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Author(s): Emily A. Buchholtz

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SWIMMING STYLES IN JURASSIC ICHTHYOSAURS

EMILY A. BUCHHOLTZ

Department of Biological Sciences, Wellesley College, Wellesley, Massachusetts 02481

ABSTRACT—Postcranial axial anatomy of six Jurassic ichthyosaurs is described and used to define a generalized pattern of regional anatomy with four structural units (neck, trunk, tail stock, fluke). Functional interpretation of each unit predicts a generalized swimming mode that used a laterally compressed, laterally oscillating caudal fluke as the propulsive organ. Fluke displacement was accomplished by the undulation of a dorsoventrally compressed posterior tail stock acting on a stabilized anterior tail stock. The trunk was largely uninvolved in locomotion. Osteological predictors of postcranial flexibility in living aquatic axial locomotors are reviewed and used to identify the existence of a range of swimming styles within this generalized pattern among surveyed ichthyosaurs.

INTRODUCTION

Ichthyosaurs were obligate marine reptiles of the Mesozoic Era, isolated from their reptilian contemporaries in both anatomy and lifestyle. The famous Lower Jurassic fossil beds of western England and Germany (Urlich et al., 1994), and the Middle to Upper Jurassic beds of central England (Martill, 1987; Martill et al., 1991) have provided numerous ichthyosaurs over the past two hundred years. The dominant data sets for most phylogenetic and functional analyses have come from cranial and/or fin anatomy (e.g., Appleby, 1979; McGowan, 1974a, b, 1979; Godefroit, 1993; Maisch, 1997, 1998a, b, c; Caldwell, 1996; Motani, 1999a, b). Postcranial axial anatomy is less well documented, but both bony and occasional soft tissue evidence suggest the presence of a deep body and a narrow-necked, high aspect ratio tail fluke in Jurassic species. Similar body shapes are typical of those bony fish, sharks, and whales that are capable of rapid and sustained swimming, and an extensive literature evaluates the possibility that ichthyosaurs shared this locomotor style (McGowan, 1973, 1992; Riess, 1986; Taylor, 1987; Massare, 1988; Massare and Faulkner, 1997; Klima, 1992; Motani, 1998; Motani et al., 1996; Lingham-Soliar and Reif, 1998). All of these animals must have faced similar challenges of propulsor displacement, drag minimization, recoil reduction, and trunk stabilization. Nevertheless, the postcranial anatomy of the secondarily aquatic reptilian ichthyosaurs differs significantly from those of the primarily aquatic bony fish and sharks, and from that of the mammalian whales, suggesting different routes to success in the marine environment.

This study examines the swimming styles of Jurassic ichthyosaurs by means of the analysis of comparative postcranial, and particularly vertebral, osteology. It is intended to supplement previous comparative analyses of stratigraphic distribution (e.g., McGowan, 1979; Godefroit, 1994), geographic distribution (e.g., McGowan, 1978; Godefroit, 1994; Maisch, 1998c), cranial and dental anatomy (e.g., Besmer, 1947; Massare, 1987; Maisch, 1998c; Motani, 1997), and body proportions (e.g., von Huene, 1926; McGowan, 1979; Massare, 1988, 1995, 1997; Motani et al., 1996) that have all contributed to an understanding of the ecological partitioning that allowed ichthyosaurs to radiate so widely and successfully in Jurassic seas.

Propulsive mechanisms in swimming vertebrates are classically defined as either undulatory or oscillatory (Webb and Blake, 1985). In undulatory movement, repeated waves pass along a mobile propulsor, which in axial swimmers is the body axis supported by the vertebral column. All or parts of the body axis may be variably stabilized or stiffened, with the result that

undulatory wavelength increases and wave amplitude decreases. Anguilliform swimmers with long, flexible bodies and short undulatory wavelengths exist at one end of a continuum of axial swimming styles. Subcarangiaform and carangiaform swimmers are intermediate, with deeper bodies and longer wavelengths. Thunniform swimmers such as tunas with short, high flukes that oscillate on nearly rigid bodies represent the other end of the continuum. Variations in body stiffness are inevitably the result of the combined actions of soft tissues (muscle, skin, and connective tissue, including intervertebral disks) and the skeleton (Long et al., 1994). Of these, skeletal evidence provides the most complete and dependable record for analysis of swimming style in extinct species. Regional variation in vertebral morphology is correlated with style and flexibility of axial movement in living vertebrates (Slijper, 1936, 1948; Worthington and Wake, 1972; Buchholtz, 1998a), and is the primary source of data in this study.

