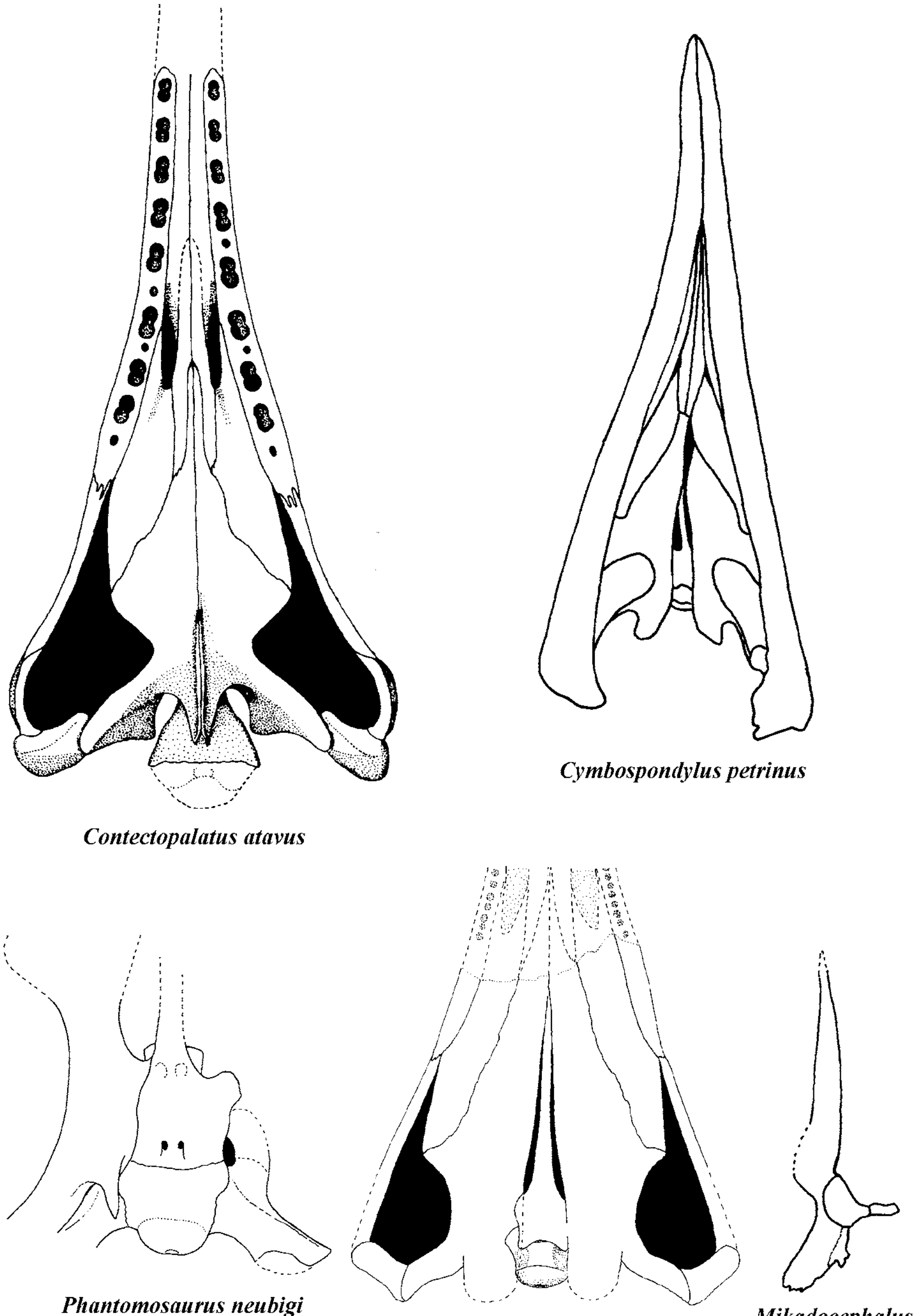
Grippia longirostris

Chaohusaurus geishanensis

Wimanius odontopalatus

Phalarodon nordenskioeldii

Fig. 14. Palates of Lower to Middle Triassic ichthyosaurs in ventral view. *Grippia longirostris* from WIMAN 1933, *Chaohusaurus geishanensis* from MAISCH in press b, *Wimanius odontopalatus* modified from MAISCH & MATZKE 1998a, *Phalarodon nordenskioeldii* modified from NICHOLLS et al. 1999.



Contectopalatus atavus

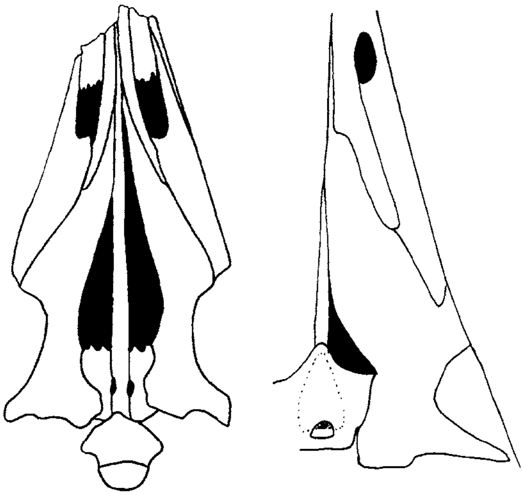
Cymbospondylus petrinus

Phantomosaurus neubigi

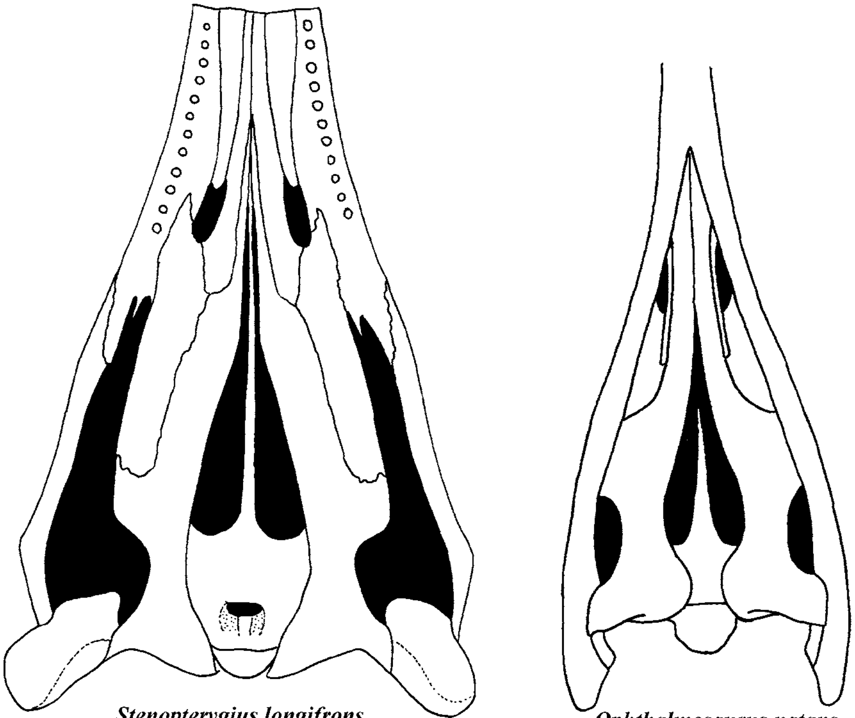
Shastasaurus alexandrae

Mikadocephalus gracilirostris

Fig. 15. Palates of Middle to Upper Triassic ichthyosaurs in ventral view. *Contectopalatus atavus* from MAISCH & MATZKE in press b, *Cymbospondylus petrinus* from MERRIAM 1908, *Phantomosaurus neubigi* pers. obs. (München), *Shastasaurus alexandrae* from MAISCH 2000, *Mikadocephalus gracilirostris* modified from MAISCH & MATZKE 1997a.



Temnodontosaurus trigonodon ***Eurhinosaurus longirostris*** ***Ichthyosaurus communis***



Stenopterygius longifrons ***Ophthalmosaurus natans***

Fig. 16. Palates of Jurassic ichthyosaurs in ventral view. *Temnodontosaurus trigonodon* from von HUENE 1931b, *Eurhinosaurus longirostris* pers. obs. (Stuttgart), *Ichthyosaurus communis* from MCGOWAN 1973, *Stenopterygius longifrons* from OWEN 1881, *Ophthalmosaurus natans* from GILMORE 1905.

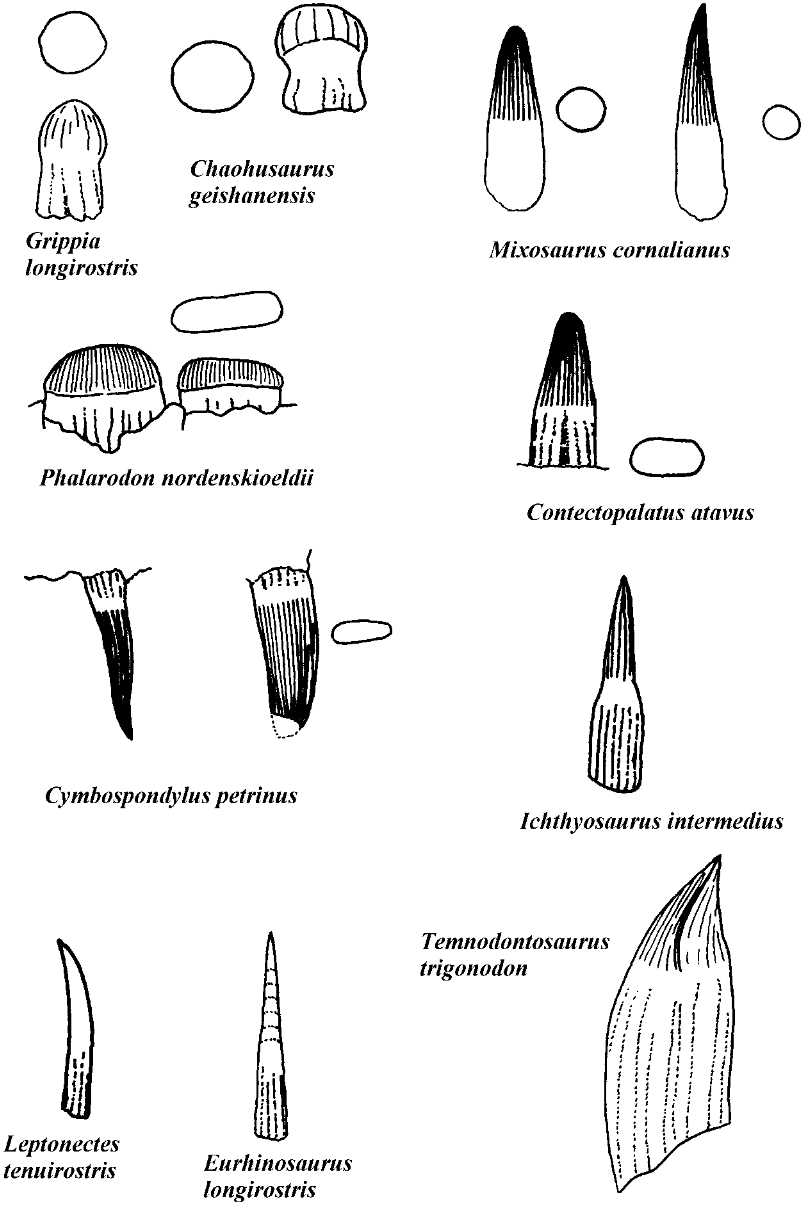


Fig. 17. Ichthyosaur teeth. *Grippia longirostris*, posterior dentary tooth, modified from Mazin 1981b, *Chaohusaurus geishanensis* posterior dentary tooth, from Maisch in press b, *Mixosaurus cornalianus* anterior and posterior dentary teeth, pers. obs. (Tübingen), *Phalarodon nordenskioeldii* posterior dentary teeth, pers. obs. (Berkeley), *Contectopalatus atavus* posterior dentary tooth, pers. obs. (Tübingen), *Cymbospondylus petrinus* anterior premaxillary tooth in labial and anterior view, pers. obs. (Berkeley), *Ichthyosaurus intermedius* posterior dentary tooth, from Owen 1881, *Leptonectes tenuirostris* dentary tooth, from Owen 1881, *Eurhinosaurus longirostris* dentary tooth, pers. obs. (Stuttgart), *Temnodontosaurus trigonodon*, dentary tooth, from von Theodori 1854.

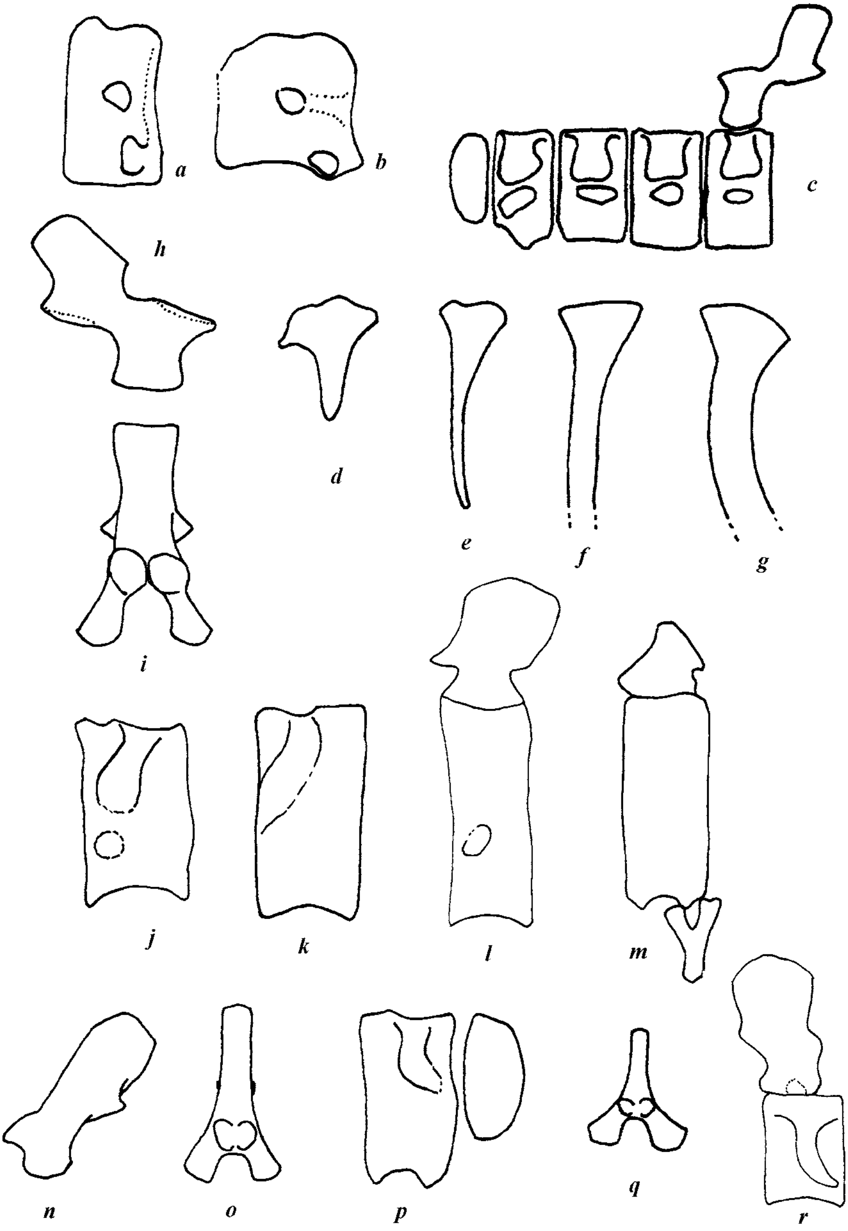


Fig. 18. Triassic ichthyosaur vertebrae and ribs, a: *Toretocnemus californicus*, posterior thoracal centrum, modified from Merriam 1908, b: *Toretocnemus zitteli*, posterior thoracal centrum, pers. obs. (Berkeley), c: *Cymbospondylus petrinus*, atlas-axis and anterior cervicals, from Merriam 1908, d–g: *Cymbospondylus petrinus*, anterior and posterior cervical, anterior and middle thoracal ribs, from Merriam 1908, h–i: *Cymbospondylus petrinus*, anterior cervical neural arch, from Merriam 1908, j–m: *Cymbospondylus petrinus*, anterior cervical, anterior thoracal, anterior and posterior caudal vertebrae, from Merriam 1908, n–p: *Shastasaurus alexandrae* anterior thoracal neural arch, atlas-axis complex, from Merriam 1908, q–r: *Californosaurus perrini* thoracal neural arch, posterior thoracal vertebra, from Merriam 1908.

