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EVOLUTION OF FISH-SHAPED REPTILES (REPTILIA: ICHTHYOPTERYGIA) IN THEIR PHYSICAL ENVIRONMENTS AND CONSTRAINTS

Ryosuke Motani
Department of Geology, University of California, Davis, California 95616;
email: motani@geology.ucdavis.edu

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■ **Abstract** Ichthyosaurs were a group of Mesozoic marine reptiles that evolved fish-shaped body outlines. They are unique in several anatomical characters, including the possession of enormous eyeballs sometimes exceeding 25 cm and an enlarged manus with sometimes up to 20 bones in a single digit, or 10 digits per manus. They are also unique in that their biology has been studied from the perspective of physical constraints, which allowed estimation of such characteristics as optimal cruising speed, visual sensitivity, and even possible basal metabolic rate ranges. These functional inferences, although based on physical principles, obviously contain errors arising from the limitations of fossilized data, but are necessarily stronger than the commonly made inferences based on superficial correlations among quantities without mechanical or optical explanations for why such correlations exist.

INTRODUCTION

Ichthyosaurs were a group of marine reptiles that first diversified near the end of the Early Triassic. They remained one of the main predators in the Mesozoic ocean until their disappearance near the Cenomanian-Turonian boundary (Bardet 1992). They were the first tetrapod to evolve a fish-shaped body profile with a well-demarcated caudal fluke, long before cetaceans came up with a similar design some 150 million years later (McGowan 1991, Motani 2002a). They evolved the largest eyes of all vertebrates, sometimes exceeding 25 cm in maximum diameter (Motani et al. 1999). They also hold the records for hyperphalangy and hyperdactyly—the number of phalanges (finger bones) in a single digit (finger) reached as many as 20 in the genus *Ichthyosaurus* (McGowan 1974a), and the number of digits per manus was up to 10 in *Caypullisaurus* (Motani 1999a, Fernández 2001). They have one of the earliest records of live-birth in amniotes (Dal Sasso & Pinna 1996, Brinkmann 1996), and they were the first marine tetrapod to reach a total length of ~20 m (Nicholls & Manabe 2004). And finally, they were the first major fossil collected by Mary Anning in the 1800s (McGowan 1991), and, together with the plesiosaurs that she discovered later, they symbolize the early phase of scientific movements in England that cultivated the grounds for Darwin's evolutionary theory (McGowan 2001).

The first scientific description of ichthyosaurs was published by Homes (1814), and the first genus *Ichthyosaurus* was named by de la Beche & Conybeare (1821). Despite such a long history of scientific study, our knowledge of the evolution of the group was limited until recently because interest in the group flagged, especially after the recognition of the Dinosauria (Owen 1842). It was not until the late 1980s that the ichthyosaurian study was revitalized, and many of the noteworthy facts listed above were recognized during the past decade. The purpose of the present review is to summarize these newer discoveries and list future perspectives.

It is noteworthy that the unique evolution of ichthyosaurs enabled paleontologists to use simple physical principles to probe aspects of how ichthyosaurian body parts functioned in their physical environments. This is possible partly because they were under stringent physical constraints, being a large animal in water. These relatively new lines of studies are summarized in the third section of this review. The first two sections provide overviews of basic knowledge that illuminate the evolution of the group, namely the systematics and fossil record, respectively.

PHYLOGENY AND SYSTEMATICS

Phylogeny and systematics provide the framework for evolutionary discussions, so they are reviewed first.

Overview

The latest taxonomic overview recognized that 235 species in 76 genera of ichthyosaurs had been proposed, of which 80 species in 36 genera were considered valid (McGowan & Motani 2003). The number, however, is increasing year by year because of new discoveries.

The sister group of ichthyosaurs is unknown. Many different hypotheses have been proposed as to where ichthyosaurs belong in the tree of vertebrates, and all major groups, including mammals, amphibians, and osteichthyes, have been proposed (Callaway 1989). A consensus is beginning to emerge among cladistic studies (e.g., Caldwell 1996, Motani et al. 1998) that ichthyosaurs are diapsids that are close to the basal node of the Sauria (the last common ancestor of lepidosaurs and archosaurs). It is unknown whether they are outside or inside the saurian clade. Only new specimens of very basal ichthyosaurs will clarify the problem.

Phylogenetic analyses of ichthyosaurs using cladistic methods started to appear in the early 1980s, when Mazin (1982) published the first cladogram. There was no data matrix associated with this manually drawn tree. Callaway (1989) conducted the first objective cladistic analysis based on a data matrix for the clade Shastasauridae. Motani (1999b) published the first comprehensive phylogenetic hypothesis for the entire Ichthyopterygia based on a data matrix, and Sander (2000) and Maisch & Matzke (2000) followed with different analyses.

None of the published phylogenetic trees is uncontroversial; however, there seems to be a consensus regarding the basic phylogenetic relationship among major groups. A topology from Motani (1999b) is given in Figure 1 because it contains the least number of problems with methodology (McGowan & Motani 2003). This basic phylogenetic outline of the group is briefly explained below. McGowan & Motani (2003) should be consulted for more extensive information on systematics.

Basic Group Names—Clades and Grades

The common name "ichthyosaur" refers to the group Ichthyopterygia, which contains a smaller group Ichthyosauria (Figure 2). To be precise, the word ichthyosaur should refer to the group Ichthyosauria, but it is becoming customary to use it for the entire Ichthyopterygia, and that is how the word is used in this review.

It is useful to recognize a few grades and clades within the Ichthyopterygia. The most "primitive" grade of ichthyosaurs is referred to as "basal" ichthyosaur. These are exclusively Early Triassic forms that appeared somewhat like a lizard with flippers (Figure 2), although there is a new undescribed species form the Middle Triassic that may fall into this grade. These include, for example, *Utatsusaurus*, *Grippia*, and *Chaohusaurus*. They retained some characters that are found in terrestrial diapsids.

In the Middle and Late Triassic, many clades of ichthyosaurs appeared, forming an intermediate grade (Figure 2). The word intermediate is used here in a sense that they diversified along the stem of the phylogenetic tree that led from the basal grade to the very successful clade of fish-shaped ichthyosaurs that appeared later. The intermediate grade includes such famous clades as Cymbospondylidae, Mixosauridae, and Shastasauridae.

Fish-shaped ichthyosaurs probably evolved in the Late Triassic (Motani 1998). The term fish-shaped is used here to refer to a body configuration with streamlined trunk and demarcated caudal fin that is used as an oscillating foil. This may be a misnomer sensu stricto because not all osteichthyes (bony fish) share this configuration, but the design at least matches their stereotypic image. The exact phylogenetic position for the appearance of the fish-shaped design in ichthyosaurs is controversial. It is possible that the poorly known Shastasauridae was already fish-shaped, especially given the new fossils being described from the lower Carnian of China. The most important group of fish-shaped ichthyosaurs is the clade Parvipelvia, or the ichthyosaurs with a small pelvis (Figure 2). Parvipelvians dominated soon after they emerged in the early Norian, and soon became the only group of ichthyosaurs, probably by the late Norian.