MATERIALS AND METHODS

Six Jurassic ichthyosaurs (*Suevoleviathan disinteger*, *Temnodontosaurus trigonodon*, *Eurhinosaurus longirostris*, *Ichthyosaurus communis*, *Stenopterygius quadricissus*, and *Ophthalmosaurus icenicus*) were chosen for analysis. These species were chosen because they share both close phylogenetic relationship (recognized by Motani (1999b) as members of the Parvipelvina) and close chronological relationship. Additionally, at least one specimen that was complete or nearly complete, adult or nearly adult, and minimally deformed was available for each species. Nevertheless, it is not only possible but likely that some of the data presented below contain errors introduced by differences in completeness, ontogeny, and/or deformation, as is true in almost all paleontological studies. A total of 52 specimens were measured, but only the most complete individuals are formally presented below.

The specimens occur in two dominant preservation modes. Specimens from the Lower Jurassic beds of southern England and southern Germany are typically compressed laterally, and are found in nearly full articulation and original vertebral sequence with spectacular preservation of detail. Lateral compression often deforms the vertebrae, and lateral “slab mount” presentation typically allows only height or width, but usually not both, to be measured for a given vertebra. Bones that are not fused to the column, including limbs, limb girdles, gastralia, and neural spines, are often found in or near life position. Soft tissue body outlines are occasionally present. These specimens have in some cases been modified by preparators for presentation purposes. In contrast, specimens from the Middle and

Upper Jurassic of England are three-dimensional, and often almost undeformed. Nevertheless, the columns are much less likely to be complete. Associated elements are rarely in life position, and were often dispersed before preservation. These two preservation modes provide complementary information. Column counts and unit length data are most complete on the slab mounts; vertebral dimensions are most complete on the 3-dimensional specimens.

Vertebral measurements were made with digital calipers. Centrum heights and widths were measured anteriorly, centrum lengths both dorsally and ventrally when possible. Centrum widths are maximal widths, but do not include diapophyses. Centrum height was used to standardize vertebral measurements (centrum length, centrum width, neural spine height). The lengths of column units were calculated by summing averaged centrum length measurements of individual vertebrae. Tail stock and fluke lengths were standardized to precaudal length, which was also calculated by summing averaged centrum length measurements. Rib measurements were curvilinear.

Institutional Abbreviations—**BMNH**, Natural History Museum, London; **BRSMG**, Bristol Museum and Art Gallery; **FSF**, Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt; **GPIT**, Institut und Museum für Geologie und Palaeontologie der Universität Tübingen; **PMAG**, Peterborough Museum and Art Gallery; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart. The cetacean specimen was measured at the National Museum of Natural History (**USNM**).

COMPARATIVE VERTEBRAL COLUMN ANATOMY

In the descriptions below, each vertebral column is divided into four major structural units: neck, trunk, tail stock, and fluke, that can be differentiated on the basis of centrum dimensions. The tail stock is further subdivided into anterior and posterior subunits. Rationale for these divisions and functional interpretation of each unit are deferred until the discussion section. Specimen dimensions are summarized in Table I.

Suevoleiathan disinteger

Suevoleiathan disinteger was defined by Maisch (1998a) to contain the specimen SMNS 15390 (Fig. 1A), previously described as *Leptopterygius disinteger* by von Huene (1926) and by McGowan (1979). This single documented specimen of the species is fortunately very well preserved and almost completely intact in a slab mount. It is unlikely that the tail has been altered in preparation.

SMNS 15390 is a long (≈ 4 m), thin animal; the relatively short, curved ribs (greatest rib length = 0.44 precaudal length) accentuate its elongate appearance. Maisch (1998a) described the skull as low, with a medium-sized orbit and a weakly concave dorsal profile. It lacks both gastralia and an interclavicle. Ischium and pubis are not fused. The pectoral fin is large and broadly spatulate (length = 0.51 precaudal length). The pelvic fin is shorter and narrower (length = 0.39 precaudal length). The fluke is very long ($=0.73$ precaudal length) and the presence of a mid-fluke vertebral "loop" suggests that it was flexible in life.

The vertebral column is composed of 44 precaudal, 45 tail stock, and 98 fluke vertebrae, for a total count of 187 and a total length of 3,011 mm. Atlas and axis are separate. The first 86 vertebrae apparently bore ribs, although articulation facets for ribs are unclear anteriorly. Only the first 16 ribs were bicapital; dorsal and ventral articulation facets are confluent or fused after this point. Centrum edges in the trunk and fluke are crisp, while those of the tail stock are uniformly but minimally rounded.