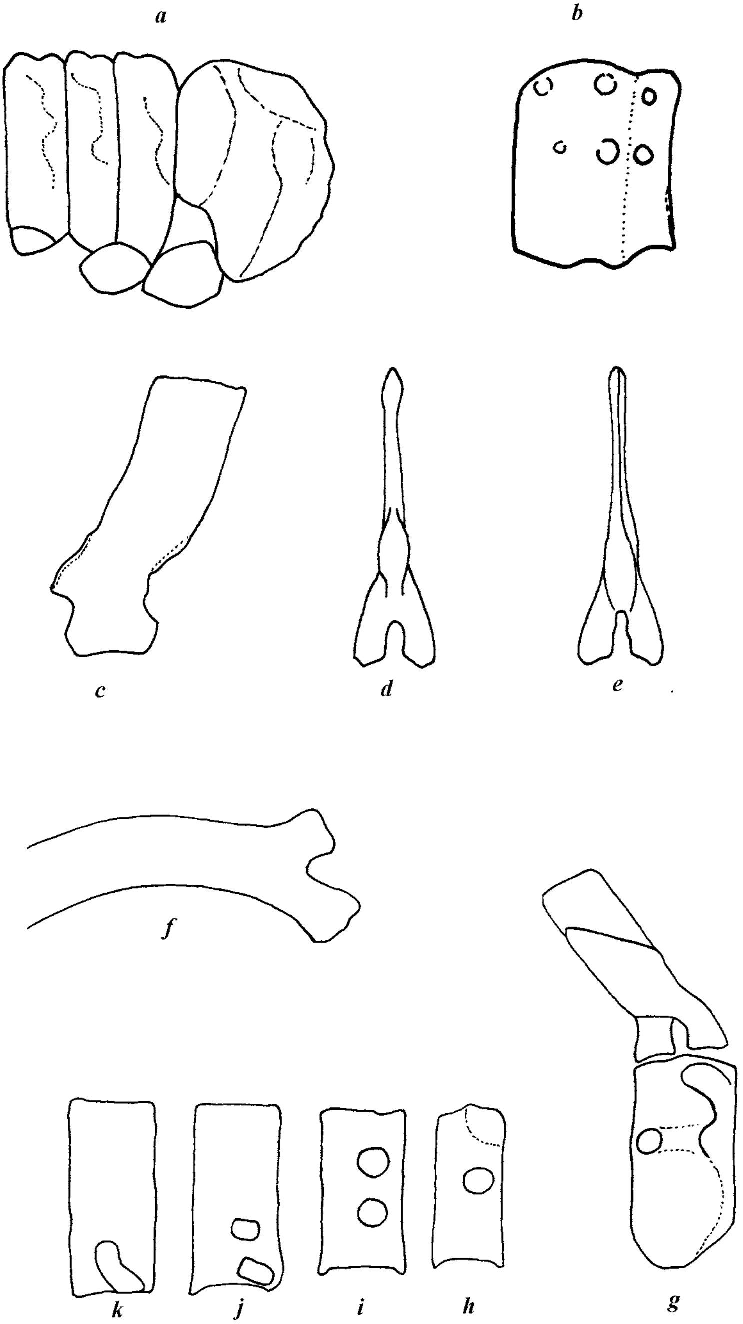


Fig. 19. Jurassic-Cretaceous vertebrae and ribs, a: *Temnodontosaurus platyodon*, juvenile, anteriormost cervicals, from Hawkins 1840, b: *Platypterygius platydactylus*, atlas-axis complex, Broili 1907, c–f: *Ophthalmosaurus icenicus*, thoracal neural arch, thoracal rib head, from Andrews 1910, g–k: *Ophthalmosaurus natans*, atlas-axis, cervical, anterior and posterior thoracal, anterior caudal centra, from Gilmore 1905.

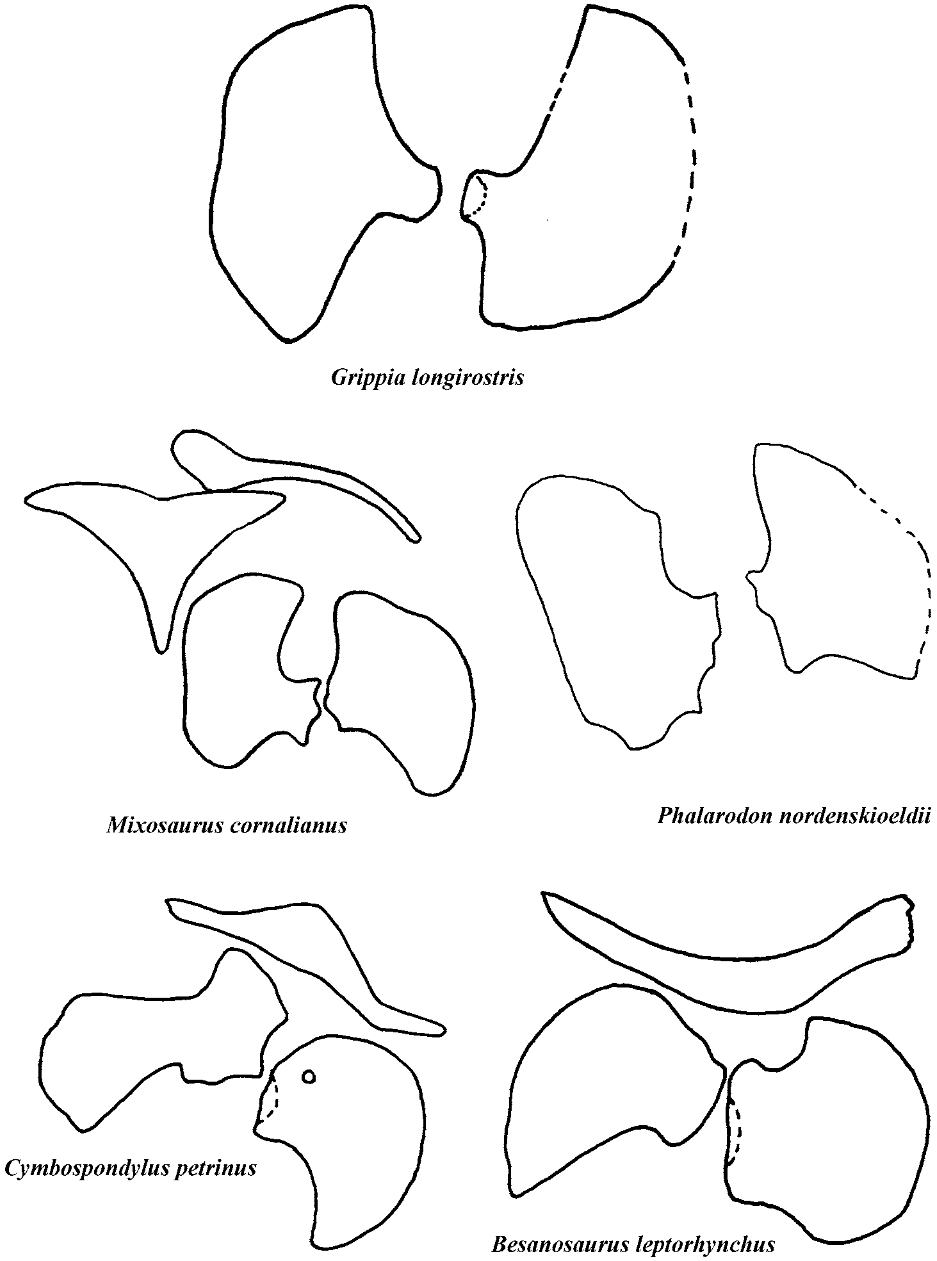
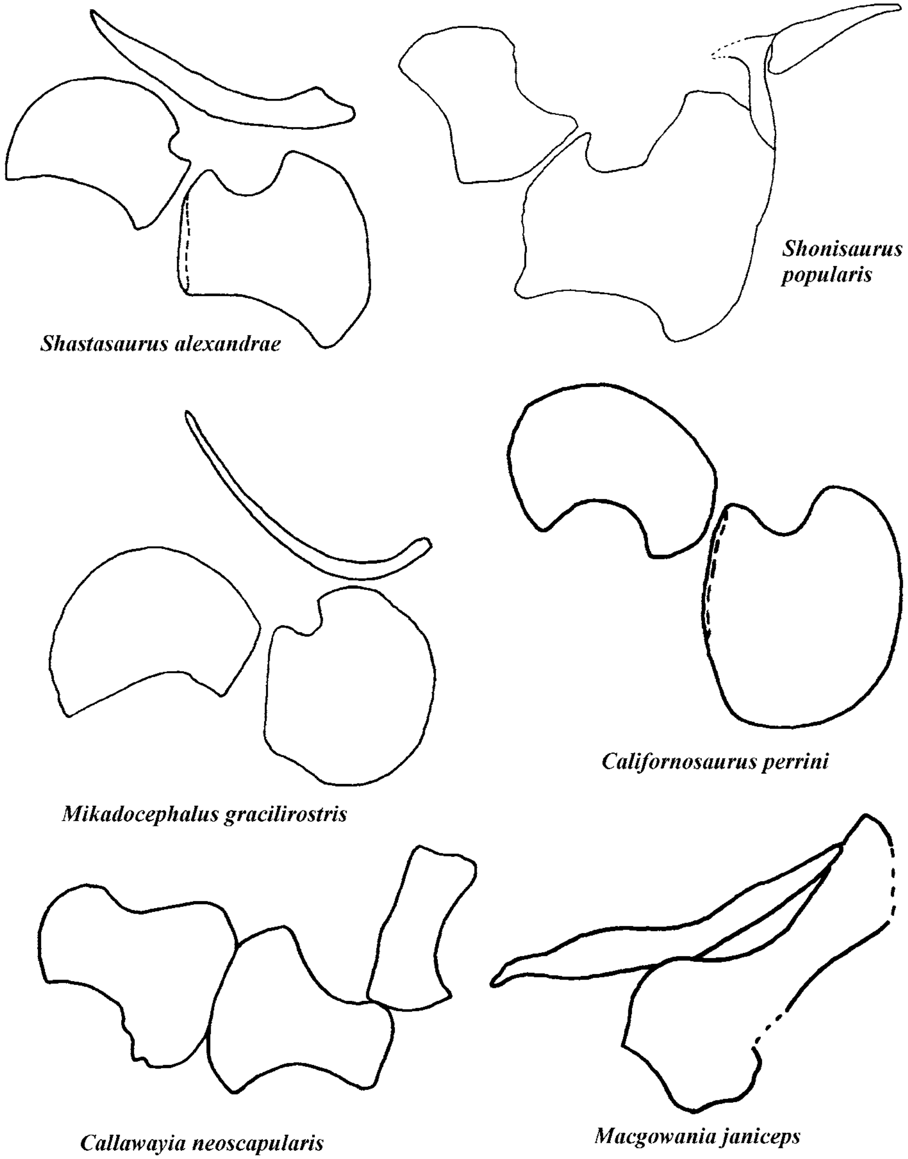


Fig. 20. Lower to Middle Triassic ichthyosaur shoulder girdles. *Grippia longirostris* modified from Wiman 1933, *Mixosaurus cornalianus* pers. obs. (Tübingen, Stuttgart, Zürich), *Phalarodon nordenskioeldii* modified from Nicholls et al. 1999, *Cymbospondylus petrinus* from Merriam 1908, *Besanosaurus leptorhynchus* from Dal Sasso & Pinna 1996.



Shastasaurus alexandrae

Shonisaurus popularis

Mikadocephalus gracilirostris

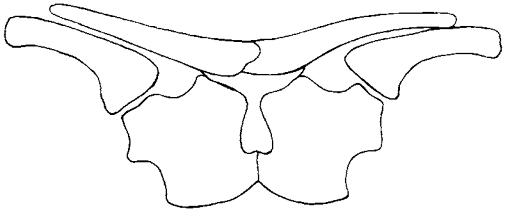
Californosaurus perrini

Callawayia neoscapularis

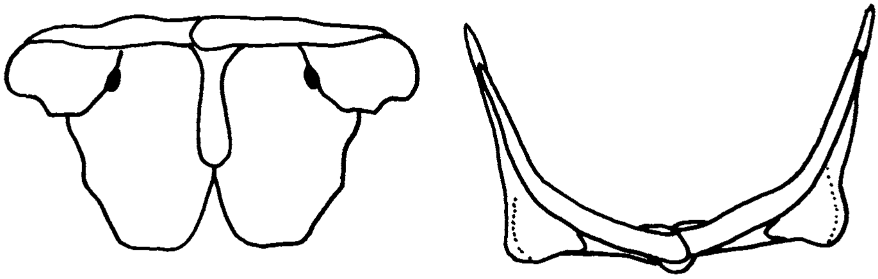
Macgowania janiceps

Fig. 21. Middle to Upper Triassic ichthyosaur shoulder girdles. *Shastasaurus alexandrae* from MERRIAM 1908, *Shonisaurus popularis* from CAMP 1980 and McGOWAN & MOTANI 1999, *Mikadocephalus gracilirostris* pers. obs. (Zürich), *Californosaurus perrini* from MERRIAM 1908, *Callawayia neoscapularis* from McGOWAN 1994a, *Macgowania janiceps* from McGOWAN 1996a.

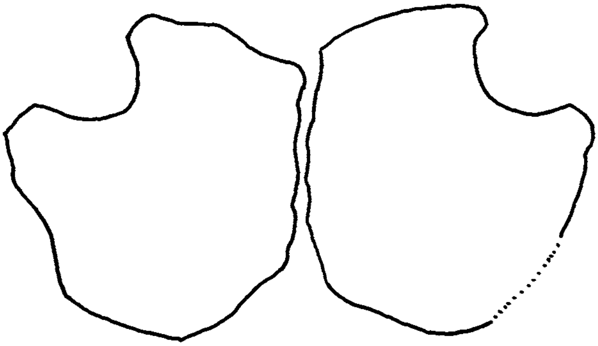
Temnodontosaurus platyodon ***Eurhinosaurus longirostris***



Ichthyosaurus communis

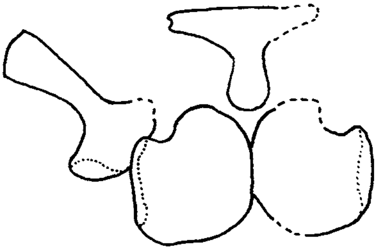


Stenopterygius quadriscissus

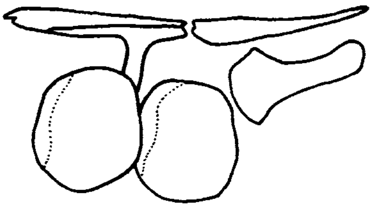


Aegirosaurus sp.