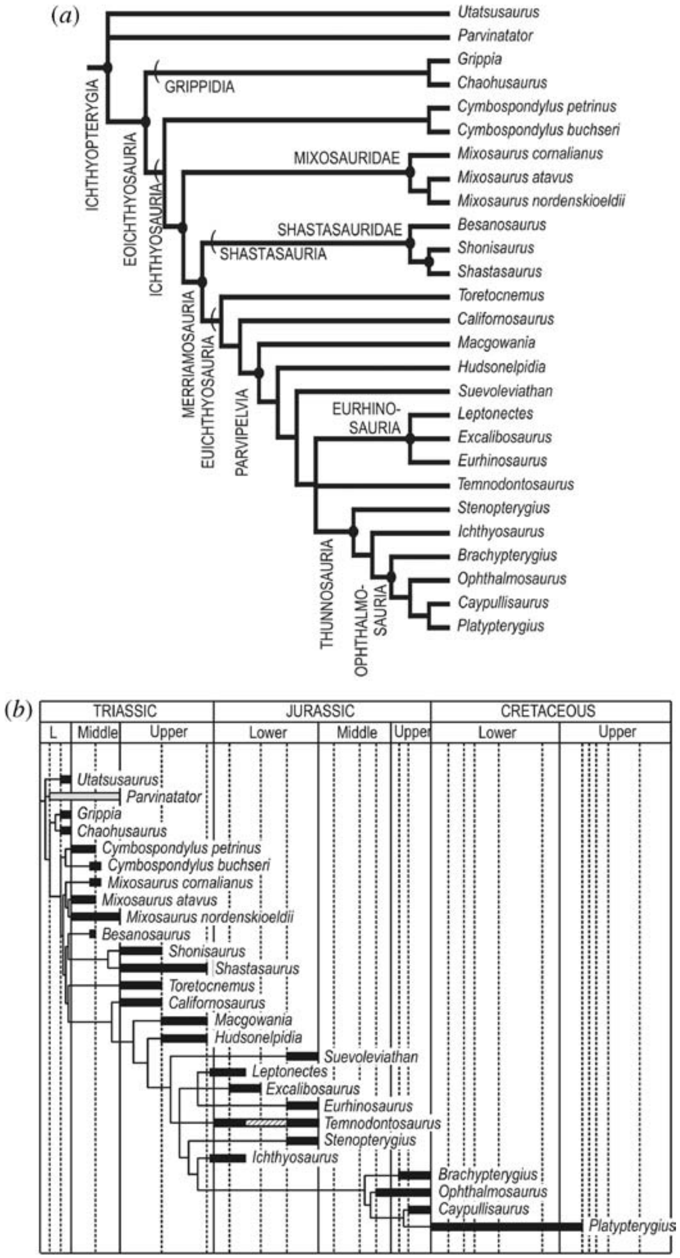

Figure 1 (*a*) Cladogram of better known ichthyosaurs (based on Motani 1999b). (*b*). Stage-level stratigraphic distribution of the taxa appearing in (*a*). Absolute ages follow 2004 stragraphic column by International Commission on Stratigraphy (http://www.stratigraphy.org).

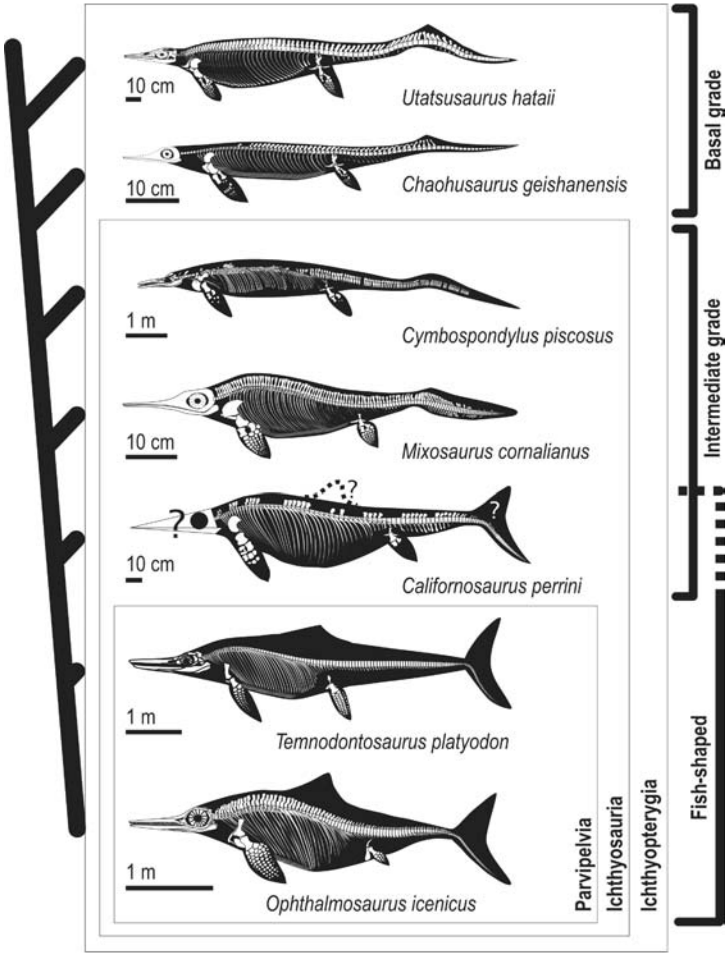

Figure 2 Body plans of basic ichthyosaurian clades and grades plotted along an abbreviated phylogenetic tree, with their names.

FOSSIL RECORD

Overview

Ichthyosaurs were a diverse group, with various body forms and sizes. Several species are represented by well-articulated skeletons, whereas others are known only from fragmentary remains. They share several common characteristics that are easily recognizable. For example, they all had an elongated and somewhat constricted snout that was narrower than the rest of the skull, although fossil compression may obscure the feature. The snout may be long or short, relative to the skull width (Figure 3, see color insert). Their tooth crowns were conical, with variations in ratios among the height, width, and length, and with occurrence of occasional blunt cutting edges. The exceptions to this rule are the posterior teeth of some mixosaurids, such as *Phalarodon fraasi* (Figure 3). These teeth are mound-shaped, sometimes with ridges on the top of the crown. It has been suggested that the teeth were used for crushing hard prey items, but there is no evidence from fossilized stomach contents. Ichthyosaurian teeth were not very large even in large species. The only exception is *Himalayasaurus tibetensis*, which had large, blade-like tooth crowns (Figure 3). Even without specialized teeth, it is known that ichthyosaurs preyed upon other vertebrates (McGowan 1974b, Böttcher 1989), including turtles (Kear et al. 2003). However, the most abundant stomach contents are the remains of dibranchiate cephalaopods and fish (Pollard 1968, Keller 1976, Böttcher 1989).

Postcranially, all ichthyosaurs had a "kink" or "bend" in the tail. In basal ichthyosaurs, this structure is referred to as the caudal peak (Motani 1999b). It is easily recognized because the direction of the neural spine changes in the area (Figure 2). In fish-shaped ichthyosaurs, this bending became steep, giving rise to a structure called the tailbend (McGowan 1974a,b). In *Californosaurus*, which is one of the transitional forms between the fish-shaped and more basal ichthyosaurs, it is clearly seen that the change of the orientation of the neural spines corresponds to the position of the tailbend.

Ichthyosaurs had flippers instead of limbs with distinctive fingers. The evolution of the flipper has been studied comparatively (e.g., Caldwell 1997a,b; Motani 1999a), and it is possible to trace the continuous evolutionary transformation series for the forelimb (Figure 4, see color insert). Although the series is continuous, it is difficult to single out a feature that is shared by all ichthyosaurian front flippers. Ichthyosaurs initially had five digits as in many amniotes, including humans. Some time in the Late Triassic, a form without the first digit, or the thumb, appeared (e.g., *Toretocnemus* in Figure 4), and this lineage eventually gave rise to the Parvipelvia. Extra digits started to appear in some species of Norian ichthyosaurs, and many Jurassic ichthyosaurs added digits both anteriorly and posteriorly in the forelimb (Figure 4), a phenomenon referred to as hyperdactyly. Ichthyosaurs also added extra finger bones, or phalanges, to their digits. Such hyperphalangy was present even in the most basal ichthyosaurs, such as *Utatsusaurus* (Figure 4). See Fedak & Hall (2004) for the latest review of hyperphalangy. Late Triassic ichthyosaurs started to loose a well-define shaft of the zeugopodial and autopodial bones. Caldwell (1997b) suggested that this may be related to the loss of perichondral ossification.

Stratigraphy

The first definitive records of ichthyosaurs appear suddenly and almost simultaneously over a wide range of the Northern Hemisphere, including Canada, China, Japan, and Spitsbergen, in the last ammonite-conodont zone of the Olenekian (Upper Triassic; McGowan & Motani 2003). Suspected earlier occurrences (Callaway & Brinkman 1989, Brinkman et al. 1992) are based on specimens floating on the surface. Therefore, it is difficult to discuss the geographic origin of the group. These Early Triassic ichthyosaurs, including *Utatsusaurus* and *Grippia*, form the basal grade of the ichthyosaurian phylogenetic tree. In appearance, they looked like a long-snouted lizard with flippers and a small caudal fin (Motani et al. 1996), with a relatively small skull, an elongated trunk containing approximately 40 vertebrae in front of the pelvic girdle, and a short tail. Smaller species did not reach 1 m in total length, and the largest species was less than 3 m.

In the Anisian (Middle Triassic), two clades diverged from the stem lineage, namely Cymbospondylidae and Mixosauridae. Cymbospondylids are large ichthyosaurs with an elongated trunk containing some 65 vertebrae in front of the pelvic girdle and possibly reaching 9 m in total length. Their skulls were small compared to their bodies, as in the basal ichthyosaurs. In contrast, mixosaurids were small ichthyosaurs, probably not growing much larger than 2 m in total length even in large species—small species did not reach 1 m. They had relatively large skulls for the body, unlike the basal ichthyosaurs, but resembled fish-shaped ichthyosaurs that appeared later, and had some 50 vertebrae in front of the pelvic girdle. The two groups were widely distributed across the Northern Hemisphere (Sander 1992, Sander & Mazin 1993).