Centrum length increases gradually to a maximum at the sacral vertebra, is nearly uniform in the anterior tail stock, and

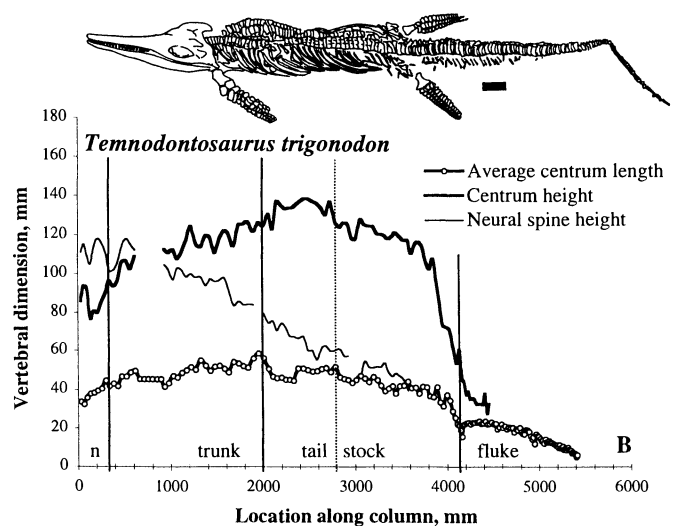
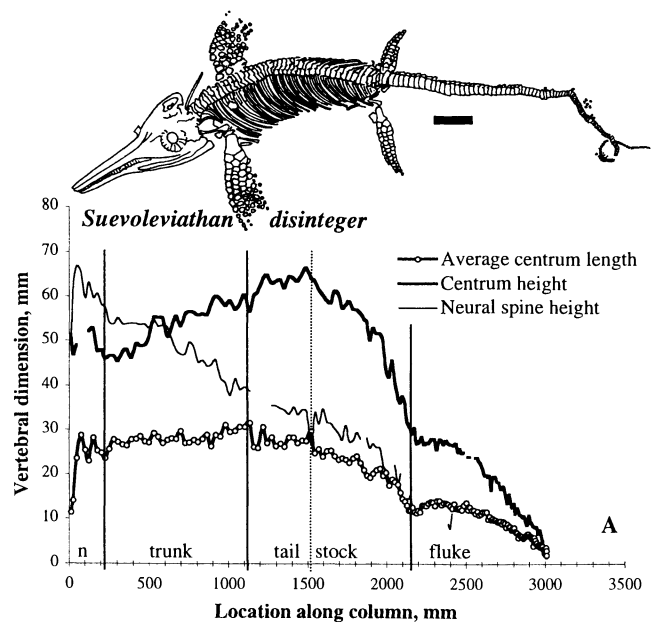


FIGURE 1. Centrum dimensions of (A) *Suevoleiathan disinteger* (SMNS 15390) and (B) *Temnodontosaurus trigonodon* (SMNS 15950). Centrum height measurements of SMNS 15950 posterior to vertebra 87 were made from a photographic image. Skeletal outlines were traced and reduced from photographs originally published in Urlichs et al. (1994:51; A) and Hauff (1953: B). The image of *S. disinteger* was reversed for consistency of presentation. Skeletons differ in size, as indicated by dimensions on axes and scale bars, which are 25 cm in length. **Abbreviation n**, neck.

then decreases throughout the posterior tail stock to the fluke base. Centrum height increases from the neck to the midstock boundary, which occurs less than half of the distance along the tail stock. Its decrease through the posterior tail stock is more rapid than that of centrum length, with the result that relative centrum length increases.

Neural spine height is short relative to other vertebral dimensions: its maximum of 1.36 times centrum height occurs in the neck. Relative neural spine height decreases below 1.0 before mid trunk and remains below 0.6 throughout the tail stock and fluke. Shape transitions occur at column locations anterior to those of other species, as noted by Maisch (1998a): anterior trunk neural spines are rectangular, posterior trunk spines are square, and anterior tail stock spines are obliquely polygonal.

Temnodontosaurus trigonodon

Temnodontosaurus is a genus of very large ichthyosaurs whose length may have reached 11 meters (von Huene, 1922). Among cranial traits of the genus McGowan (1996) listed small orbits, teeth of moderate size, and a relatively long maxilla. Three species are typically recognized, of which *T. eurycephalus* is known only from a skull and *T. platyodon* from mostly incomplete or inaccessible skeletons (McGowan, 1996). The third species has traditionally been identified as *T. burgundiae*, but Maisch (1998c) identified this name as a junior synonym of *T. trigonodon*, which he now accepts for all temnodontosaurids from southwestern Germany.