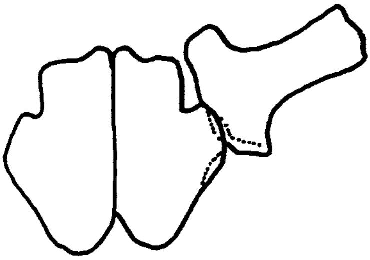
Fig. 22. Lower to Upper Jurassic ichthyosaur shoulder girdles. *Temnodontosaurus platyodon* from von HUENE 1922, *Eurhinosaurus longirostris*, modified from von HUENE 1928, *Ichthyosaurus communis* from MCGOWAN 1974b, *Stenopterygius quadriscissus* in ventral and anterior views, from JOHNSON 1979, *Aegirosaurus* sp. from GASPARINI 1988.



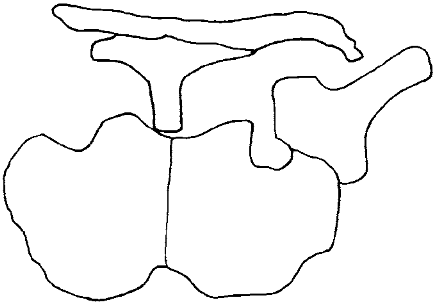
Brachypterygius pseudoscythius



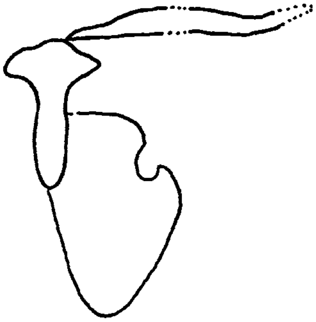
Platypterygius bedengensis



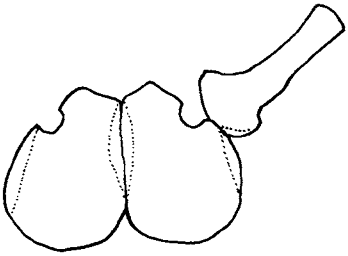
Ophthalmosaurus yasykovi



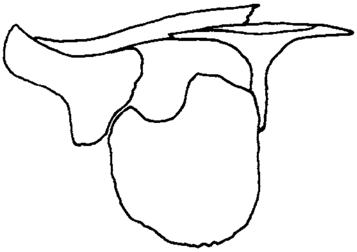
Ophthalmosaurus natans



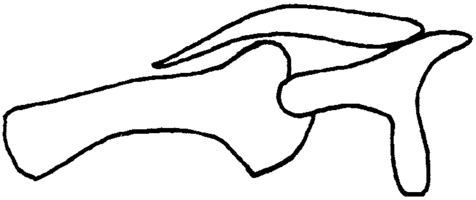
Ophthalmosaurus saveljeviensis



Ophthalmosaurus gorodischensis

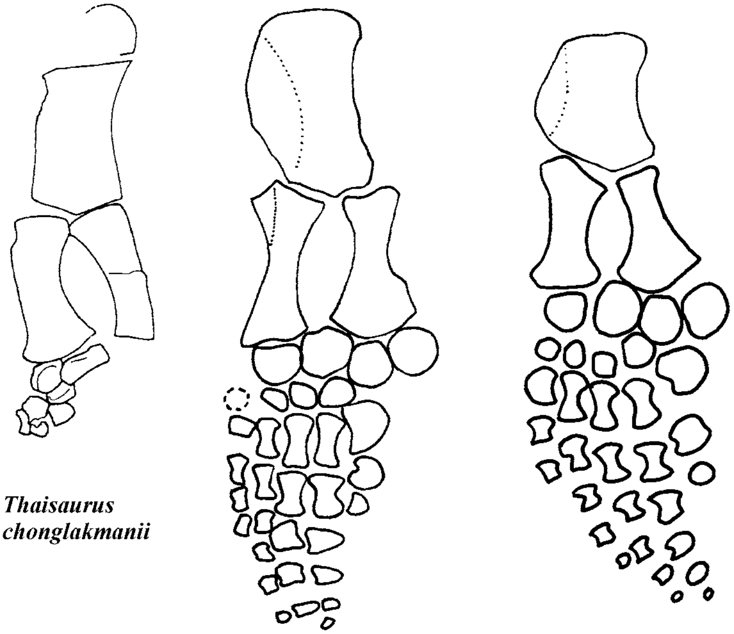


Ophthalmosaurus icenicus



Caypullisaurus bonapartei

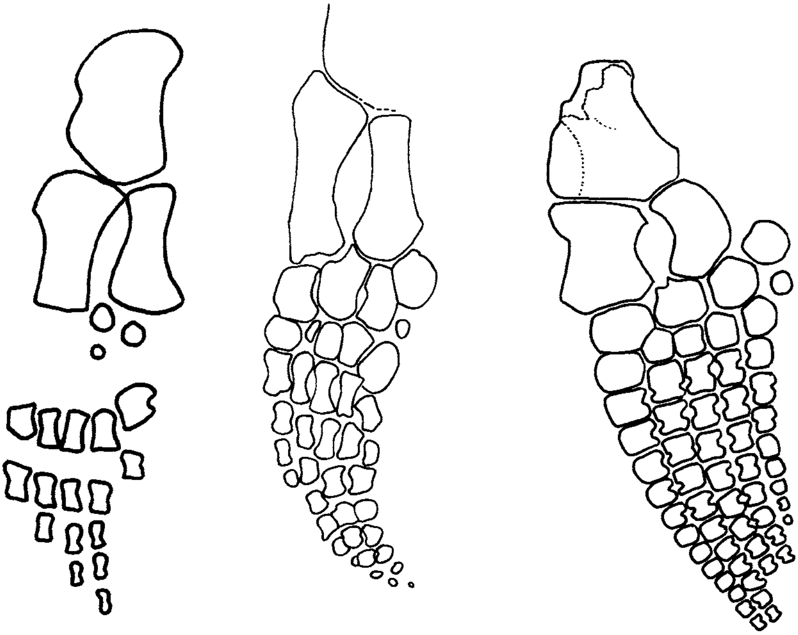
Fig. 23. Middle Jurassic to Cretaceous ichthyosaur shoulder girdles. *Brachypterygius pseudoscythius* from EFIMOV 1998, *Platypterygius bedengensis* from EFIMOV 1997, *Ophthalmosaurus yasykovi* from EFIMOV 1999b, *Ophthalmosaurus natans* from GILMORE 1905, *Ophthalmosaurus saveljeviensis* from ARKHANGELSKY 1997, *Ophthalmosaurus gorodischensis* from EFIMOV 1999a, *Ophthalmosaurus icenicus* from ANDREWS 1910, *Caypullisaurus bonapartei* from FERNÁNDEZ 1997.



Thaisaurus chonglakmanii

Utatsusaurus hataii

Grippia longirostris



Chaohusaurus geishanensis

Parvinatator wapitiensis

Mixosaurus cornalianus

Fig. 24. Lower to Middle Triassic ichthyosaur forefins. *Thaisaurus chonglakmanii* from Mazin et al. 1991, *Utatsusaurus hataii* from Motani 1997a, *Grippia longirostris* from Motani 1998b, *Chaohusaurus geishanensis* from Maisch in press b, *Parvinatator wapitiensis* from Nicholls & Brinkman 1996, *Mixosaurus cornalianus* pers. obs. (Tübingen).

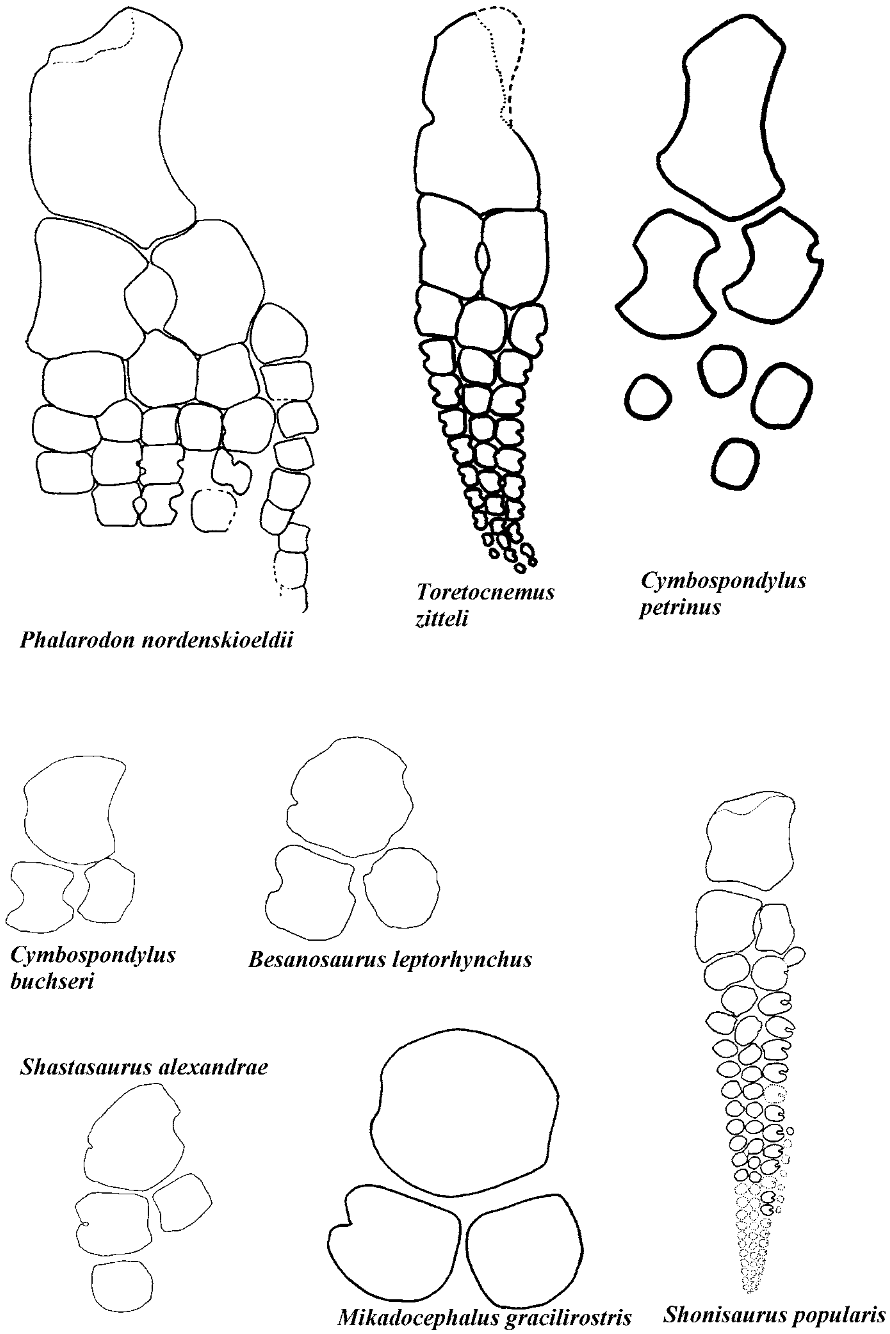
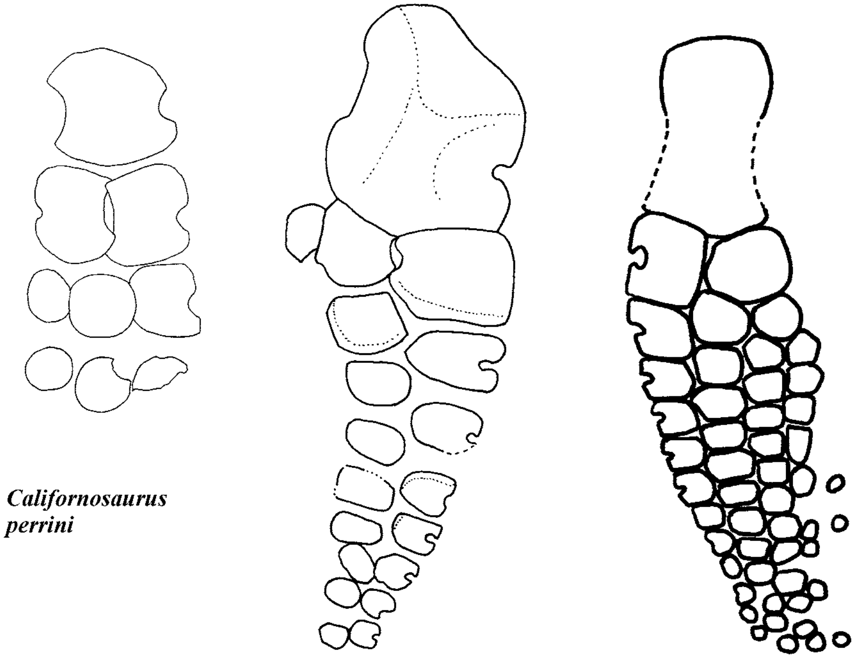


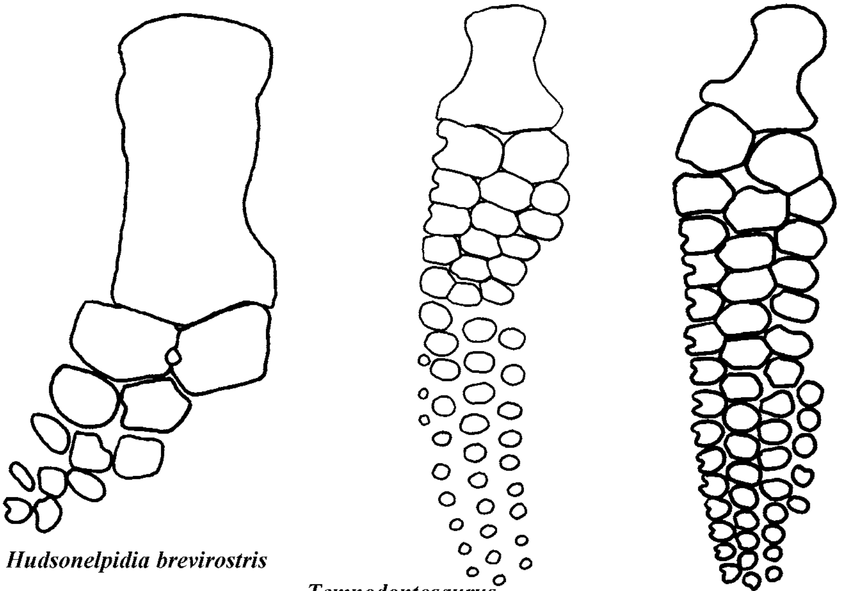
Fig. 25. Middle to Upper Triassic ichthyosaur forefins. *Phalarodon nordenskioeldii* from Wiman 1910, *Toretocnemus zitteli* from Merriam 1908, *Cymbospondylus petrinus* from Merriam 1908, *Cymbospondylus buchseri* from Sander 1989, *Besanosaurus leptorhynchus* from Dal Sasso & Pinna 1996, *Shastasaurus alexandrae* from Merriam 1908, *Mikadocephalus gracilirostris* pers. obs. (Zürich), *Shonisaurus popularis* from Camp 1980.