The stem lineage during the Middle Triassic is represented by *Besanosaurus* from the Anisian (Dal Sasso & Pinna 1996) and the poorly known *Pessosaurus* from the Ladinian (Wiman 1910), which is now considered undiagnostic by many authors (McGowan & Motani 2003). *Besanosaurus* was a moderately sized ichthyosaurs (approximately 5 m in total length), with a relatively small skull for the body. Isolated bones probably belonging to a similar ichthyosaur are found in the Lower Saurian Level of Spitsbergen (McGowan & Motani 2003), which is now correlated to the last conodont zone of the Lower Triassic. It is therefore possible that a *Besanosaurus*-type ichthyosaur preceded cymbospondylids and mixosaurids, despite the current cladogram (Figure 1). *Pessosaurus* was somewhat similar to *Besanosaurus*, and although it shows the existence of the stem lineage in the Ladinian, it is too poorly known to be discussed further.

Mixosaurids and cymbospondylids became extinct by the Carnian (Late Triassic), with the latter possibly disappearing before the Ladinian (Middle Triassic). The stem lineage continued into the Carnian, without much difference in body shape. The evolution of ichthyosaurs during the Carnian is poorly documented, having been based on partial skeletons from the Hosselkus Limestone of the upper Carnian (Merriam 1902, 1903, 1908). These Californian ichthyosaurs have been customary assigned to the family Shastasauridae, but are now considered paraphyletic (Motani 1999b). A new locality representing the lower Carnian was recently discovered in Guizhou Province of Southern China, yielding many complete ichthyosaurian skeletons. The overview of this Guanling Fauna has yet to be established firmly, and our knowledge will be remarkably improved as the study progresses over the next several years.

During the Norian, the evolution of ichthyosaurs took a major turn, with the appearance of the clade Parvipelvia, or the ichthyosaurs with a small pelvic girlde. Some shastasaurids were still surviving until the middle Norian (R. Motani, personal observation), but there is no record of them from the upper Norian. As the name implies, the pelvic girdles of parvipelvian ichthyosaurs were much reduced in size, with each element being somewhat rod-shaped rather than platelike. The femur was also small. The reduced size indicates that the majority of caudal muscle series did not insert to, or originate from, the pelvic girdle or femur. Instead, they probably were connected to the trunk area, as in cetaceans, which would have increased the length of the propulsive wave passing through the body, leading to more oscillatory, as opposed to undulatory, body movement during swimming. At the same time, the length of the tail increased, with 30 to 50 vertebrae existing between the pelvic girdle and the caudal fluke. Early parvipelvians include *Hudsonelpidia* (McGowan 1995) and *Macgowania* (Motani 1999b).

The Rhaetian record of ichthyosaurs is scarce, but there are undescribed specimens from this stage. One is from the Williston Lake in British Columbia, Canada, probably representing a new genus that is similar to *Ichthyosaurus* (R. Motani, personal observation). The other is from the White Lias of southern England, which is now correlated with the Rhaetian despite its name. This specimen unmistakably represents the genus *Ichthyosaurus* (R. Motani, personal observation) and brings back the origin of this otherwise Jurassic genus into the Triassic.

A diversity of typically fish-shaped ichthyosaurs is known from the Lower Jurassic, including such major genera as *Ichthyosaurus* and *Stenopterygius*. The evolution of the group during the Early Jurassic can be considered as continued experimentation along the fish-shaped parvipelvian design that appeared in the Norian. There are two main ichthyosaurian localities for the Lower Jurassic, namely southern England, where Mary Anning collected the first skull, and southern Germany. Rocks ranging in age from the Hettangian (possibly including uppermost Rhaetian) to Pliensbachian are exposed in the former, whereas the lower half of the Toarcian occurs in the latter. The famous Lagerstätten of Holzmaden, yielding excellent fossils, some with approximate body outlines (Martill 1987), is located in the southern Germany.

Middle Jurassic ichthyosaurs are not very abundant, except in the Callovian, where *Ophthalmosaurus* occur in the Oxford Clay. None of the few reported Aalenian ichthyosaurs (Arnaud et al. 1976, Motani 1991) is complete. The Bajocian ichthyosaurs *Chacaicosaurus* (Fernández 1994) and *Mollesaurus* (Fernández 1999) are also incomplete, but they do show that nonophthalmosaurid ichthyosaurs were surviving at least early in the Middle Jurassic, being mixed with the new lineage (i.e., ophthalmosaurids).

The ichthyosaurian fossil record in the Upper Jurassic is much better than in the Middle Jurassic. At least six genera are recognized based on reasonable specimens, all belonging to the clade Ophthalmosauridae, which is a well-diagnosed clade with some definitive characters of the skull and forefin. *Caypullisaurus* (Fernández 1997) and *Aegirosaurus* (Bardet & Fernández 2000) are better-known Upper Jurassic ichthyosaurs.

McGowan & Motani (2003) recognized only two genera of ichthyosaurs from the Cretaceous, namely *Platypterygius* and *Brachypterygius*. However, a diverse set of morphology is known in fragmentary specimens stored at the Sedgwick Museum in Cambridge, so the generic diversity is probably largely underestimated.

The last record of ichthyosaurs occurs in the Cenomanian of the Upper Cretaceous. It is possible that ichthyosaurs became extinct during the end Cenomanian extinction event of marine organisms, but it is not possible to establish at this point that ichthyosaurs survived until the event because of the scarcity of fossil record (Bardet 1992).

Impression Fossils

Approximate body outlines of ichthyosaurs are known based on some excellently preserved fossils (Figure 5, see color insert). At least four localities have yielded ichthyosaurian fossils indicating a part of body outlines. These are:

- Sulphur Mountain Formation in the Wapiti Lake area, British Columbia (Lower to Middle Triassic) (Nicholls & Manabe 1999)
- Barrow-upon-Soar, England (Lower Jurassic) (Owen 1881, Martill 1995)
- Holzmaden area, Germany (Lower Jurassic) (e.g., Hauff & Hauff 1981, Martill 1987)
- Solnhofen area, Germany (Upper Jurassic) (e.g., Bauer 1898, Bardet & Fernández 2000)

Caudal flukes are known from all four localities above. Jurassic fossils all belong to the Parvipelvia, showing that they had crescent-shaped caudal flukes, as in cetaceans (although vertical rather than horizontal in orientation). The Triassic fossil, from the first locality, seems to represent a basal ichthyosaur (Nicholls & Manabe 1999), probably of *Utatsusaurus* or *Grippia* grade, which had a caudal fin with only the dorsal lobe.

A specimen of the basal ichthyosaur *Chaohusaurus geishanensis* from the Lower Triassic of Anhui, China, which was described by Motani et al. (1996) as *Chensaurus chaoxianensis* (now considered subjective junior synonym of *Chaohusaurus geishanensis*), showed an impression of the dorsal lobe of the caudal fluke, much resembling the same in the specimen from the Sulphur Mountain Formation. The outline was reported to be clear when the specimen was first examined in the early 1990s, but it was less conspicuous by 1995 when it was studied for the 1996 publication, and it was not possible to detect the outline with naked eyes in 1998 when the specimen was examined again (R. Motani, personal observation). Figure 5 shows yellowish coloring of the dorsal lobe of the caudal fin that was still seen in 1996.

Dorsal fin fossils are known only from the Holzmaden area (Figure 5), where some specimens of the genus *Stenopterygius* with approximate body outlines, preserved as fossilized bacterial mats that grew under the carcasses after deposition, are known. The preservation is very different from that in other localities, such as Barrow upon Soar (Figure 5). Because of this preservation, Martill (1987) questioned the accuracy of the body outlines, and also the existence of the dorsal fins as a whole, in these ichthyosaurs. It is true that some of these specimens have been prepared to show clear outlines, yet bacterial mats are not expected to terminate cleanly. Therefore, at least parts of some body outlines are probably not precise in that they have been smoothed through fossil preparation. However, it is still likely that many of these fossils at least preserve approximate body outlines. For example, Motani (2002a) found that the span of the caudal fluke for ten such specimens, when plotted against the fork length (the length between the tip of the snout and the fork of the tail), showed a positive allometry, as seen in living cruisers of similar body size (see Swimming Evolution, below). It is unlikely that such a scaling is artificial, given that these specimens were found at various points of time and prepared by different individuals. Also, some specimens, such as R158 of the Paleontologiska Museet, Uppsala Universitet, Sweden, show gradual fading of the bacterial mat toward periphery, especially around the torso, indicating that preparators did not alter the outline; yet the distribution of the bacterial mat indicate a tuna-like outline, with a single dorsal fin. Therefore, it seems that the body outline fossils from the Holzmaden area show at least approximate extent of the flesh, especially where the body is not very thick and tightly contacted the substrate after the deposition, as would be expected for the caudal fluke and dorsal fin. In some specimens, however, there is more than one dorsal projection of the outline that is not very smooth overall. It is possible that the dorsal fins were not deposited horizontally to the substrate in these specimens, and the validity of the outline should be questioned.