Of the specimens available for study, SMNS 15950 (Fig. 1B) most clearly exhibits vertebral anatomy, despite some disruption of the trunk vertebral sequence. It is a slab mount; the tail may have been modified during preparation. Like *Suevoleviathan disinteger*, SMNS 15950 has relatively short ribs (greatest rib length = 0.39 precaudal length), and lacks preserved gastralia. Pelvic elements are separate, although McGowan (1996) mentions in his emended diagnosis of the species that partial fusion between ischium and pubis may sometimes occur. The pectoral fin is robust and long (0.47 precaudal length). The pelvic fin is markedly shorter (=0.36 precaudal length). The fluke as mounted is relatively shorter than that of *Suevoleviathan disinteger* (0.61 precaudal length) but relatively longer than those of the other species surveyed.

The vertebral column of SMNS 15950 is composed of 44 precaudal, 51 tail stock, and 84 fluke vertebrae, for a total count of 179 and a column length of 5,414 mm. These numbers differ modestly from those reported by McGowan (1996) for the same specimen. Atlas and axis appear to be separate, although McGowan (pers. comm.) reports fusion in at least one very large specimen. Rib articulations indicate the presence of bicapital ribs on vertebrae 1–45, unicipital ribs on vertebrae 46–93, and no ribs from vertebra 94 to the fluke tip. Centrum edges are modestly, but noticeably, rounded in vertebrae immediately adjacent to the fluke base.

As in *Suevoleviathan disinteger*, centrum length increases gradually throughout the torso, is relatively stable in the anterior tail stock, and then decreases again in the posterior tail stock. It drops abruptly just anterior to the fluke base. Dorsal centrum length exceeds ventral centrum length in the vertebrae immediately anterior and posterior to the fluke. Centrum height peaks and plateaus in the anterior tail stock; its decrease in the posterior tail stock is at first gradual, but then accelerates anterior to the fluke base. Relative centrum lengths of the trunk (average = 0.44) and of the tail stock (average = 0.37) are shorter than those of *Suevoleviathan disinteger*, producing more discoidal vertebrae.

Neural spines decrease rapidly in height from their anterior trunk maximum (=1.47 centrum height), and remain below 0.6 centrum height in the tail stock. Neural spine shape follows the same progression as in *Suevoleviathan disinteger*, but transitions occur at more posterior points in the column. Rectangular shape is retained until the posterior trunk, and square shape until the anterior tail stock. Polygonal shape is replaced by rod shape in the posterior tail stock.