Californosaurus perrini

Callawayia neoscapularis

Macgowania janiceps



Hudsonelpidia brevirostris

Temnodontosaurus platyodon

Temnodontosaurus trigonodon

Fig. 26. Upper Triassic to Lower Jurassic ichthyosaur forefins. *Californosaurus perrini* from Merriam 1908, *Callawayia neoscapularis* pers. obs. (Toronto), *Macgowania janiceps* from McGowan 1991, *Hudsonelpidia brevirostris* from McGowan 1995, *Temnodontosaurus platyodon* from Hawkins 1840, *Temnodontosaurus trigonodon* from McGowan 1996c.

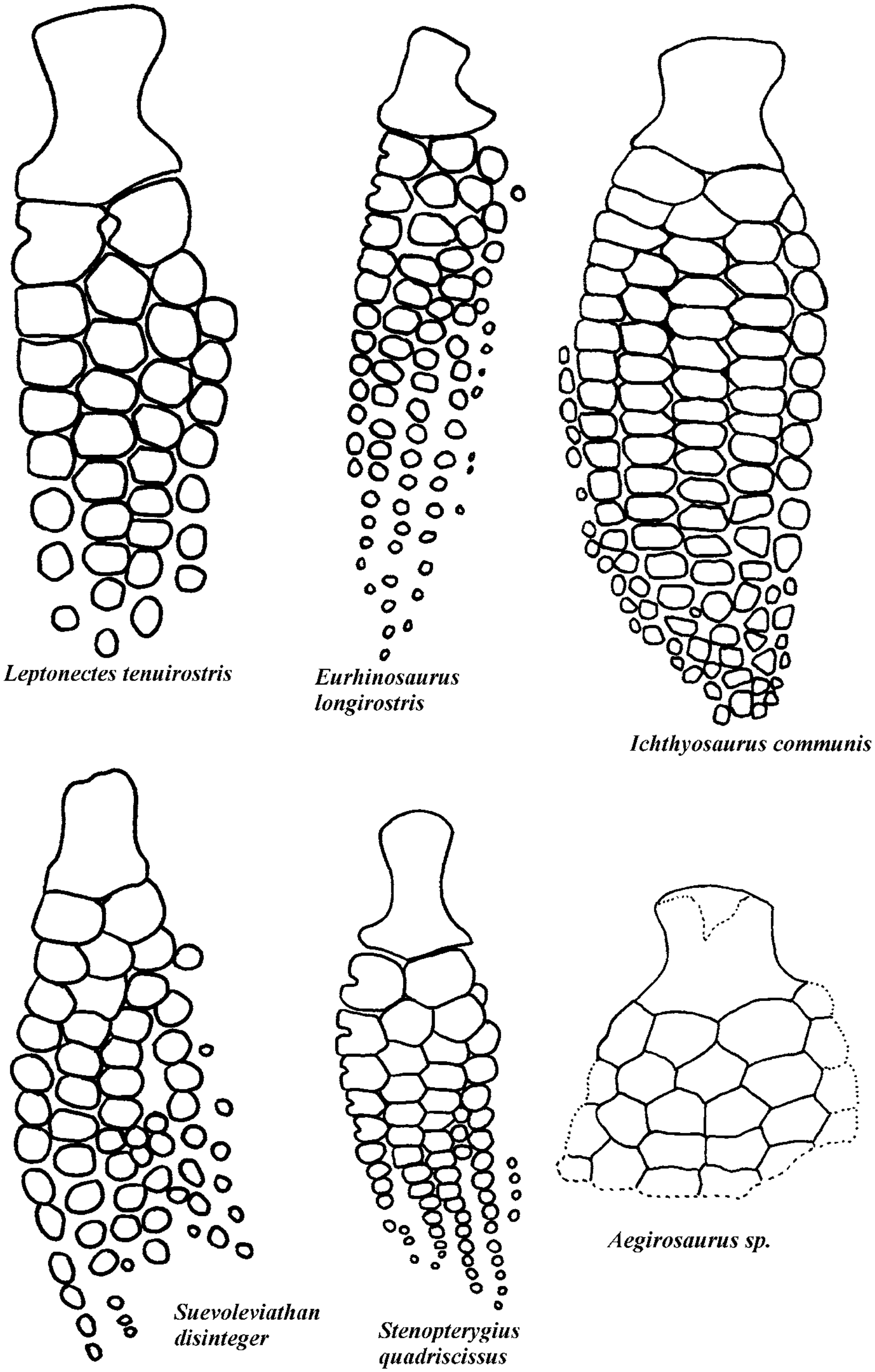
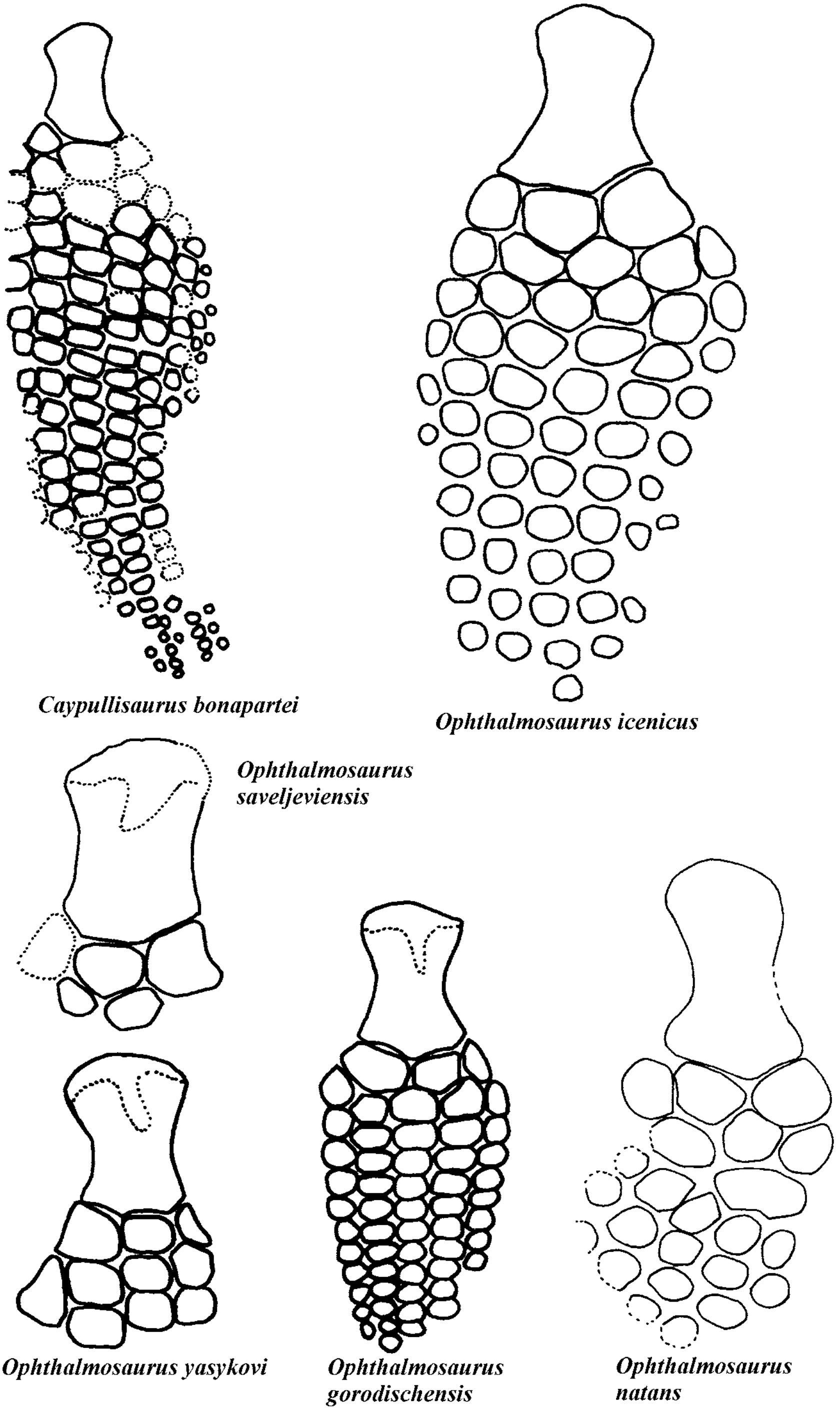


Fig. 27. Lower to Upper Jurassic ichthyosaur forefins. *Leptonectes tenuirostris* from Owen 1881, *Eurhinosaurus longirostris* from von Huene 1928, *Ichthyosaurus communis* from von Huene 1922, *Suevoleviathan disinteger* from Maisch 1998b, *Stenopterygius quadriscissus* from von Huene 1922, *Aegirosaurus* sp. from Gasparini 1988.



Caypullisaurus bonapartei

Ophthalmosaurus icenicus

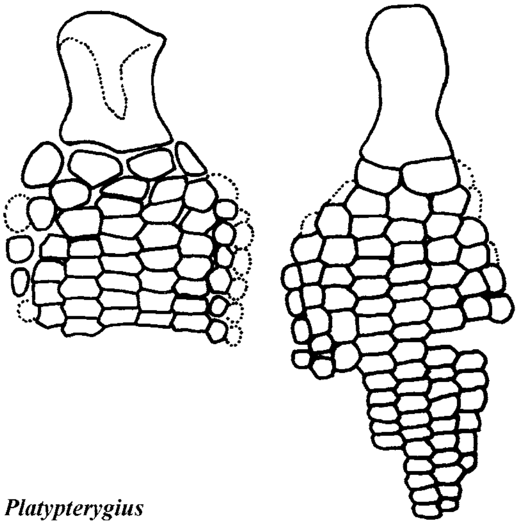
Ophthalmosaurus saveljeviensis

Ophthalmosaurus yasykovi

Ophthalmosaurus gorodischensis

Ophthalmosaurus natans

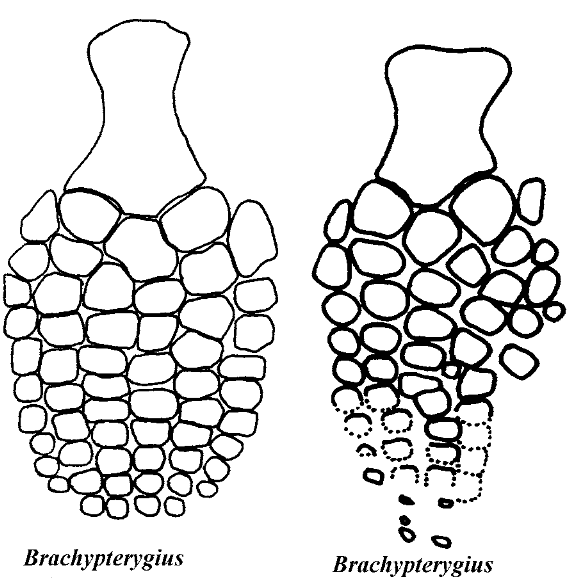
Fig. 28. Middle to Upper Jurassic ichthyosaur forefins. *Caypullisaurus bonapartei* from Fernández 1997, *Ophthalmosaurus icenicus* from Kirton in McGowan 1997b, *Ophthalmosaurus saveljeviensis* from Arkhangelsky 1998a, *Ophthalmosaurus yasykovi* from Efimov 1999b, *Ophthalmosaurus gorodischensis* from Efimov 1999a, *Ophthalmosaurus natans* from Gilmore 1905.



Platypterygius hercynicus

Platypterygius platydactylus

Platypterygius bedengensis



Brachypterygius extremus

Brachypterygius mordax

Brachypterygius pseudoscythius

Fig. 29. Upper Jurassic to Cretaceous ichthyosaur forefins. *Platypterygius hercynicus* from KUHN 1946, *Platypterygius platydactylus* from BROILI 1907, *Platypterygius bedengensis* from EFIMOV 1997, *Brachypterygius extremus* from VON HUENE 1922, *Brachypterygius mordax* from MCGOWAN 1997b, *Brachypterygius pseudoscythius* from EFIMOV 1998.

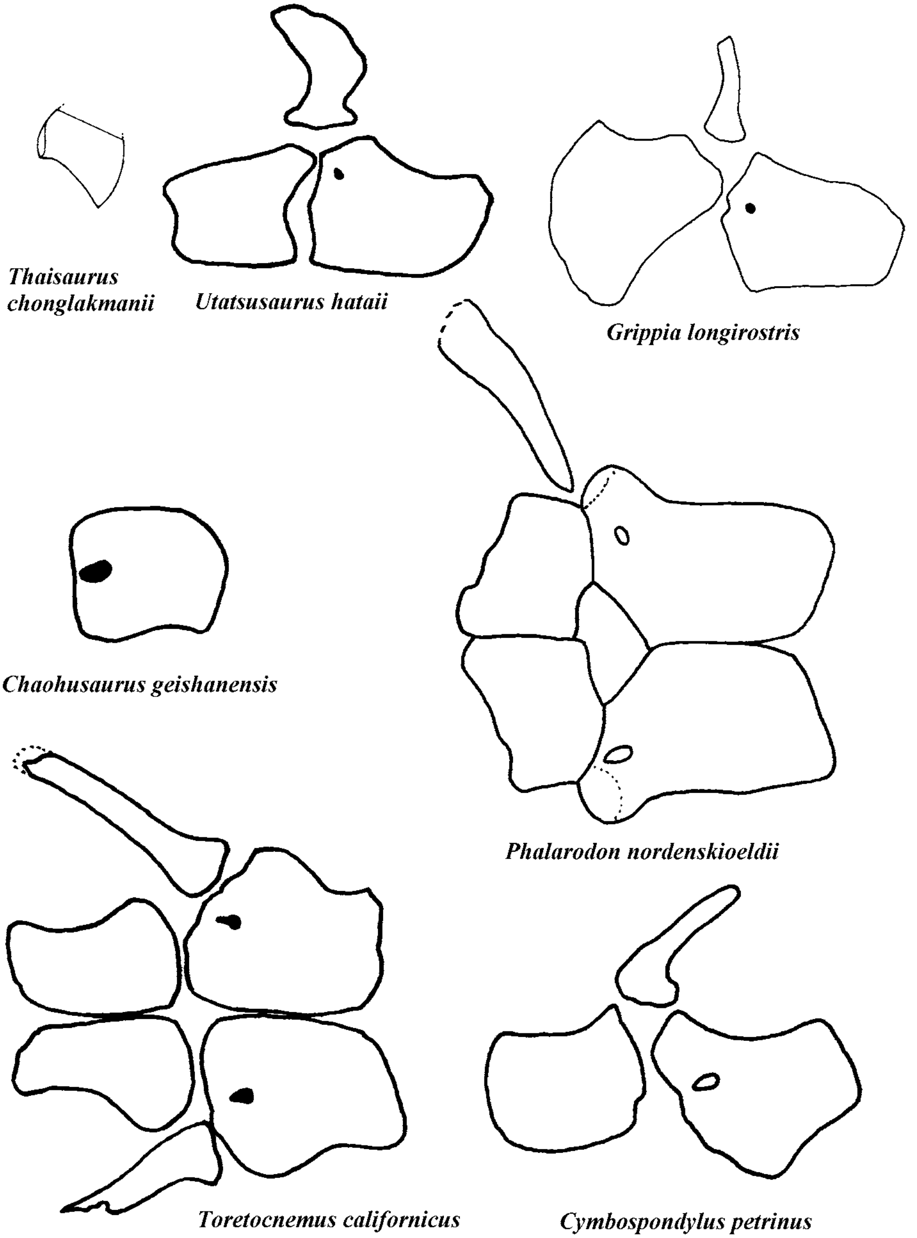


Fig. 30. Lower to Middle Triassic ichthyosaur pelvic girdles. *Thaisaurus chonglakmanii*, ischium, from Mazin et al. 1991, *Utatsusaurus hataii* from Motani et al. 1998, *Grippia longirostris* modified from Wiman 1933, *Chaohusaurus geishanensis*, pubis, from Maisch in press b, *Phalarodon nordenskioeldii* from Wiman 1910, *Toretocnemus californicus* from Merriam 1908, *Cymbospondylus petrinus* from Merriam 1908.