Fossil Embryos

Occurrence of embryos inside adult individuals is known for at least six genera of ichthyosaurs: *Besanosaurus* (Dal Sasso & Pinna 1996) and *Mixosaurus* (Brinkmann 1996) from the Middle Triassic (Anisian and Ladinian, respectively); *Ichthyosaurus* (Woodward 1906, Deeming et al. 1993), *Stenopterygius* (Woodward 1906), and *Temnodontosaurus* (Böttcher 1990) from the Lower Jurassic (Sinemurian, Toarcian, and Toarcian, respectively); and an undetermined ophthalmosaurid from the Lower Cretaceous (Maxwell & Caldwell 2003). None of the presumed embryos show indications of chemical or physical damages that would be expected from cannibalistic ingestion, so it is likely that they represent true embryos. In some cases, the small individuals inside adults have incompletely developed vertebral columns that are curled, without limbs (Figure 5), as would be expected for embryos (e.g., Deeming et al. 1993).

There is a famous specimen of *Stenopterygius* in the Staatliches Museum für Naturkunde, Stuttgart, that has a small ichthyosaur with its snout penetrating between the right and left pelvic girdle elements of an adult (Figure 5). The common interpretation is that the mother died when giving birth to the baby. However, the likelihood of the smooth and narrowing snout of the baby being stuck inside the cloaca of the mother has been questioned. Alternative interpretation is that the baby was still in the birth canal when the mother died, and it was pushed out later by gasses generated by the decaying soft tissues (McGowan 1991).

There is no record of ichthyosaurian embryo from the Lower Triassic, but it is also true that Lower Triassic ichthyosaurs are not very abundant. Given that ichthyosaurs did not appear until very late in the Early Triassic, live-birth clearly evolved early in the ichthyosaurian evolution, at least during the first few million years or possibly less, of their 150-million-year evolutionary history.

Body Size

There was no simple trend in ichthyosaurian body sizes through geological time. Large as well as small ichthyosaurian species seem to have coexisted from the beginning. One exception could be the Early Triassic, when well-established species did not exceed 3 m in total length. However, there are multiple fragmentary records of larger species (e.g., Wiman 1910) of unknown body size (possibly more than 6 m).

The smallest adult body size of ichthyosaurs stayed between 0.5 and 1 m in total length through geological time—note that this is not small compared to most marine vertebrates. These include *Chaohusaurus geishanensis* (Early Triassic), *Mixosaurus cornalianus* type A (Middle Triassic; see Brinkmann 1998), *Toretocnemus californicus* and *Hudsonelpidia brevirostris* (Late Triassic), and *Ichthyosaurus breviceps* (Early Jurassic). Clear records do not exist of ichthyosaurs in this body size range after the Early Jurassic, when the overall fossil record of the group is not very robust.

Most ichthyosaurs did not exceed 10 m in total length, except in the Late Triassic *Shonisaurus* and its relatives. The most complete specimen of the type species *S. popularis*, from the upper Carnian of Nevada, was probably slightly less than 15 m, when missing parts are estimated (Camp 1980, McGowan & Motani 1999). This individual is not the largest of the species: There are larger but fragmentary individuals from Nevada (Camp 1980). An even larger individual, belonging to a new species of *Shonisaurus*, is being described from the Norian of British Columbia (Nicholls & Manabe 2004). It was probably approximately 20 m, or possibly more, when missing parts are estimated. This is by far the most complete of all the marine reptilian fossils that have been estimated to have reached 20 m. *Himalayasaurus tibetensis*, a very fragmentary ichthyosaur from the Norian of Himalayas (Dong 1972), is another giant. The type and only specimen is too incomplete, but it can be recognized that it was related to *Shonisaurus* and comparable in size (Motani et al. 1999). McGowan (1996) discussed isolated elements of giant ichthyosaurs from the Lower Jurassic of England, possibly approaching 15 m. Otherwise, there is no clear record of ichthyosaurs exceeding 10 m in the Jurassic and later.

PHYSICS AND INFERENCE OF BODY FUNCTIONS

Physics and Functional Inferences—The Framework

Ichthyosaurs do not have any descendants today, so our knowledge of the group is limited to what has been preserved in fossils. This poses difficulty in studying the function of their body parts, and ultimately how they interacted with their environment. Functional inferences in paleontology are frequently made from the shapes found in fossils, and some are more scientifically robust than others. In this review, the scientific value of such functional inferences is judged based on the involvement of physics, as explained below.

The most basic principle of inferring body part functions from fossils is uniformitarianism, which posits that physical processes have not changed since the time when the animal in question was alive, and thus that shapes perform functional roles according to their known physical characteristics. Functional hypotheses explicitly incorporating physics (and that make valid assumptions about animal behavior and body material properties) should be considered more viable than those that do not. At the same time, quantitative hypotheses should be given higher consideration than nonquantitative ones because of the repeatability and objectivity. When these factors are combined, it is possible to divide functional inferences in paleontology into three categories (modified from McGowan & Motani 2003):

- Level 1: Intuitive functional morphology. These are inferences on body part function based on qualitative assessment of the shapes of fossils and analogies made based on that assessment. See Visual Optics and Swimming Evolution, below, for examples.
- Level 2: Quantitative functional morphology. These are functional inferences based on assessment of fossil shapes, on which analogies to modern organisms are made quantitatively. However, physical principles are not incorporated into the quantification process. See Visual Optics and Swimming Evolution, below, for examples.
- Level 3: Physical functional morphology. These are functional inferences based on quantitative assessment of fossil shapes based on physical laws (e.g., mechanics and optics). See Visual Optics and Swimming Evolution, below, for examples.

Level 3 inferences are the strongest of the three, being both physics-based and quantitative. The reality, however, is that this level of inference is very rare in paleobiological studies. Many inferences are quantitative yet based on correlations among measurements that lack explicit physical meaning.

It is inevitable that functional hypotheses become more explicit as the inference level, as defined above, increases. This may appear as if more assumptions have to be made at higher levels, but it is not so. At lower levels, implicit assumptions that there is no need to know certain constants or variable ranges exist. The number of the implicit assumptions equals that of the variable and constants that are ignored. Higher level inferences are more honest about implicit assumptions hidden behind the superficial logic of lower level counterparts.

Visual Optics

Ichthyosaurs are exceptional among vertebrates in having very large eyeballs. It is usually difficult to estimate the size of eyeballs in fossil vertebrates, but in ichthyosaurs, and some other marine reptiles such as mosasaurs, scleral ossicles are so well developed that they not only form a ring, but also cover more than a hemisphere of the eyeball (Figure 6, see color insert). The ring is not very thick in cross-section, despite its robust external appearance (Figure 6). Because of these scleral rings, it is possible to measure not only the approximate diameter of the eyeball but also the size of the bony aperture in the middle.

It is not known why such an extensive bony coverage of the eyeball evolved. One possible explanation may be found in hydrodynamics. In fish, water pressure is positive (i.e., pushing toward the animal) at the anterior tip of the animal as it swims through the water, but gradually becomes negative toward the operculum (Wardle 1977). The transition between the positive and negative pressures is usually found in the area where the eyes are located; thus the eyeballs are least affected by the pressure arising from the water movement around the fish during swimming. The eyeballs of ichthyosaurs were exceptionally large, and it is possible that the anterior part of the eyeball was pushed by the moving water, whereas the posterior part was pulled. Such differential pressures could modify the shape of eyeballs if there was no protective mechanism, such as a hemisphere of bone. This hypothesis requires further testing using actual ichthyosaurian models in the flume or by computer simulation.

Ichthyosaurs had enormous eyeballs, but the size has only been quantified recently (Motani et al. 1999). The largest ichthyosaurian eyeball belongs to the genus *Temnodontosaurus*. There are at least two skulls of *T. platyodon*, from England, showing scleral rings exceeding 25 cm in maximum diameter, and one of the scleral rings, still incompletely prepared, was measured to be 26.3 cm (Figure 6). These are the largest eyes of any animal that have been measured; there are comparable estimates for the Giant Squid (Roper & Boss 1982). These large individuals of *T. platyodon* probably approached 9 m in total length.