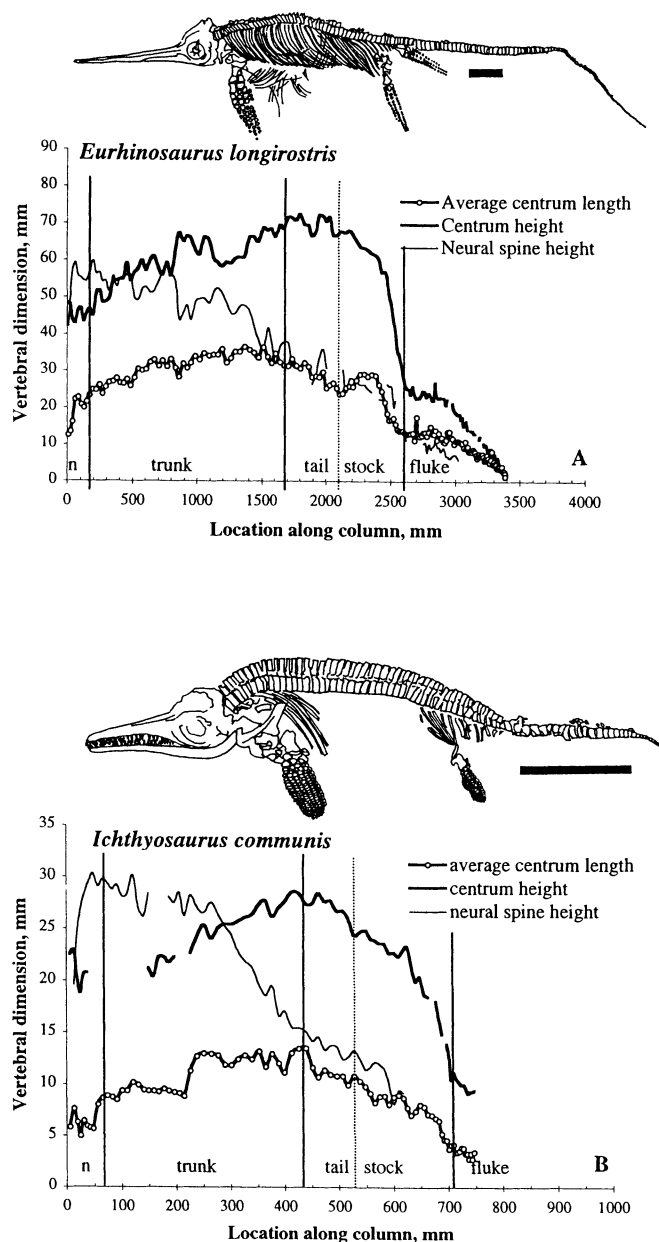


FIGURE 2. Centrum dimensions of (A) *Eurhinosaurus longirostris* (GPIT 1025/18/1) and (B) *Ichthyosaurus communis* (BRSMG Cb3578). Skeletal outlines were traced and reduced from photographs originally published in Hungerbühler et al. (1989:15; A) and McGowan (1974b: 7; B). Skeletons differ in size, as indicated by dimensions on axes and scale bars, which are 25 cm in length. **Abbreviation n**, neck.

Eurhinosaurus longirostris

Eurhinosaurus is a large-bodied, small-toothed, slender ichthyosaur most easily recognized by the elongate upper jaw that greatly exceeds the lower in length (Fig. 2A). Despite some frequency in the fossil record, complete skeletons of the species are rare (Maisch, 1998a). The fluke of SMNS 14931 differs so radically from others in vertebral count that it raises questions of authenticity. The small London and very large Senckenberg Museum specimens are on exhibit, and could be studied only through glass. The mid-size University of Tübingen specimen (GPIT 1025/18/1) described by von Huene in 1951 is used for this study. It seems likely that the orientation of the fluke has

been altered during preparation of most if not all of these specimens, as discussed by Riess (1986).

The vertebral column of GPIT 1025/18/1 is composed of 49 precaudal, 45 tail stock, and 96 fluke vertebrae, for a total count of 190 and a postcranial length of 3,386 mm. These numbers differ very slightly from those of von Huene (1951), primarily in the location of the contact between tail stock and fluke. Atlas and axis abut closely, but are not clearly fused. The transition from bicapital to unicapital ribs occurs between vertebrae 41 and 42; no rib articulations are present on fluke vertebrae. Centrum edges are modestly but noticeably rounded in vertebrae at and immediately posterior to the fluke base. The slenderness of the specimen is accentuated by the short ribs (longest rib = 0.40 precaudal length). Gastralria are present in the anterior trunk. The pectoral fin is long and narrow (=0.44 precaudal length); the pelvic fin is nearly equal to the pectoral in length (=0.41 precaudal length); ischium and pubis are separate. The fluke is relatively shorter than that of *Suevoleviathan disinteger* or *Temnodontosaurus trigonodon* at 0.56 precaudal length.

Centrum length increases throughout the precaudal column, peaking just anterior to the sacral vertebra. Its decrease in the rest of the column is interrupted by a prominent increase in the caudal tail stock. Despite some irregularity, centrum height increases gradually to peak and plateau in the anterior tail stock. A gradual and then precipitous decline in height occurs in the posterior tail stock, clearly distinguishing tail stock subunits. Precaudal centra are relatively quite long (average relative centrum length = 0.51), and become gradually more discoidal throughout the tail stock (minimum = 0.33). A local peak in relative centrum length (=0.47) occurs just before the fluke base.

Neural spine height falls rapidly from its maximum of 1.38 centrum height in the neck to less than centrum height in the anterior trunk, and remains below 0.6 centrum height in the tail stock. The rectangular neural spines of the anterior trunk become rounded squares in the posterior trunk. Posterior inclination increases gradually. Shape becomes polygonal in the anterior tail stock and rod-shaped in the posterior tail stock. Neural spines of fluke vertebrae are very short and again almost erect.