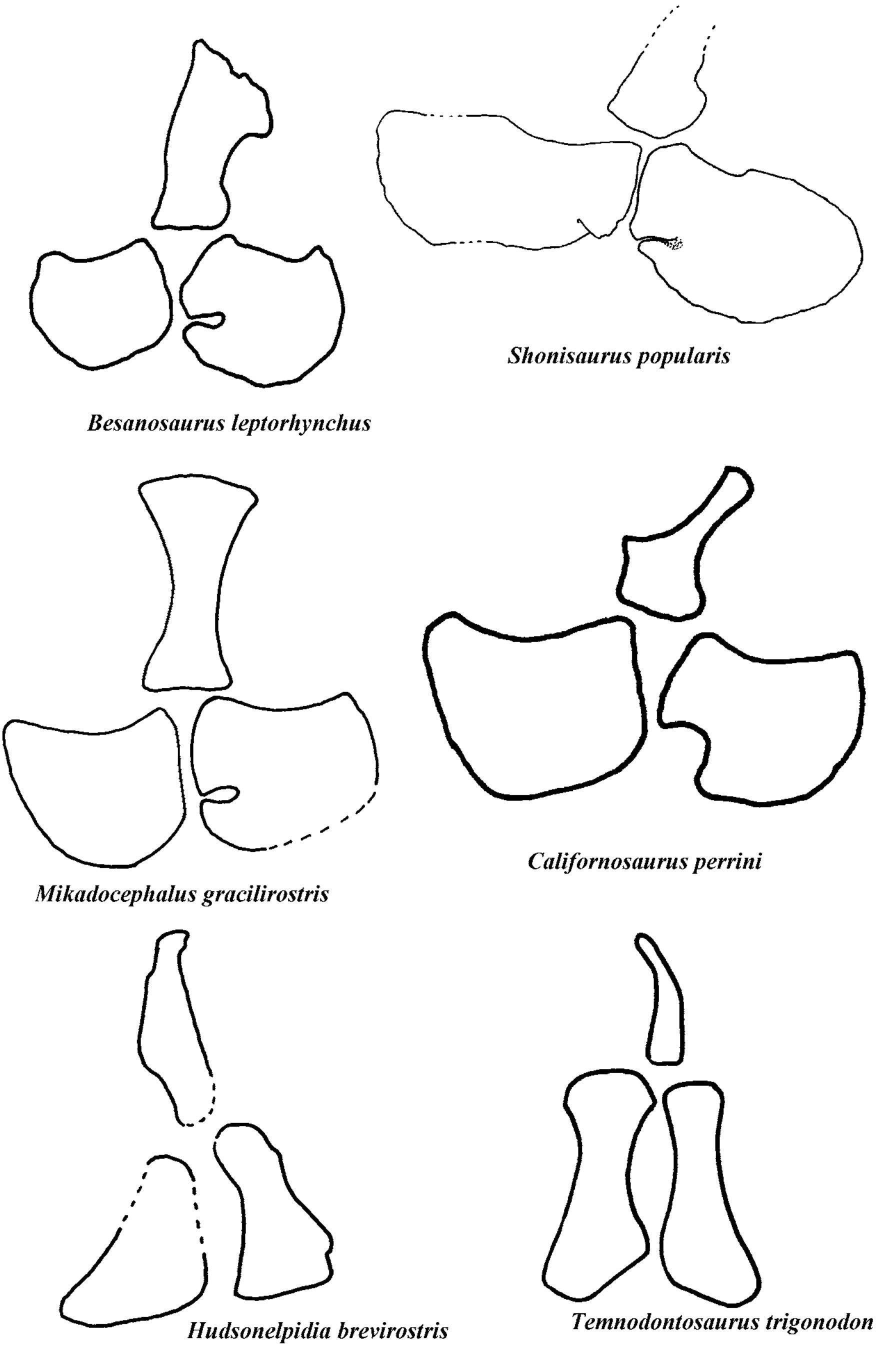


Fig. 31. Middle Triassic to Lower Jurassic ichthyosaur pelvic girdles. *Besanosaurus leptorhynchus* from Dal Sasso & Pinna 1996, *Shonisaurus popularis* modified from Camp 1980, *Mikadocephalus gracilirostris*, pers. obs. (Zürich), *Californosaurus perrini* from Merriam 1908, *Hudsonelpidia brevirostris* modified from McGowan 1995, *Temnodontosaurus trigonodon* from von Huene 1922.

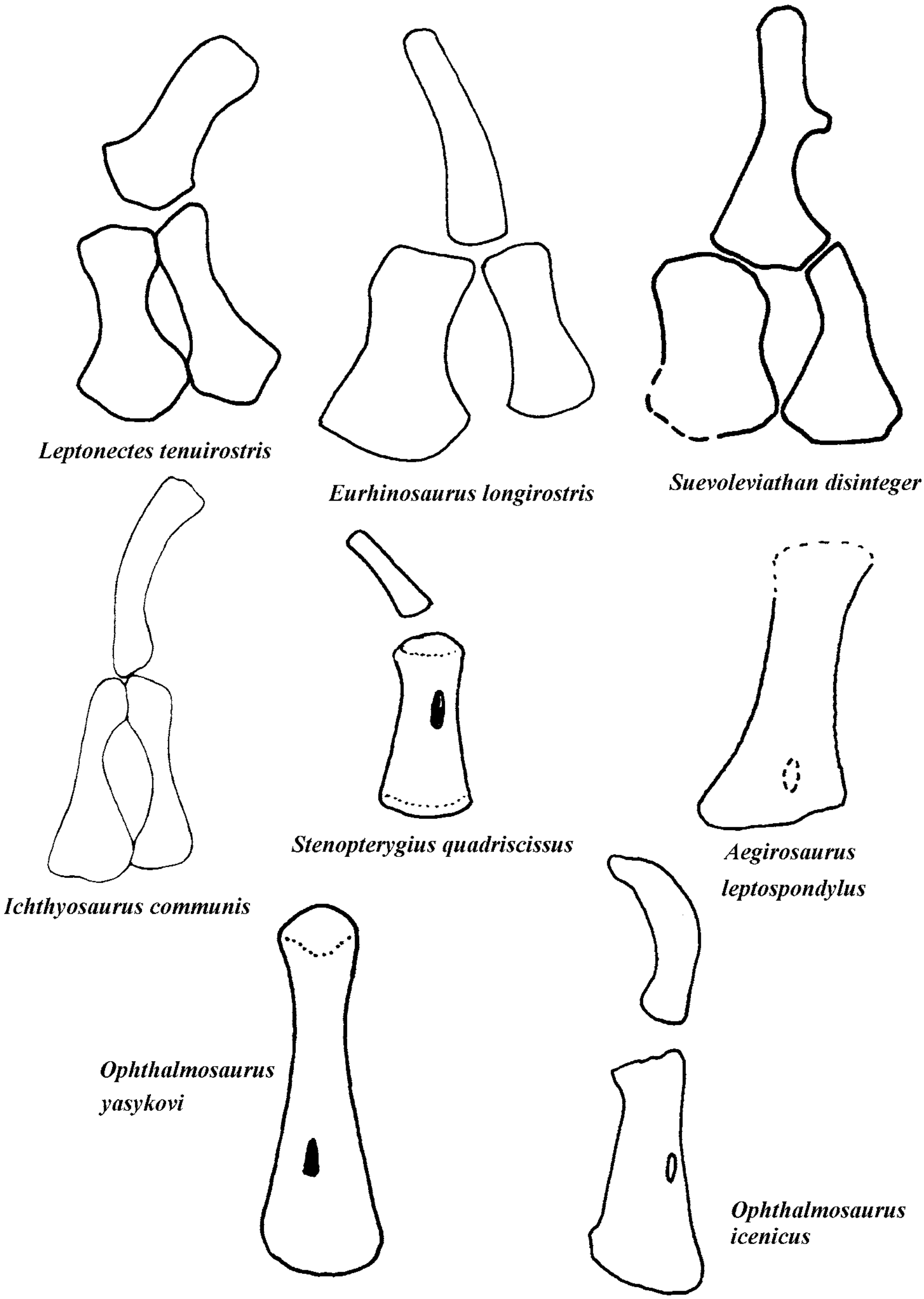
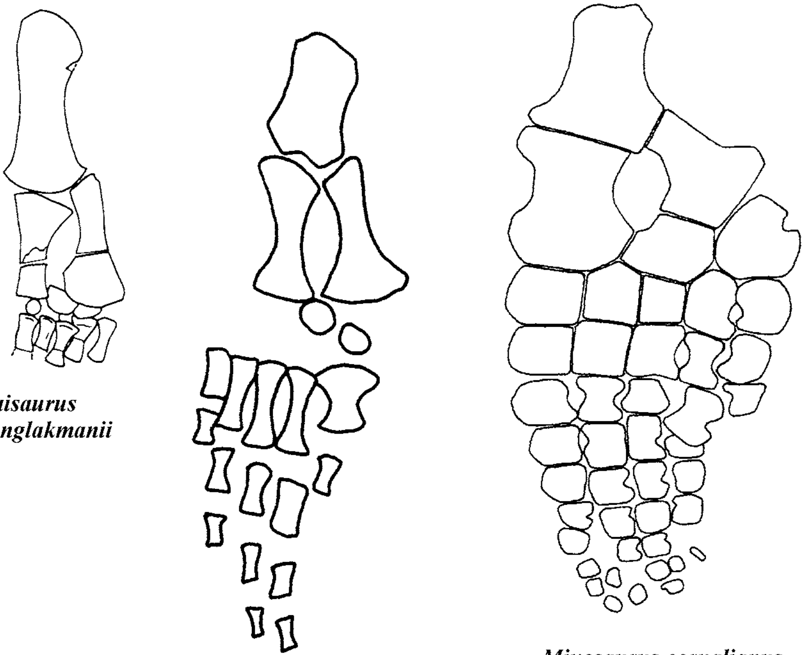


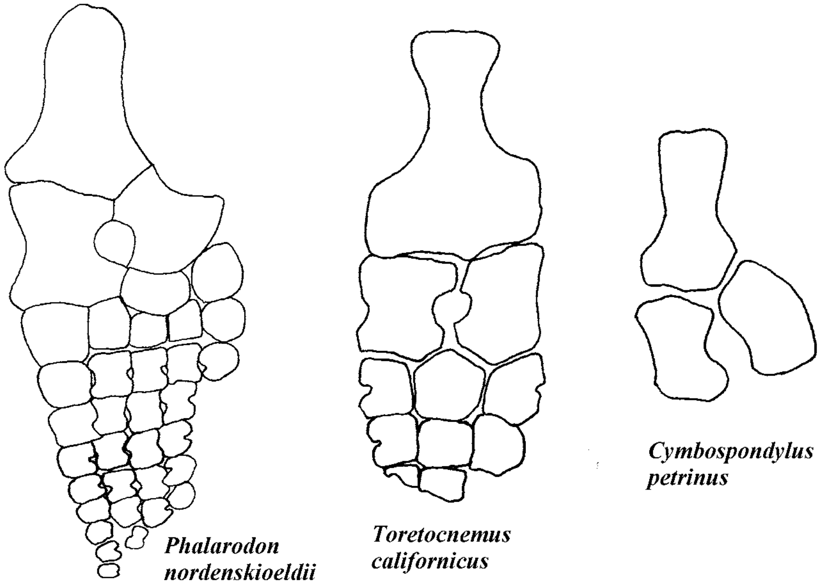
Fig. 32. Lower to Upper Jurassic ichthyosaur pelvic girdles. *Leptonectes tenuirostris* from Owen 1881, *Eurhinosaurus longirostris* pers. obs. (Tübingen), *Suevoleviathan disinteger* from Maisch 1998b, *Ichthyosaurus communis* from McGowan 1974b, *Stenopterygius quadriscissus* pers. obs. (Tübingen), *Aegirosaurus leptospondylus* pers. obs. (München), *Ophthalmosaurus yasykovi* from Efimov 1999b, *Ophthalmosaurus icenicus* from Andrews 1910.



Thaisaurus chonglakmanii

Chaohusaurus geishanensis

Mixosaurus cornalianus

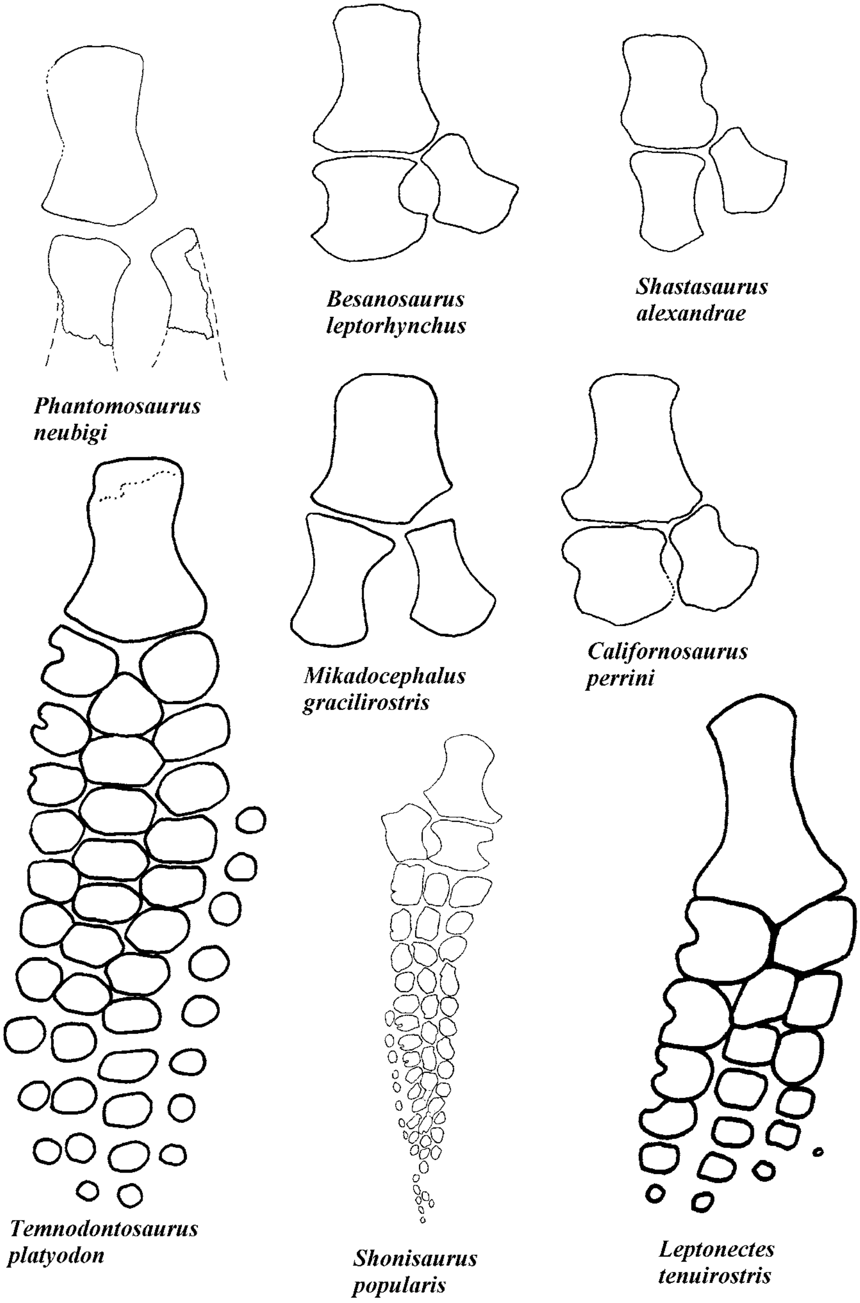


Phalarodon nordenskioeldii

Toretocnemus californicus

Cymbospondylus petrinus

Fig. 33. Lower to Middle Triassic ichthyosaur hindfins. *Thaisaurus chonglakmanii* from MAZIN et al. 1991, *Chaohusaurus geishanensis* from MAISCH in press b, *Mixosaurus cornalianus* from MCGOWAN 1995, *Phalarodon nordenskioeldii* from WIMAN 1910, *Toretocnemus californicus* from MERRIAM 1908, *Cymbospondylus petrinus* from MERRIAM 1908.