Large eye size usually indicates high visual capacity by a simple fact that there could be a high number of photoreceptive cells, whose size is physically constrained, although loosely (Hughes 1977, Ali & Klyne 1985). Intuitively, ichthyosaurs with their large eyes must have had high visual capacity (Level 1 inference).

It is possible to make this inference more quantitative (Level 2). From a plot of the maximum eyeball diameter against the fork length (the length from the tip of the snout to the fork of the caudal fluke, which is a standard measurement in cetaceans), it is clear that ichthyosaurs had unusually large intercepts for the

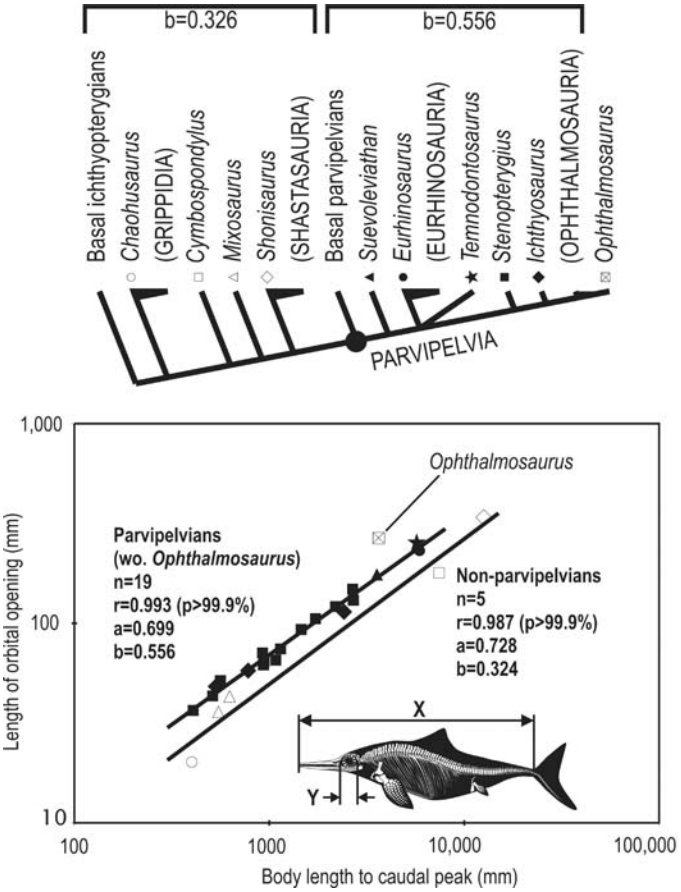

Figure 7 Change of eye size relative to the body length among ichthyosaurs, with an abbreviated cladogram to show the phylogenetic position of the taxa involved. Note that the relative eye size increased in parvipelvians and then in *Ophthalmosaurus* (based on Motani et al. 1999).

allometric line (Figure 7). Compared to most other vertebrates, ichthyosaurs had large eyes for their body, and presumably higher visual capacity. Among ichthyosaurs, parvipelvian ichthyosaurs had relatively larger eyes for the body compared to the more basal ichthyosaurs, and within the Parvipelvia, the genus *Ophthalmosaurus* (meaning "eye-lizard") had markedly larger eyeballs relative to the body than the rest (Figure 7). Most display specimens of this genus only have the central portion of the scleral rings spanning approximately 15 cm, but the actual extent is much larger, reaching 23 cm in maximum diameter. *Ophthalmosaurus* probably did not exceed 4 m in total length, but its eyeball was almost as large as those of *Temnodontosaurus*, with twice the body size.

The function of the large ichthyosaurian eyes may be further probed using simple optical principles (Level 3 inference). Motani et al. (1999) devised a method to estimate the minimum f-numbers of ichthyosaurian eyes from the eye socket depth and the diameter of the bony aperture of the scleral rings. The eyes are closely packed in ichthyosaurian skulls (Figure 6), enabling estimation of the maximum possible socket depth given the skull width. This gives the maximum possible eyeball length, which is correlated to the posterior nodal distance of the optical system of the eyeball (Hughes 1977). The diameter of the dilated pupil can be estimated based on the scleral ring aperture. The f-numbers thus calculated obviously contain error margins but still give sufficient grounds to discuss the relative sensitivity of various ichthyosaurian eyes. The results, given in Figure 8, indicate that the basal ichthyosaur *Cymbospondylus* from the Middle Triassic of Nevada had a relatively high minimum f-number, comparable to those of living diurnal animals (∼2.0), whereas *Ophthalmosaurus* had a very small minimum f-number, as in some living nocturnal animals (∼1.0). The database size is still limited, but it seems that the minimum f-number became smaller with the appearance of parvipelvians, and within the group, *Ophthalmosaurus* alone had even smaller values. Small f-numbers indicate, on average, high visual sensitivity that enables better performance under low-light conditions.

Humphries & Ruxton (2002) argued that ichthyosaurian eyes were larger than those of some deep diving mammals, so they must have provided not only the

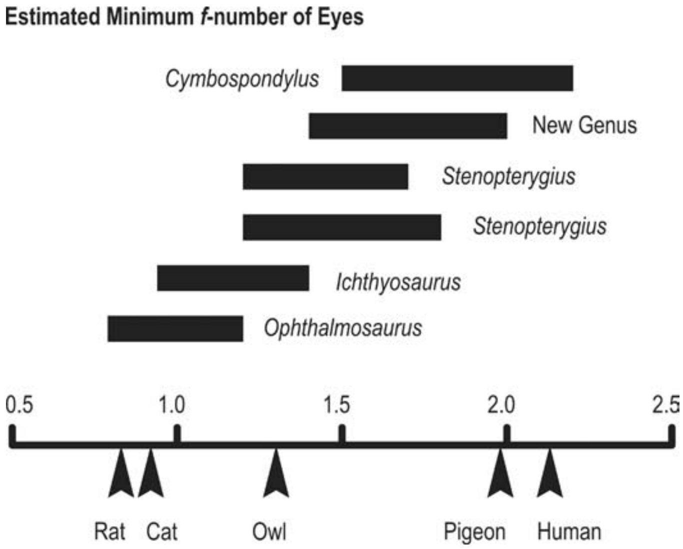

Figure 8 Estimated minimum f-number ranges for selected ichthyosaurian genera compared to values generally known in some living vertebrates (based on Motani et al. 1999).

sensitivity but also the acuity that are useful for other aspects of life, such as species recognition. This is a Level 2 inference (i.e., there is little physical logic behind the superficial quantification) that may or may not be valid and cannot overturn the Level 3 inference described above. One possible obstacle against this hypothesis is the general arrangement of photoreceptive cells in vertebrate eyes. Cone cells usually occur centrally and do not occupy much space. Rod cells fill the peripheral part of the retina and they can become very large. It is most likely that the giant eyes of ichthyosaurs had a high number of large rod cells, which are usually useful for sensitivity but not for acuity. There is no vertebrate living today with such large eyeballs, and there is much doubt as to whether the small brain of ichthyosaurs could have handled the amount of information that would have resulted from having a high number of cone cells, as the hypothesis necessarily assumes. Although the hypothesis is interesting, it is not truly testable.

To summarize what can be said with confidence, ichthyosaurian eyes became relatively large when parvipelvians appeared, and at the same time, their visual sensitivity increased. The same pattern repeated again when *Ophthalmosaurus* appeared among parvipelvians.

Swimming Evolution

Ichthyosaurian swimming styles have been inferred by analogy with living vertebrate swimmers. All ichthyosaurs are considered axial swimmers, i.e., they undulated their body axis to generate propulsive thrusts that were eventually released by the caudal fin (Massare 1988). The alternative swimming mechanism seen among living vertebrates, namely paraxial propulsion that uses appendages, as in sea turtles and sea lions, seems to have never evolved in the group (Massare 1988). The shoulder and pelvic girdles were never large in ichthyosaurs, possibly except in *Leptonectes solei* from the Sinemurian of England, indicating the lack of a muscular system to facilitate paraxial swimming. A possibility of pectoral propulsion has been proposed in the past for some ichthyosaurs (Riess 1986), but the evidence is weak and confused (e.g., citation of a large pectoral girdle, which actually does not exit).

Although all ichthyosaurs most likely used their body axis for propulsion, the actual swimming manner probably differed from species to species. Limitations of fossil evidence do not allow detailed studies of their swimming styles, yet it is possible to infer approximate swimming manners.