Phantomosaurus neubigi

Besanosaurus leptorhynchus

Shastasaurus alexandrae

Mikadocephalus gracilirostris

Californosaurus perrini

Temnodontosaurus platyodon

Shonisaurus popularis

Leptonectes tenuirostris

Fig. 34. Middle Triassic to Lower Jurassic ichthyosaur hindfins. *Phantomosaurus neubigi* pers. obs. (München), *Besanosaurus leptorhynchus* from DAL SASSO & PINNA 1996, *Shastasaurus alexandrae* from MERRIAM 1908, *Mikadocephalus gracilirostris* pers. obs. (Zürich), *Californosaurus perrini* from MERRIAM 1908, *Temnodontosaurus platyodon* from HAWKINS 1840, *Shonisaurus popularis* from CAMP 1980, *Leptonectes tenuirostris* from OWEN 1881.

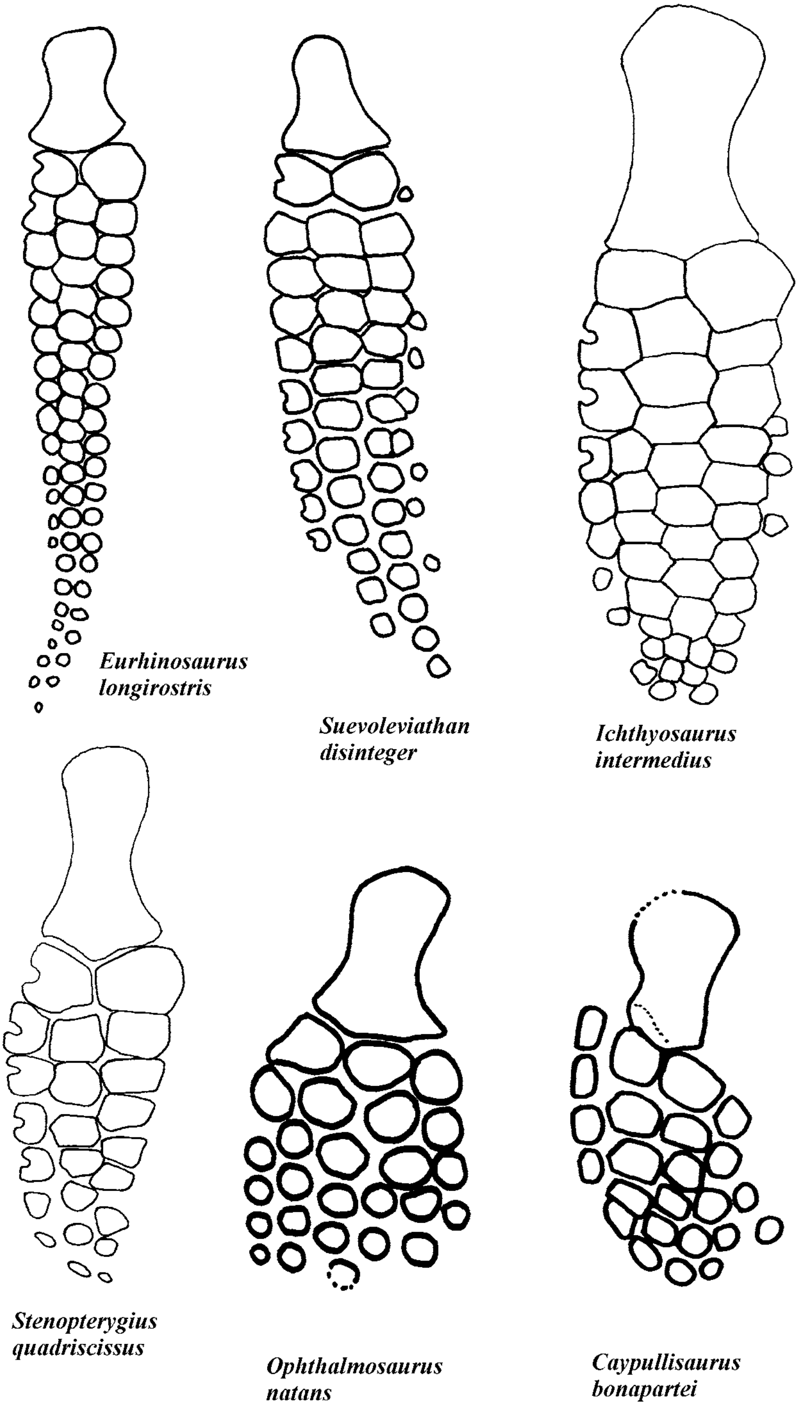


Fig. 35. Lower to Upper Jurassic ichthyosaur hindfins. *Eurhinosaurus longirostris* from VON HUENE 1922, *Suevoleviathan disinteger* from MAISCH 1998b, *Ichthyosaurus intermedius* from VON HUENE 1922, *Stenopterygius quadriscissus* from VON HUENE 1922, *Ophthalmosaurus natans* from GILMORE 1905, *Caypullisaurus bonapartei* from FERNÁNDEZ 1997.

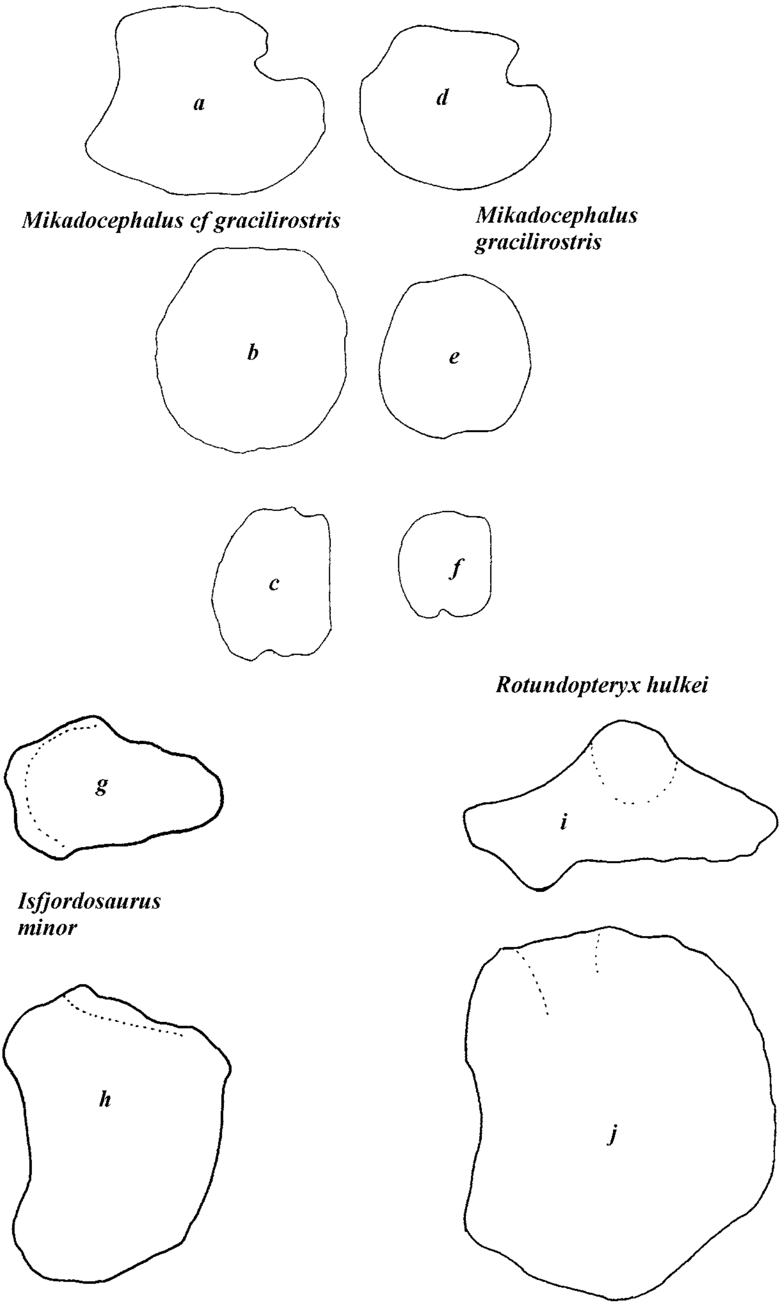


Fig. 36. Comparison of *Mikadocephalus* cf. *gracilirostris* from Spitsbergen (a–c, after WIMAN 1910) and *Mikadocephalus gracilirostris* from Monte San Giorgio (d–f, pers. obs. of Zurich specimen). Coracoid, humerus and radius, brought to the same scale. Humeri of *Isfjordosaurus minor* (g–h, after WIMAN, 1910) and *Rotundopteryx hulkei* gen. nov. sp nov. (i–j, after WIMAN 1910).

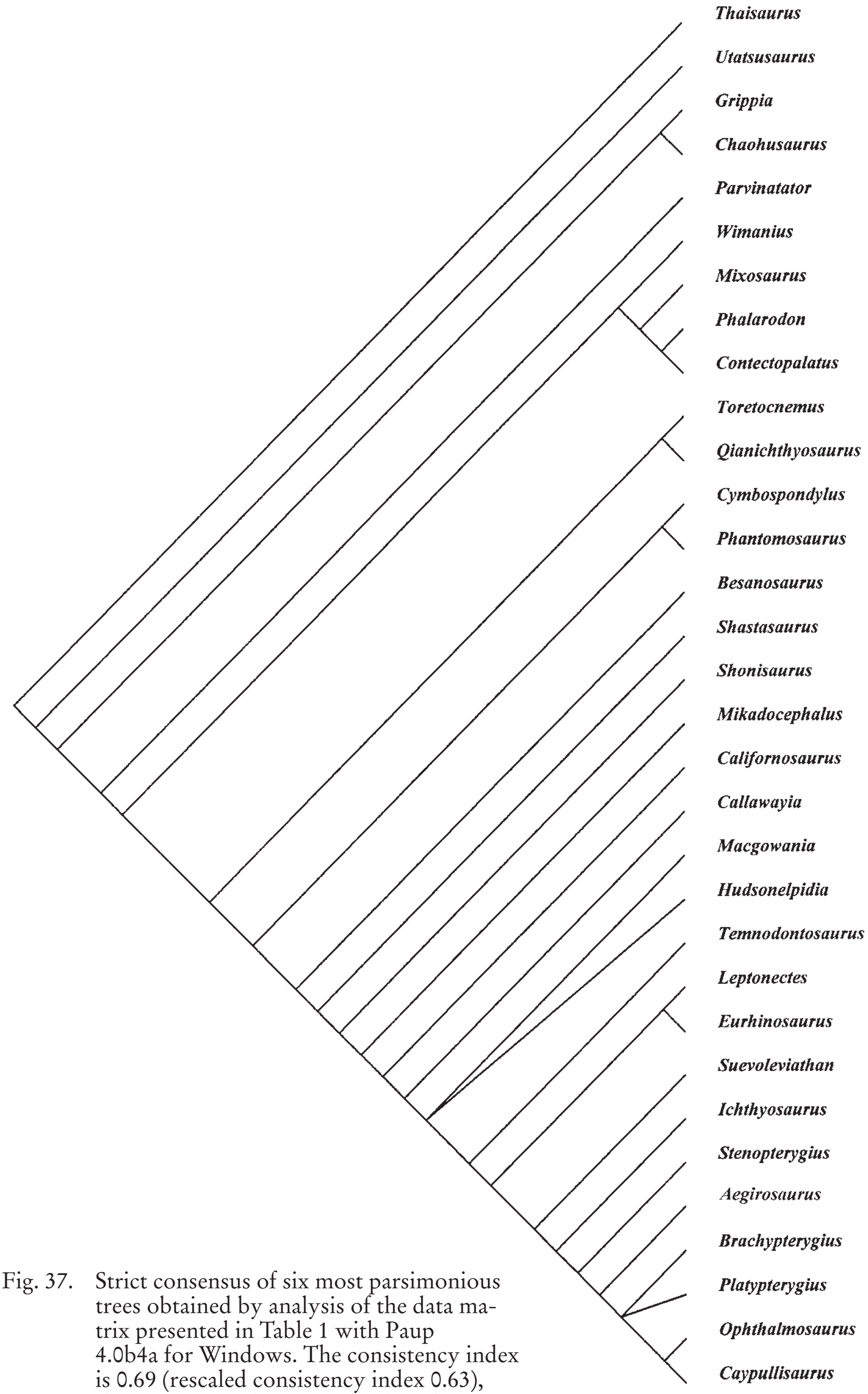


Fig. 37. Strict consensus of six most parsimonious trees obtained by analysis of the data matrix presented in Table 1 with Paup 4.0b4a for Windows. The consistency index is 0.69 (rescaled consistency index 0.63), the retention index 0.91. Tree length is 192 steps (33 taxa, 128 characters).

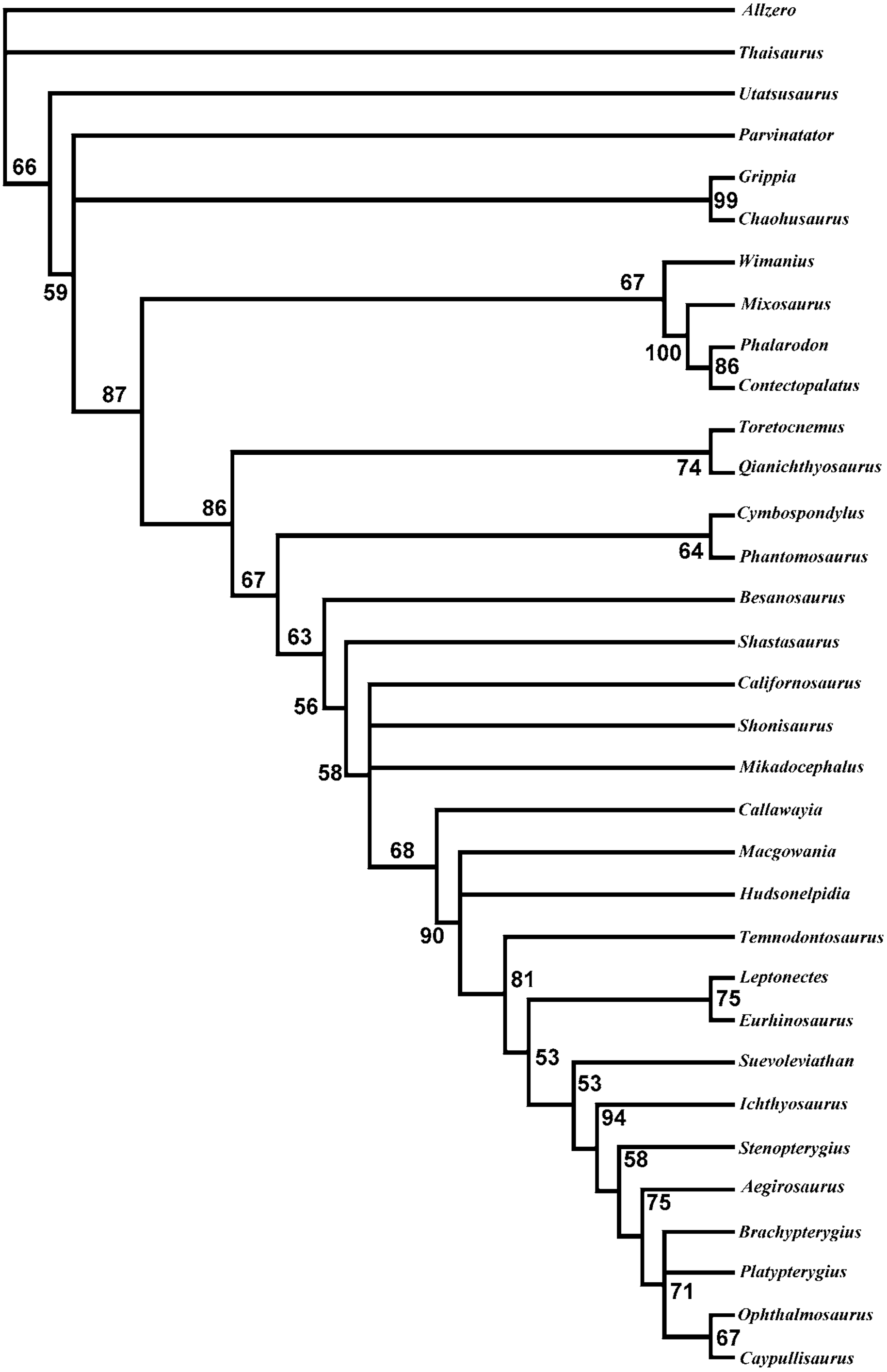


Fig. 38. Bootstrap values for the clades resulting from the phylogenetic analysis.

Lower Triassic

Middle Triassic

Fig. 39. Major Lower and Middle Triassic ichthyosaur localities. Map based on MAZIN & SANDER 1993.

Lower Triassic: 1. Japan, *Utatsusaurus*. 2. Spitsbergen, *Grippia*, *Rotundopteryx*, *Isfjordosaurus*. 3. Thailand, *Thaisaurus*. 4. Anhui, China, *Chaohusaurus*. 5. British Columbia, Canada, *Parvinatator*.

Middle Triassic: 1. Germany, *Contectopalatus*, *Phalarodon*, *Phantomosaurus*, *Cymbospondylus*. 2. Switzerland/Italy, *Mixosaurus*, *Phalarodon*, *Wimanius*, *Cymbospondylus*, *Mikadocephalus*, *Besanosaurus*. 3. Spitsbergen, *Mixosaurus*, *Phalarodon*, *Cymbospondylus*, *Mikadocephalus*. 4. Nevada, USA, *Phalarodon*, *Cymbospondylus*. 5. British Columbia, Canada, *Phalarodon*, Longipinnati indet. 6. China, Mixosauridae indet. 7. Timor, Mixosauridae indet., Cymbospondylidae indet. 8. New Zealand, Mixosauridae indet.

Upper Triassic

Lower Jurassic

Fig. 40. Major Upper Triassic to Lower Jurassic ichthyosaur localities.

Upper Triassic: 1. California/Nevada, USA, *Shastasaurus*, *Californosaurus*, *Toretocnemus*, *Shonisaurus*. 2. British Columbia, Canada, *Hudsonelpidia*, *Macgowania*, *Callawayia*, Temnodontosauridae indet. 3. Guizhou, China, *Qianichthyosaurus*. 4. England, *Leptonectes*, *Ichthyosaurus*. 5. Mexico, *Shastasaurus*. 6. Tibet, Longipinnati indet.

Lower Jurassic: 1. Germany, *Stenopterygius*, *Temnodontosaurus*, *Leptonectes*, *Eurhinosaurus*, *Ichthyosaurus*, *Suevoleviathan*. 2. England, *Leptonectes*, *Ichthyosaurus*, *Eurhinosaurus*, *Temnodontosaurus*, *Stenopterygius*. 3. France/Belgium/Luxembourg, *Stenopterygius*, *Eurhinosaurus*, *Temnodontosaurus*, *Leptonectes*, *Ichthyosaurus*. 4. Prince Edwards Island, Canada, Neoichthyosauria indet. 5. Alberta, Canada, *Ichthyosaurus*.

Middle Jurassic

Upper Jurassic

Fig. 41. Major Middle to Upper Jurassic ichthyosaur localities.

Middle Jurassic: 1. Argentina, *Ophthalmosaurus*, *Chacaicosaurus*. 2. England, *Ophthalmosaurus*. 3. Germany, ?*Stenopterygius*, *Ophthalmosaurus*. 4. Russia, *Ophthalmosaurus*.

Upper Jurassic: 1. England, *Ophthalmosaurus*, *Brachypterygius*, *Nannopterygius*. 2. Germany, *Aegirosaurus*, *Nannopterygius*. 3. France, *Ophthalmosaurus*. 4. Russia, *Ophthalmosaurus*, *Brachypterygius*. 5. Wyoming, *Ophthalmosaurus*. 6. Argentina, *Ophthalmosaurus*, *Aegirosaurus*, *Caypullisaurus*.

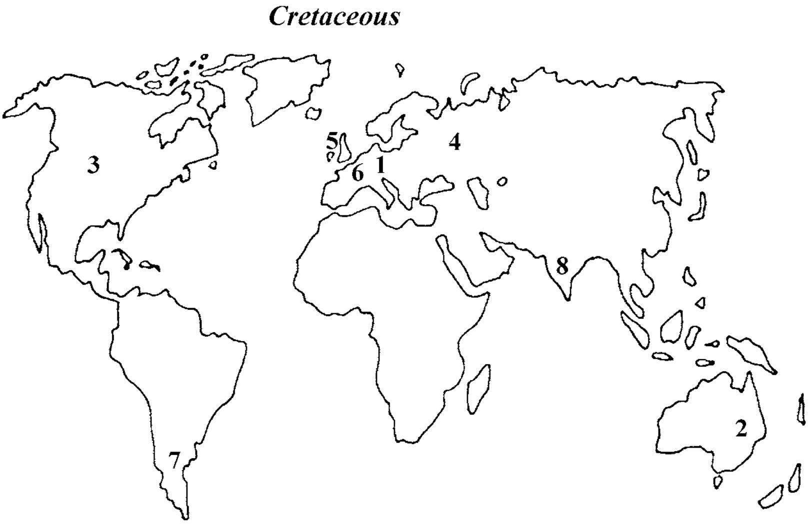


Fig. 42. Major Lower to Upper Cretaceous ichthyosaur localities.

1. Germany, *Platypterygius platydactylus*, *P. hercynicus*. 2. Queensland, Australia, *Platypterygius longmani*. 3. Wyoming, USA, *Platypterygius americanus*. 4. Russia, *Platypterygius bedengensis*, *P. birjukovi*, *P. bannovkensis*, *P. kiprijanoffi*. 5. England, *Platypterygius* sp. 6. France, *Platypterygius* sp. 7. Argentina, *Platypterygius hauthali*. 8. India, *Platypterygius* sp.

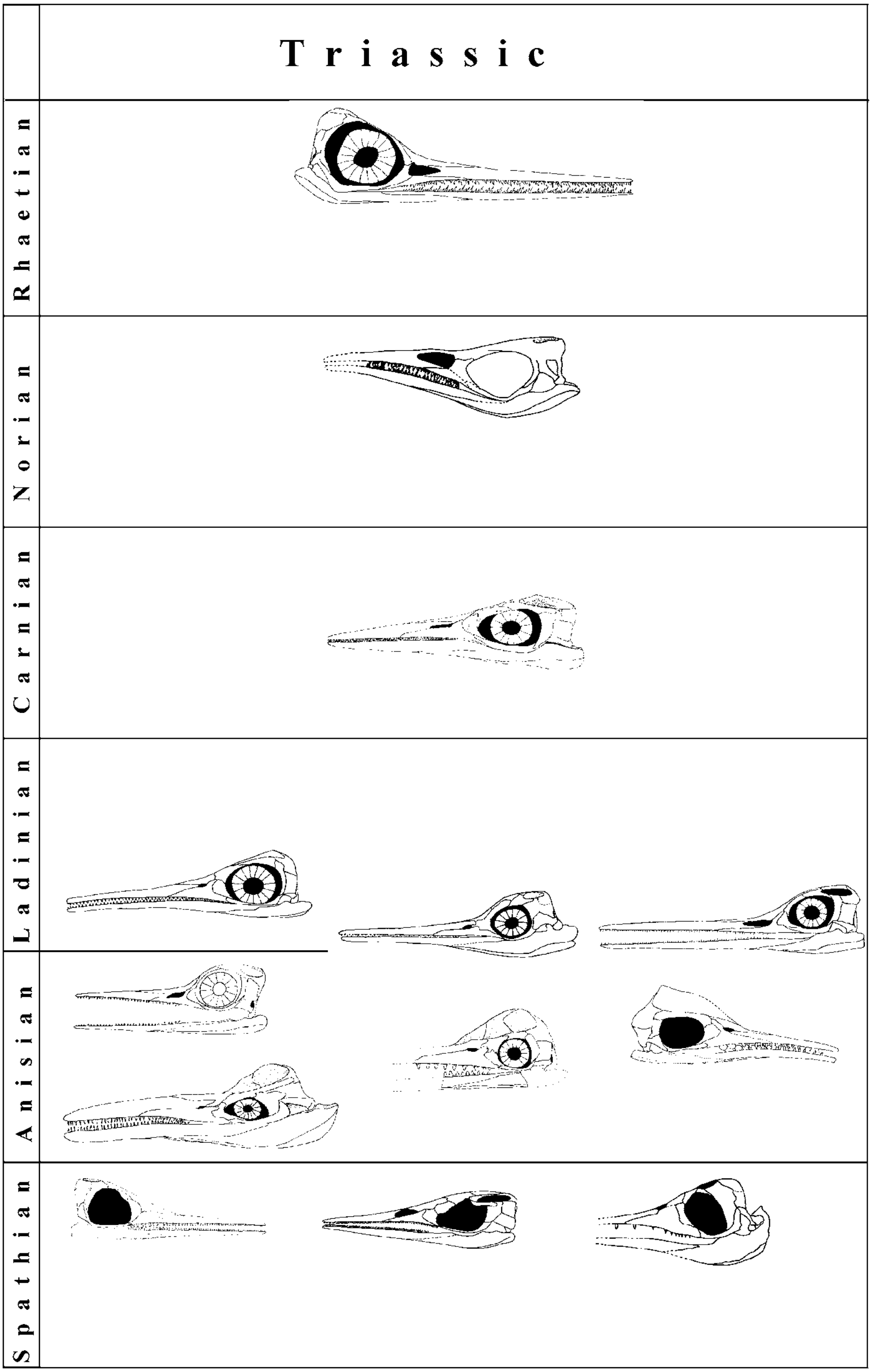


Fig. 43. Distribution of major Triassic ichthyosaur taxa in time, illustrated by skulls of well-known species (see Figs. 1–5).

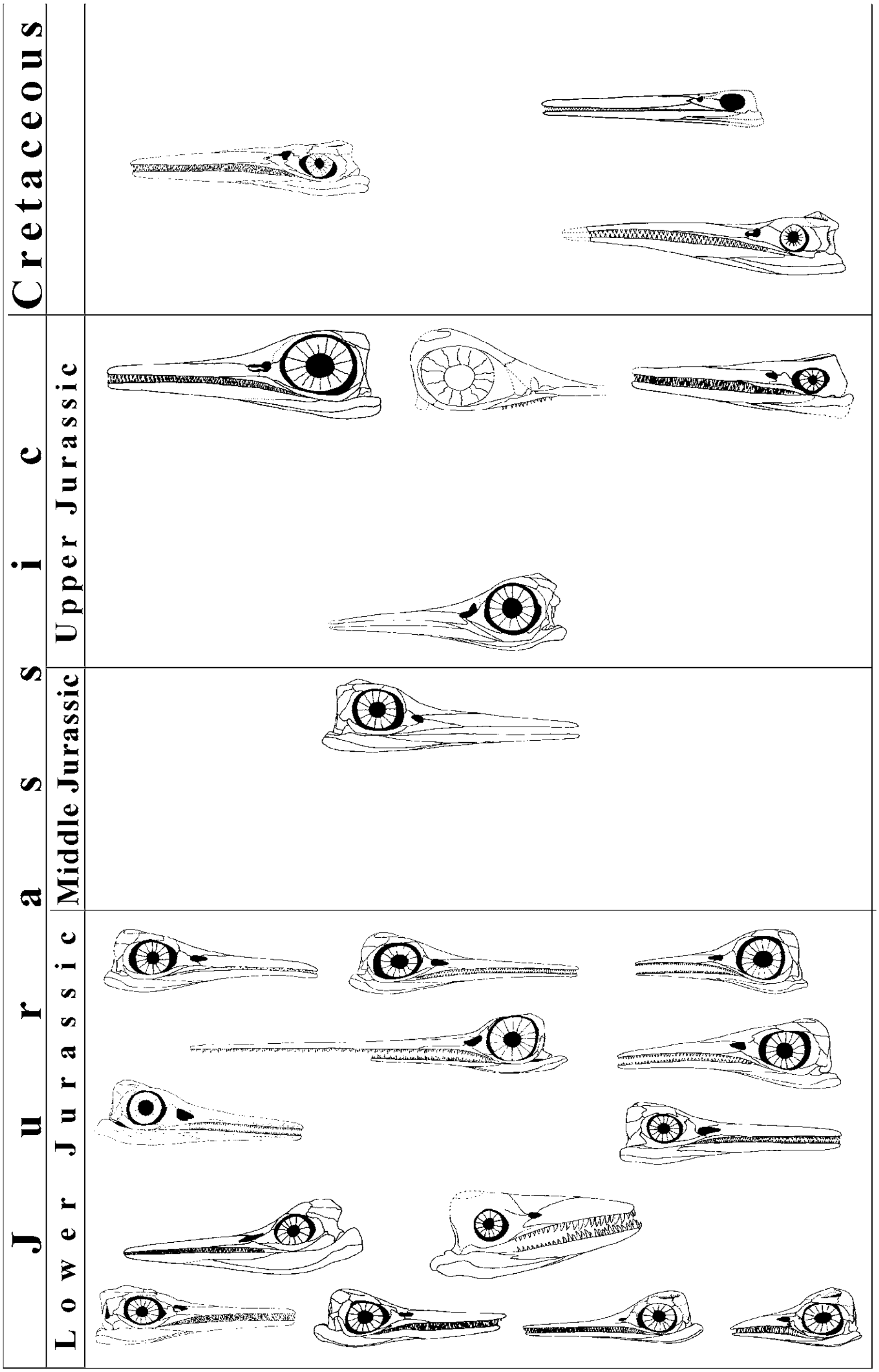


Fig. 44. Distribution of major Jurassic to Cretaceous ichthyosaur taxa in time, illustrated by skulls of well-known and important species (see Figs. 4–9).