The simplest inferences of ichthyosaurian swimming style may be intuitive (Level 1 inference). For example, parvipelvian ichthyosaurs, with crescent-shaped caudal flukes, swam like tunas or lamnid sharks, whereas lizard-looking basal ichthyosaurs swam like lizards. It is possible to raise these intuitive inferences to the next level (Level 2). By plotting the height/length ratio of the caudal fluke against the fineness ratio of the body for various sharks (Figure 9), it is possible to obtain a continuous distribution that stretches from more eel-like toward tuna-like swimmers (Motani et al. 1996). When superimposing ichthyosaurs onto this

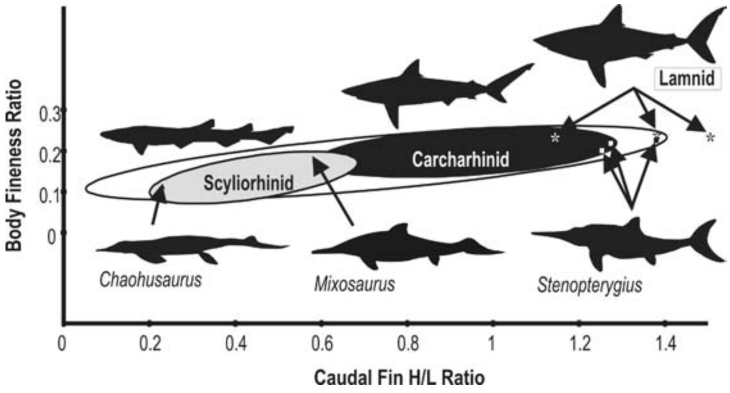

Figure 9 Body shape correlation between sharks and ichthyosaurs. *Chaohusaurus* was probably more eel-like in swimming style, as in living cat sharks (scyliorhinid), whereas *Stenopterygius* was probably more tuna-like, as in lamnid sharks (based on Motani et al. 1996).

distribution (Figure 9), it is shown that basal ichthyosaurs had body proportions similar to scyliorhinid sharks, which are known to be eel-like swimmers, whereas parvipelvian ichthyosaurs resembled lamnid sharks, which are considered tuna-like swimmers. One could argue that ichthyosaurs probably started as a more eel-like swimmer when they first appeared in the Early Triassic, and gave rise to a lineage of tuna-like swimmers that survived the end Triassic extinction.

This Level 2 inference is better than the previous Level 1 inference, but it still has its weakness; that is, the connection between the swimming styles and the simple body proportions is not justified by explicitly physical (especially mechanical in this case) analysis. The more slender body of the basal ichthyosaurs would probably have been more flexible than the more robust parvipelvian body design, but it is unknown how flexible it may have been in an absolute sense given the unknown yet undoubtedly complex internal structures of the ichthyosaurian body, comprised of many different materials.

Another Level 2 inference concerning ichthyosaurian swimming was made by Buchholtz (2000). She recorded the size change of the vertebral centra along the body of several Jurassic ichthyosaurs. By correlating the data with other characters, such as the rib length and tail length, she inferred that certain ichthyosaurs were more adapted for cruising by having stiffer trunks. The weakness of the argument, as in the previous case, is that the measurements were not integrated in a physically meaningful manner to justify the inferred relative stiffness. Moreover, the underlying premise that a stiffer body enables more efficient cruising is not currently well established based on experiments (e.g., Sepulveda et al. 2003).

There has been one Level 3 study of ichthyosaurian swimming. Motani (2002a) found that relatively large vertebrate swimmers (10^5 to 10^8 in Reynolds number) released approximately similar levels of power through the trailing edge of the caudal fins at a given Reynolds number, despite apparent variations in body outlines. The Reynolds number is a fundamental variable in fluid mechanics calculated from the size and speed of the moving object (an animal in this case) and the fluid property. Many variables in fluid mechanics scale with the Reynolds number, so it is similar to body mass in biology in that sense. The study was based on published kinematic studies. This scaling of the power output with the Reynolds number can be approximated by an exponential equation. It is also known that swimming vertebrates tend to use a certain range of Strouhal numbers at a constant speed for efficiency (Triantafyllou et al. 1993, Anderson et al. 1998, Taylor et al. 2003), and this can be expressed in the form of an equation. The Strouhal number describes the rate and density of the vortices that are formed in the wake of a moving object. A few predictions can be made when the two equations are combined. For example, optimal cruising speed and tailbeat frequency of a given large vertebrate swimmer can be estimated from its body length and the caudal fin span. Thus, the shape of the animal closely reflects its typical behavior because of the stringent physical constraints for the surrounding medium. Because the two dimensions can be measured from the body outline specimens of *Stenopterygius*, Motani (2002a) calculated the optimum cruising speed for ten such specimens (Figure 10). The result suggested that *Stenopterygius* was not as fast a cruiser as similarly sized cetaceans, but was comparable to tunas of similar body size.

Another prediction from Motani's (2002a) model is that optimal tailbeat frequency should decrease as the caudal fin span increases. It is then expected that larger individuals of a given species of cruising vertebrate have larger caudal fin span relative to the body length because the optimal contraction frequency of muscle is known to be smaller in larger individuals (Altringham & Johnston 1990, Altringham & Young 1991). Such a scaling of the caudal fin span relative to the body length is known for growth series of many large cruising vertebrates, including the blue marlin (Nakamura 1985), swordfish (Arata 1954), and cetaceans (e.g., Pilleri & Gihr 1976a,b; Best 1988). The same scaling pattern is seen in the ichthyosaur *Stenopterygius* (Motani 2002a), as mentioned above in Impression Fossils.

Massare (1988) pioneered another approach to estimating the swimming speed of ichthyosaurs. Her model is based on the assumption that the energy consumption at a constant swimming speed, apart from that for basic body maintenance, equals drag power to be overcome. Then, assuming such parameters as the surface area, drag coefficient, and the maximum sustainable metabolic rate, it is possible to calculate the maximum sustainable swimming speed (called the critical speed) for a given vertebrate swimmer. However, Massare (1988) tested her method with data from extant cetaceans and found that her estimates were larger than the published observed speeds, sometimes up to eight times larger. Motani (2002b) revisited this model and suggested several modifications, including the use of optimal speed in the calculation, rather than the critical speed. The revised version of the model was capable of predicting the optimal cruising speeds of large living vertebrate

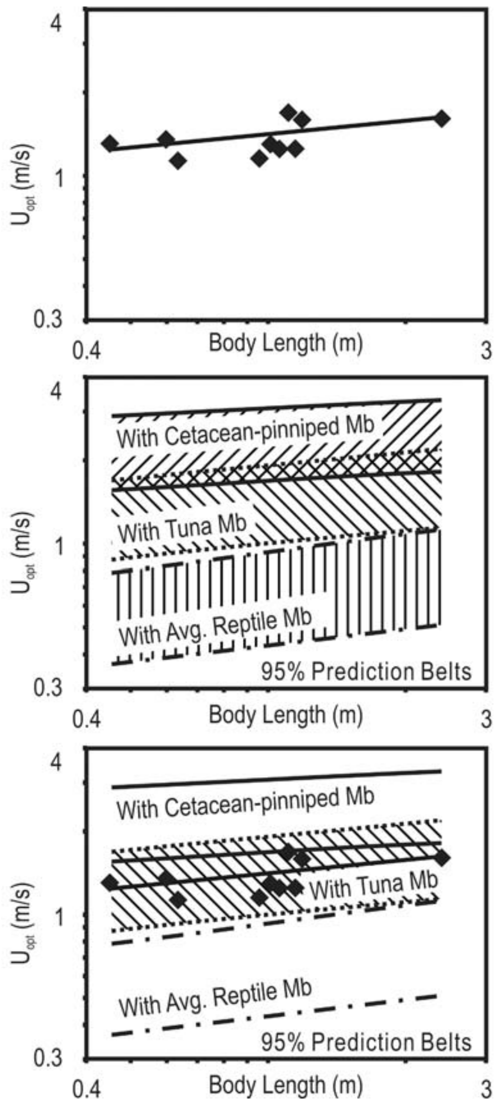

Figure 10 Speed estimates for ten individuals of *Stenopterygius* with preserved body outlines with two independent methods. Top: results from Motani (2002a). Middle: Different prediction belts indicating different assumptions of basal metabolic rates of *Stenopterygius,* results from Motani (2002b). Bottom: The top superimposed on the middle, showing that the two independent methods indicate tuna-like basal metabolic rates for *Stenopterygius*.

swimmers with less error than before. Therefore, Massare's (1988) premise is probably valid. Motani (2002b) estimated the optimal swimming speeds of some marine reptiles, including the same ten individuals of *Stenopterygius* as in the other study (Figure 10), with the revised method. However, because the metabolic rates of these animals are unknown, it was only possible to give different speed ranges depending on different assumptions of metabolic rates.

There is one pending point to the revised model, that is, the use of correction factors that were proposed by Hind & Gurney (1997). These values are considered as constants specific to swimming styles, but they may actually be variables with small ranges. Even in that case, however, the effect to speed estimates should be minor.

Metabolic Rate

The two approaches to estimating the swimming speed of ichthyosaurs are independent from each other, being based on different principles and measurements. They provide a unique opportunity to discuss the possible basal metabolic rates of ichthyosaurs in a quantitative fashion, which is usually very difficult for extinct vertebrates. Theoretically, it is possible to estimate the basal metabolic rates of the ten individuals by combining the two methods. The first method yields likely optimal speeds for the ten individuals of *Stenopterygius*. The second model can translate these estimated speeds into the basal metabolic rates if the calculation process is reversed. Such calculations suggest that *Stenopterygius* had basal metabolic rates between typical mammalian and reptilian levels at 20°C. This can be visualized by superimposing the speed estimates from Motani (2002a) on the results from Motani (2002b), as shown in Figure 10. These "raised ectothermic level" of metabolic rates are found today in such vertebrates as tunas (e.g., Dewar & Graham 1994a,b) and leatherback turtles (Paladino et al. 1990; but see also Lutcavage et al. 1992). Given the large number of assumptions that were made to make these calculations, the result cannot be taken as given. However, it is not unreasonable because living thunniform swimmers (i.e., tunas, lamnid sharks, and cetaceans) have metabolic rates somewhat higher than the typical ectothermic level (McGowan 1991).

Possibility of Deep Diving

Many air-breathing vertebrates dive deeply to forage (Kooyman 1989, Kooyman & Ponganis 1998). It would therefore be unsurprising if some Mesozoic marine reptiles did the same. A deep diving habit was proposed for ichthyosaurs by Taylor (1994), largely based on bone histology. The bony cortex of the diapophyses is spongy in ichthyosaurs, rather than being densely packed as in most vertebrates (de Buffrénil & Mazin 1990). Such spongy cortex bones are otherwise known in cetaceans, leatherback turtle, and elephant seal, all of which are known deep divers. Taylor (1994) correlated the existence of spongy cortex bones with the possession of compressible lungs (Level 2 inference). These lungs are emptied before diving and collapse at depths beyond 50 to 100 m (Ridgway & Scronce 1969), without being damaged or causing bubbles in the blood. If this correlation holds, then it is possible that most ichthyosaurs dove at least to some depth.

The possession of large and sensitive eyes in parvipelvians, as discussed above in the Visual Optics, is in accord with the evolution of deep diving in ichthyosaurs. Parvipelvian ichthyosaurs were capable of cruising, as in living tunas (see Swimming Evolution, above). Once ichthyosaurs were capable of cruising to the pelagic oceans, deeper parts of the oceans were also available to be exploited.

Motani et al. (1999) calculated the possible diving depths of *Ophthalmosaurus* given its visual optics and physiological scope. Because *Ophthalmosaurus* is extinct, Motani et al. (1999) instead used data for a cat, which has a similar minimum optic f-number as in *Ophthalmosaurus*. By simple calculations based on published data (Gunter 1951, Jerlov 1976), a cat should be capable of detecting a moving object at 300 m deep or deeper in the majority of oceanic waters. With larger eyes than in a cat, and with a comparable minimum f-number, *Ophthalmosaurus* was probably not inferior to the cat in visual capacity, suggesting that it was capable of detecting prey in the mesopelagic zone as well. This is especially true if the prey was emitting light signals, as would be expected in the deep oceans.

Schreer & Kovacs (1997) showed that the diving duration of air-breathing divers is roughly correlated with the body mass: The heavier the animal, the longer it can dive. Their data were mostly based on endothermic divers, which are more demanding in oxygen consumption and therefore cannot stay submerged as long as ectothermic divers. For example, leatherback turtles can stay underwater for three to five times longer than a marine mammal of comparable body mass (Schreer & Kovacs 1997). If *Ophthalmosaurus* shared the inferred physiology of *Stenopterygius* (see Metabolic Rate, above), then the use of the regression equation by Schreer & Kovacs (1997) would largely underestimate the diving duration of the ichthyosaur. With an underestimated body mass of 950 kg, an *Ophthalmosaurus* should be able to dive for approximately 20 min (largely underestimated as stated above). Within this time frame, with a very conservative cruising speed of 1 m/s (2 m/s is more likely from the estimation methods discussed earlier), *Ophthalmosaurus* could reach 600 m deep and resurface. Therefore, deep diving to the mesopelagic zones is in accordance with the optics and physiological scopes of *Ophthalmosaurus* (Motani et al. 1999).

NEW DISCOVERIES AND FUTURE DIRECTIONS

More and more ichthyosaurs are being discovered worldwide. These new discoveries are expected to improve our understanding of the evolution of the group remarkably. There are three stratigraphic horizons of special interest: the Middle and Upper Triassic and the Lower Cretaceous. The evolution of the intermediate grade ichthyosaurs during the Middle and Later Triassic is poorly understood at this point, and the diversity of ichthyosaurs in the Early Cretaceous requires further investigation. Middle and Late Jurassic are also important, given the scarcity of materials known at his point.

New discoveries are being made in the Middle and Upper Triassic of Guizhou Province, China. The localities have yielded very well-articulated skeletons of ichthyosaurs and other marine reptiles, and a careful review of the specimens is now required to clarify the taxonomic diversity therein. Upper Triassic localities are also being found in Alaska, which would possibly link the Chinese and Californian finds of Late Triassic ichthyosaurs.

The time has never been better to explore the mechanics, optics, and other biological aspects of ichthyosaurs using simulation modeling, given the rapid advancement in computer technology. Three-dimensional laser scanners are being used to quickly capture three-dimensional shapes of bones, in addition to CT scanners that are slower but provide internal images of fossils (Motani 2003). It is expected that the use of FEA (finite element analyses) and CFD (computational fluid dynamics) will become common in paleobiological studies of ichthyosaurs during the next decade.

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Figure 3 Normal (*bottom*, *Ichthyosaurus communis*; *middle left*, *I. breviceps*) and unusual (*top left*, *Phalarodon fraasi*; *top right*, *Himalayasaurus tibetensis*) dentition in ichthyosaurs. Note that snout length varies remarkably within one genus.

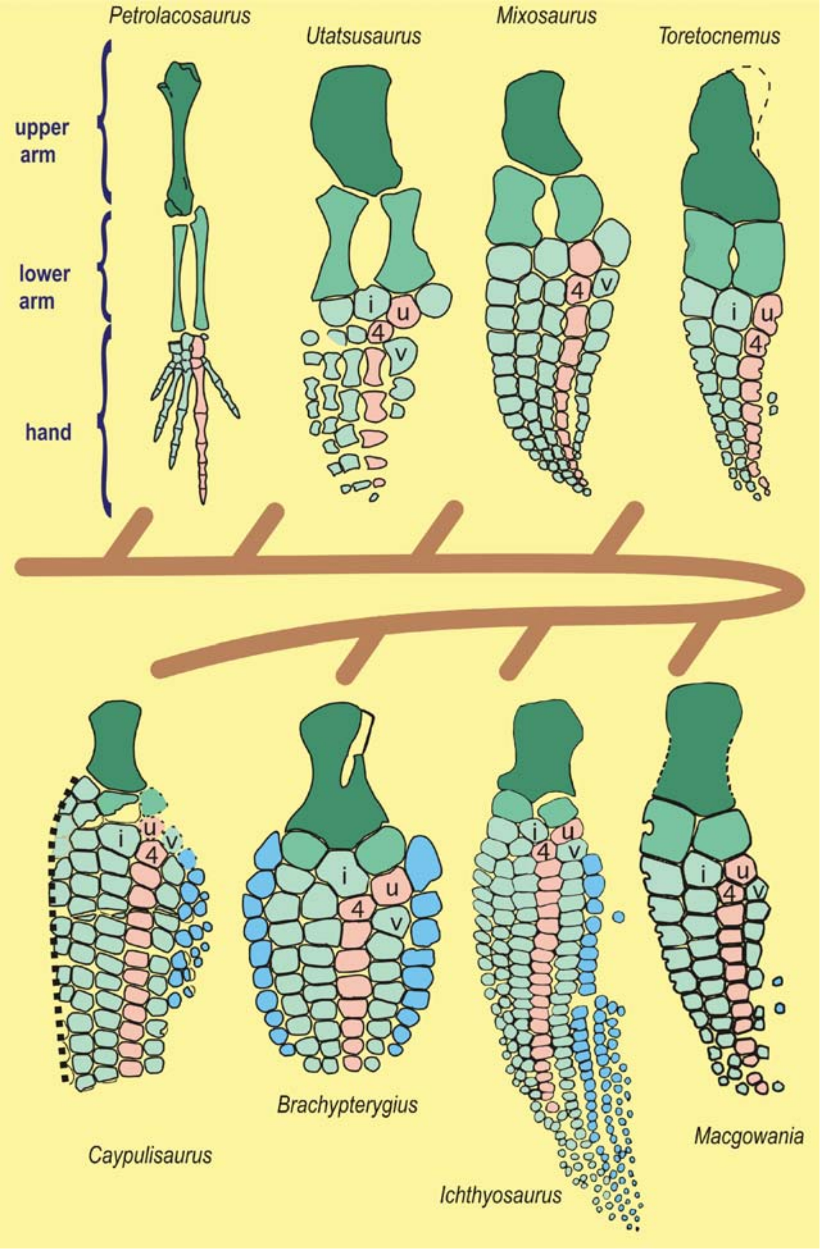

Figure 4 Evolution of forelimbs in ichthyosaurs along an abbreviated cladogram (deformed brown tree in the middle). Color coding: dark green, humerus; green, radius and ulna; pink, primary axis (fourth digit); light blue, extra digits; light green, other elements.