Tab. 1. Data matrix for the phylogenetic analysis of the Ichthyosauria.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Allzero	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thaisaurus	0	?	1	0	?	?	0	?	?	?	?	?	?	?	0	?	0	0	1	?	1	0	?	0	0
Utatsusaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grippia	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaohusaurus	0	0	0	0	?	1	1	1	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0
Parvinatator	0	0	0	0	?	0	0	0	?	?	0	?	0	0	0	?	?	?	?	?	1	?	?	0	0
Wimanius	0	0	0	0	?	0	0	0	0	?	0	?	1	0	0	0	?	?	?	?	?	0	?	?	0
Mixosaurus	0	0	0	0	?	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1	1	1	1
Phalarodon	0	1	0	0	?	1	0	1	0	1	0	1	1	0	1	0	0	?	0	0	1	1	1	1	1
Contectopalatus	0	1	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1	1	1	1
Toretocnemus	?	0	0	0	?	0	0	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Qianichthyosaurus	?	?	?	0	?	0	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	1	?	?
Cymbospondylus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	0
Phantomosaurus	0	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Besanosaurus	0	0	0	0	?	0	1	0	0	0	1	0	1	1	0	0	0	0	?	?	1	0	1	0	0
Shastasaurus	0	0	0	0	?	?	0	?	1	0	0	0	1	1	0	0	0	1	1	0	1	0	1	0	0
Shonisaurus	0	0	0	0	0	0	0	0	?	?	?	?	1	1	0	0	1	?	1	0	1	0	1	?	0
Mikadocephalus	0	0	0	0	?	0	1	0	1	0	0	1	1	1	0	0	1	1	1	1	1	0	1	0	0
Californosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Callawayia	0	0	0	0	?	0	0	0	1	0	0	0	1	1	0	?	1	?	1	1	1	0	1	1	0
Macgowania	?	0	0	0	?	0	0	0	0	?	?	?	1	?	0	?	?	?	?	?	?	0	1	?	0
Hudsonelpidia	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	?	?	?	?	?	?	0	1	?	?
Temnodontosaurus	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0
Leptonectes	1	0	1	0	?	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0
Eurhinosaurus	1	0	1	0	?	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0
Suevoleviathan	1	0	0	0	?	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0
Ichthyosaurus	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0
Stenopterygius	1	0	0	0	?	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0
Aegirosaurus	1	0	1	0	?	0	0	0	1	0	1	0	1	1	0	1	1	?	1	?	1	0	1	1	0
Brachypterygius	1	0	0	0	?	0	0	0	1	0	1	0	1	1	0	1	1	?	?	?	1	0	1	1	0
Platypterygius	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0
Ophthalmosaurus	1	0	0	1	?	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0
Caypullisaurus	?	0	0	1	?	0	?	?	1	0	1	0	1	1	0	1	1	?	1	?	1	0	1	1	0

Tab. 1. Data matrix for the phylogenetic analysis of the Ichthyosauria (continued).

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Allzero	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thaisaurus	0	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Utatsusaurus	0	0	0	?	0	0	0	0	0	0	0	0	0	?	?	?	?	?	0	0	0	?	0	0	0
Grippia	0	0	0	1	0	0	?	0	0	?	0	1	0	?	?	?	?	?	0	?	0	?	0	?	?
Chaohusaurus	?	0	0	1	0	0	0	0	0	?	0	1	0	?	0	0	0	0	0	?	0	?	0	?	0
Parvinatator	?	?	0	0	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?
Wimanius	?	?	0	0	0	0	1	0	0	0	1	?	0	?	?	?	?	?	1	?	0	?	?	?	?
Mixosaurus	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0
Phalarodon	0	0	0	1	1	0	?	0	0	0	1	1	0	?	?	0	?	0	1	?	0	?	1	1	0
Contectopalatus	0	0	0	1	1	0	1	1	0	0	1	1	0	0	?	0	0	0	1	?	0	?	?	?	?
Toretocnemus	?	?	?	?	?	?	?	0	0	?	?	1	?	?	?	?	?	?	0	?	0	?	?	?	?
Qianichthyosaurus	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Cymbospondylus	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	?	1	0	0	0	0
Phantomosaurus	?	?	0	0	?	?	?	1	?	0	?	1	?	?	0	0	1	0	0	?	1	?	?	?	?
Besanosaurus	0	0	0	0	0	0	?	1	?	?	?	?	?	?	0	?	?	?	?	?	0	?	0	1	0
Shastasaurus	0	0	0	?	?	0	1	1	0	0	1	1	0	?	0	0	?	0	0	?	0	0	?	0	0
Shonisaurus	?	1	0	?	?	?	?	1	?	?	1	?	0	0	0	?	?	?	0	0	1	1	0	1	0
Mikadocephalus	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	1	1	1	0
Californosaurus	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Callawayia	0	1	0	?	?	0	?	1	1	1	1	1	0	?	0	1	1	1	0	?	1	1	1	1	0
Macgowania	?	?	0	0	0	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
Hudsonelpidia	?	1	0	0	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	?
Temnodontosaurus	1	1	0	1	0	0	1	1	1	1	1	1	0	?	0	1	1	1	0	1	1	1	1	1	1
Leptonectes	1	1	1	1	0	0	1	1	1	1	1	1	?	0	0	1	?	1	0	?	1	1	1	1	1
Eurhinosaurus	1	1	1	1	0	0	1	1	1	1	1	1	0	?	0	1	2	1	0	?	1	1	1	1	1
Suevoleviathan	1	1	0	1	0	0	1	1	1	1	1	1	0	?	0	1	2	1	0	?	1	1	1	1	1
Ichthyosaurus	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	2	1	0	1	1	1	1	1	1
Stenopterygius	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	2	1	0	1	1	1	1	1	1
Aegirosaurus	1	1	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	?
Brachypterygius	1	1	0	1	1	?	?	1	1	?	?	?	?	0	1	1	2	?	0	?	1	1	?	1	1
Platypterygius	1	1	0	1	?	1	?	1	1	1	1	1	?	0	1	1	2	1	0	?	1	1	1	1	1
Ophthalmosaurus	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	2	1	0	1	1	1	1	1	1
Caypullisaurus	1	1	0	1	1	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1	1

Tab. 1. Data matrix for the phylogenetic analysis of the Ichthyosauria (continued).

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Allzero	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thaisaurus	?	?	0	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Utatsusaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grippia	0	0	0	?	0	0	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0
Chaohusaurus	0	0	0	?	0	0	?	?	0	0	0	0	0	0	0	0	?	0	0	?	?	?	?	?	0
Parvinatator	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Wimanius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mixosaurus	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Phalarodon	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Contectopalatus	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Toretocnemus	?	?	1	?	?	1	0	1	1	?	0	0	0	?	?	0	?	?	?	?	?	?	1	1	1
Qianichthyosaurus	?	0	1	?	0	1	?	?	1	?	?	0	0	0	0	0	?	?	?	0	?	?	?	?	1
Cymbospondylus	0	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	?	0	0	0	0	0	0	1	1
Phantomosaurus	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Besanosaurus	0	1	0	0	1	1	1	1	1	1	1	0	0	1	0	0	?	1	1	1	0	1	0	1	1
Shastasaurus	0	1	0	1	?	1	1	1	1	?	1	0	0	?	?	?	?	1	1	1	0	1	0	1	1
Shonisaurus	0	0	0	?	1	1	1	1	1	1	1	0	0	1	0	0	2	1	1	1	0	1	0	0	1
Mikadocephalus	0	1	0	1	1	1	1	1	1	1	1	0	0	1	0	0	?	1	1	1	0	1	0	1	1
Californosaurus	0	0	0	1	0	1	1	1	1	0	1	0	0	?	0	0	?	1	1	1	0	1	0	1	1
Callawayia	?	0	?	?	?	?	?	?	1	?	?	0	0	?	?	0	?	1	1	1	1	1	1	1	1
Macgowania	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1	1	1	1	1	?	1	1
Hudsonelpidia	?	0	?	?	0	1	?	?	1	?	1	1	0	1	?	?	?	?	?	?	?	?	?	?	1
Temnodontosaurus	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	0	2	1	1	1	1	1	1	1	1
Leptonectes	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	0	2	1	1	1	1	1	1	1	1
Eurhinosaurus	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	0	2	1	1	1	1	1	1	1	1
Suevoleviathan	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	1	?	1	1	1	1	1	1	1	1
Ichthyosaurus	1	0	1	1	0	1	1	1	1	1	1	0	1	1	1	1	2	1	1	1	1	1	1	1	1
Stenopterygius	1	0	1	1	0	1	1	1	1	1	1	0	1	1	1	1	2	1	1	1	1	1	1	1	1
Aegirosaurus	1	0	1	1	0	1	1	1	1	1	1	0	1	1	?	?	1	1	?	?	?	?	1	1	1
Brachypterygius	?	0	1	1	0	1	1	?	1	?	?	0	1	?	?	?	?	?	1	1	1	1	1	1	1
Platypterygius	1	0	1	1	1	1	1	1	1	1	1	0	1	?	1	1	2	1	1	1	1	1	1	1	1
Ophthalmosaurus	1	0	1	1	0	1	1	1	1	1	1	0	1	?	1	1	2	1	1	1	1	1	1	1	1
Caypullisaurus	1	0	1	1	0	1	1	1	1	?	?	0	1	?	?	?	2	1	1	1	1	1	?	?	1

Tab. 1. Data matrix for the phylogenetic analysis of the Ichthyosauria (continued).

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Allzero	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thaisaurus	0	1	?	1	0	?	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Utatsusaurus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grippia	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Chaohusaurus	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0
Parvinatator	?	?	?	0	?	?	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Wimanius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mixosaurus	1	0	0	0	1	1	1	0	0	1	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1
Phalarodon	1	0	0	0	1	1	1	0	0	1	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1
Contectopalatus	1	0	0	0	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Toretocnemus	1	0	1	1	1	1	1	0	0	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Qianichthyosaurus	1	0	?	0	1	1	1	0	0	1	1	1	1	1	0	0	1	?	0	?	1	1	1	1	1
Cymbospondylus	1	1	0	0	1	1	1	0	0	1	0	1	1	?	0	0	?	1	0	?	?	1	1	?	?
Phantomosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Besanosaurus	1	0	0	0	1	1	1	0	0	1	1	1	1	0	0	0	1	?	0	?	?	1	1	?	?
Shastasaurus	1	0	0	0	1	1	1	0	1	1	1	1	1	0	0	0	?	?	0	?	?	1	1	?	?
Shonisaurus	1	0	0	0	1	1	1	1	1	1	1	1	1	?	0	0	1	?	0	0	1	1	1	?	?
Mikadocephalus	1	0	0	1	1	1	1	0	0	1	1	1	1	0	0	0	1	?	0	?	?	1	1	?	?
Californosaurus	1	0	0	1	1	1	1	0	1	1	1	1	1	0	0	0	?	1	0	?	?	1	1	?	?
Callawayia	1	0	?	0	1	1	1	1	1	1	1	1	1	1	0	0	1	?	0	0	1	1	1	1	1
Macgowania	2	1	?	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Hudsonelpidia	2	1	?	1	1	?	1	0	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Temnodontosaurus	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Leptonectes	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Eurhinosaurus	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Suevoleviathan	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Ichthyosaurus	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Stenopterygius	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1
Aegirosaurus	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	?	0	0	1	1	1	1	1
Brachypterygius	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1
Platypterygius	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1
Ophthalmosaurus	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1
Caypullisaurus	2	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1

Tab. 1. Data matrix for the phylogenetic analysis of the Ichthyosauria (continued).

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128
Allzero	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thaisaurus	?	?	0	?	0	?	?	?	?	?	?	0	0	0	1	0	0	0	0	0	1	1	?	1	?	?	0	0
Utatsusaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1
Grippia	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	?	1	1	1	1	1	1	1	1
Chaohusaurus	?	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1
Parvinatator	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1	?	1	1
Wimanius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	?	?	?	?
Mixosaurus	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	1
Phalarodon	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	1
Contectopalatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1
Toretocnemus	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	1	1	?	?	1	1	1	?	?
Qianichthyosaurus	1	1	?	?	?	?	?	?	?	?	0	0	1	0	1	1	0	1	0	1	1	1	?	1	1	1	?	?
Cymbospondylus	1	?	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	?	?	1	1	1	1	1	1	1	1
Phantomosaurus	?	?	?	?	?	?	?	?	?	?	?	0	?	0	1	0	0	?	?	?	1	1	?	?	?	1	1	1
Besanosaurus	1	1	0	1	0	0	0	1	1	1	0	0	1	0	1	0	0	1	1	1	1	1	?	1	1	1	1	1
Shastasaurus	1	1	0	1	0	0	1	1	1	1	0	0	1	0	1	0	0	1	1	?	1	1	1	1	1	1	1	1
Shonisaurus	1	1	0	1	0	0	1	1	1	1	0	0	1	0	1	?	0	1	1	1	1	1	?	1	1	1	1	1
Mikadocephalus	1	1	0	1	0	0	1	1	1	1	0	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1
Californosaurus	1	1	0	1	0	0	1	1	1	1	0	0	1	0	1	0	0	1	1	?	1	?	?	?	1	1	?	?
Callawayia	1	1	0	?	?	?	?	?	?	?	?	?	1	?	?	?	0	1	1	?	1	1	1	1	1	1	1	1
Macgowania	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	1	?	1	1
Hudsonelpidia	1	1	0	1	1	1	0	1	1	2	0	1	1	0	1	1	1	1	1	0	?	1	?	1	1	1	?	1
Temnodontosaurus	1	1	0	1	1	1	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Leptonectes	1	1	0	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Eurhinosaurus	1	1	0	1	1	1	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Suevoleviathan	1	1	0	1	1	1	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ichthyosaurus	1	1	0	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Stenopterygius	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Aegirosaurus	1	1	1	1	1	1	1	1	1	2	1	1	?	?	?	?	?	?	?	?	1	1	?	1	1	1	1	1
Brachypterygius	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	1	1	1	1
Platypterygius	1	1	1	1	?	?	?	?	1	?	?	?	1	1	1	?	1	1	1	?	1	1	1	1	1	1	1	1
Ophthalmosaurus	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1
Caypullisaurus	1	1	?	?	?	?	?	?	?	?	1	?	1	1	?	?	0	1	1	?	1	1	?	1	1	1	1	1

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