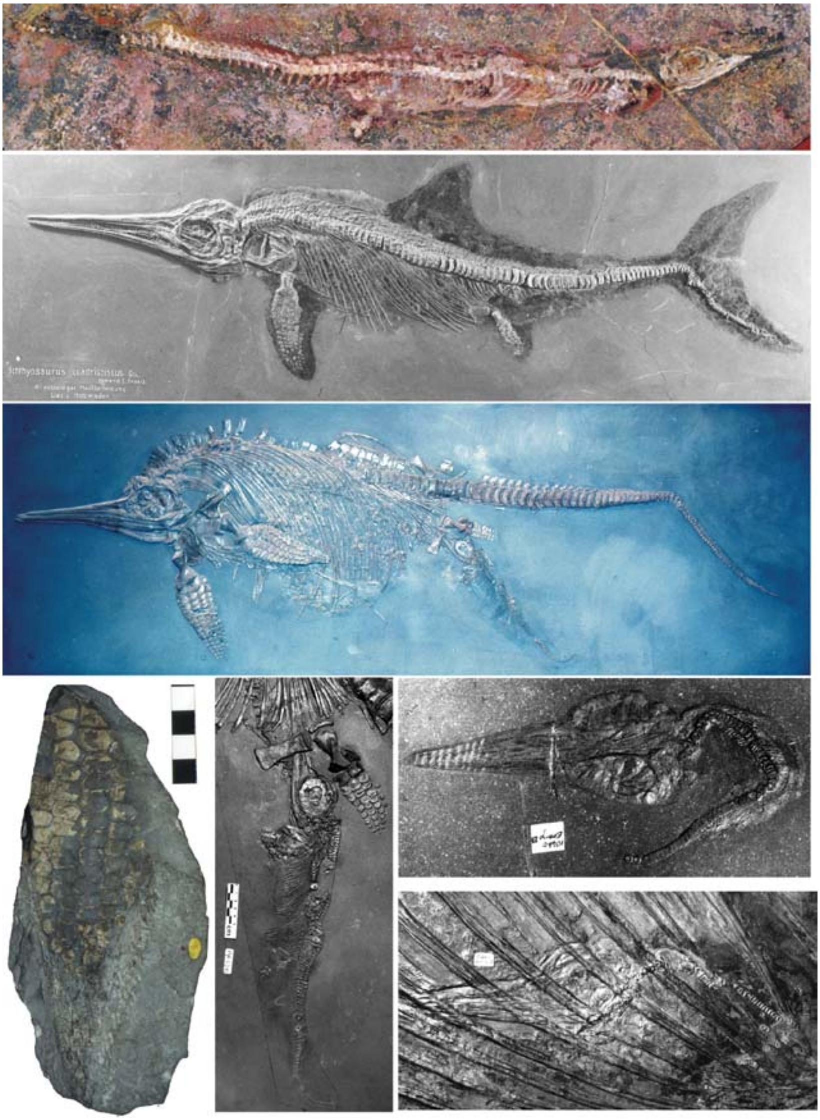

Figure 5 Body outline fossils and embryos. Top, the basal ichthyosaur *Chaohusaurus geishanensis* with yellowish outline of the dorsal lobe of the caudal fin; second from the top, the parvipelvian *Stenopterygius quadriscissus* with body outlines preserved; third from the top, *S. quadriscissus* with a baby; bottom left, forelimb fossil of Ichthyosaurus with outline impression from Barrow upon Soar; bottom middle, close-up of the *Stenopterygius* baby in the above photograph; bottom right, two curled embryos from a single individual of *S. quadriscissus*, one inside the rib cage and the other drifted out.

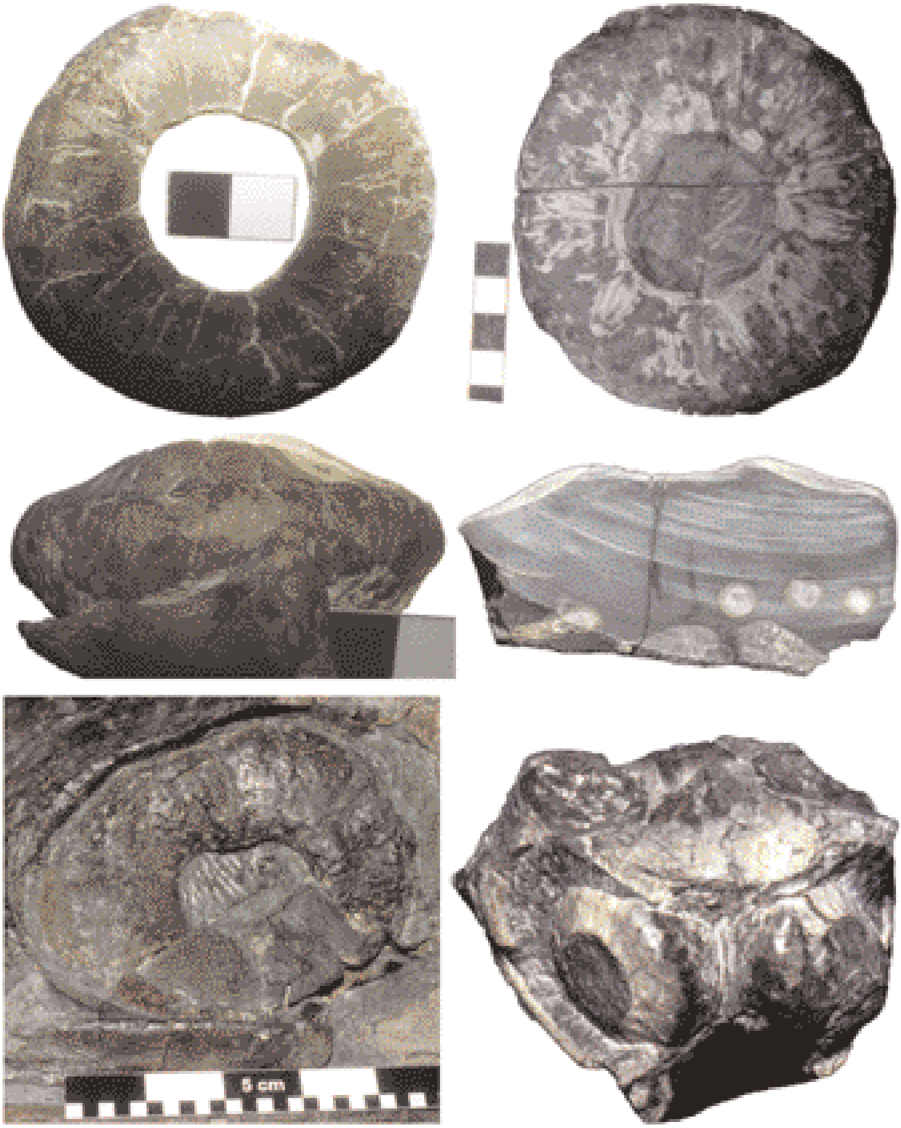

Figure 6 Scleral rings of some Jurassic ichthyosaurs. Top two, left: Two orthogonal views of the scleral ring of *Stenopterygius longifrons*. Top two, right: Scleral ring of an unidentified Liassic ichthyosaur from England (probably small *Temnodontosaurus*), with a cross-section to show the thinness of the ring bones. Bottom left: The largest eyeball to be measured so far, spanning 26.3 cm, belonging to *Temnodontosaurus platyodon*. Bottom right: Unidentified Liassic ichthyosaur missing the snout, showing the close packing of eyeballs.

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