Ichthyosaurus communis

McGowan (1974b) revised the "latipinnate" ichthyosaurs of the Lower Jurassic of England, consolidating 60 specimens into four species. Of these four, *Ichthyosaurus communis* is the most common. McGowan described it as a medium-sized ichthyosaur with a maximum size of about 2.5 meters. Two beautifully preserved, but incomplete, specimens were chosen for this study. BRSMG Cb3578 (Fig. 2B) is a rather small animal with a vertebral column that terminates in the mid fluke. BM(NH) 14563 is a larger individual; its skeleton is present from the posterior trunk to all but the very tip of the tail. Both specimens are slab mounts.

By "overlapping" the two specimens, it can be estimated that this species possessed 43 precaudal, 33–37 tail stock, and more than 41 fluke vertebrae, for a total count of 117–121, plus the missing terminal caudals. This is in close agreement with McGowan's (1974b) tallies of 44 trunk, 33 tail stock, and 58 fluke vertebrae. It was not possible to calculate the total postcranial length of either animal. Atlas and axis of BRSMG Cb3578, a subadult animal, are separate. In both animals, the transition from bicapital to unicapital ribs occurs posterior to the sacral vertebra, although it occurs later in the larger (estimated vertebra # 50) than in the smaller (vertebra # 46) specimen. Relative rib, forelimb, and hind limbs lengths are estimated from published images (McGowan, 1974b:fig. 2C, D) at 0.43,

0.41, and 0.21 precaudal length. Gastralria are present in the anterior trunk.

Centrum length increases gradually to a maximum near the sacral vertebra, and then decreases to the fluke base. In BMNH 14563 there is a slight increase in centrum length in the posterior tail stock. Centra in the immediate fluke base area are slightly wedge-shaped. A zone of six to ten centra with moderately rounded edges exists around the fluke. As in other species, centrum height increases throughout the trunk to peak in the anterior tail stock. Centrum height decreases steadily from its peak without a plateau, with the result that tail stock vertebrae (minimum relative length = 0.35) are only slightly more discoidal than trunk vertebrae.

Neural spine height peaks in the neck (=1.42 centrum height) and remains very high throughout all precaudal vertebrae (average = 0.99 centrum height). It falls rapidly in the tail stock. Transition in neural spine shape and orientation is similarly very rapid. Rectangular spines that stand erect occur throughout the trunk and into the anterior tail stock. A rapid transition to posteriorly pointing polygonal and rod-shaped spines follows.

Stenopterygius quadricissus

Stenopterygius is a small to medium-sized genus, well represented in the European Jurassic by numerous individuals of multiple species. McGowan (1979) identified seven species, while more recently Godefroit (1993, 1994) recognized three and Maisch (1998c) four. A Senckenberg Museum specimen, FSF R4154, a slab mount of the well-known species *S. quadricissus*, is used as the primary specimen here (Fig. 3A). Although the anterior trunk of this specimen is significantly disrupted, the column posterior to this point is beautifully preserved, and includes the extreme tail tip. SMNS 50963 is used to supplement missing data.

FSF R4154 has 47 precaudal, 34 tail stock, and 74 fluke vertebrae, for a total count of 155 and a column length of 1,764 mm. Atlas and axis are fused, although in this specimen the line of fusion between them is clear. Unicapital ribs replace bicapital ribs at vertebra 47, and vertebra 80 is the last with a rib facet. The longest rib is 545 mm in length (=0.62 precaudal length), making this animal very deep-bodied. Gastralria are present in the anterior and mid trunk. The forelimb is 350 mm in length, or 0.41 precaudal length. The hind limb at 190 mm is markedly shorter, only 0.22 precaudal length. Ischium and pubis are fused.

Centrum length increases gradually to a peak in the posterior trunk, decreases rapidly and then stabilizes in the anterior tail stock, and then decreases again in the posterior tail stock. It is relatively uniform in the fluke. Vertebrae of the posterior tail stock and anterior fluke have rounded edges, and ventral centrum length is markedly less than dorsal centrum length in the vertebrae immediately surrounding the fluke base. Maximum centrum height occurs in the posterior trunk, plateaus throughout the anterior tail stock, and drops abruptly in the posterior tail stock. Trunk vertebrae are very discoidal (average relative centrum length = 0.42), and tail stock vertebrae still more so (minimum relative centrum length = 0.29).

Because the precaudal neural spines of FSF R4154 are severely disrupted, relative height measurements were taken from SMNS 50963, where they reach 1.71 centrum height. Precaudal neural spines are rectangular in shape, abut each other along almost their entire height, and have robust zygapophyses. Neural spines of the posterior trunk grade into square shapes, and those of the anterior tail stock grade into polygonal shapes. Posterior tail stock spines are short, rod-shaped, and steeply inclined posteriorly.

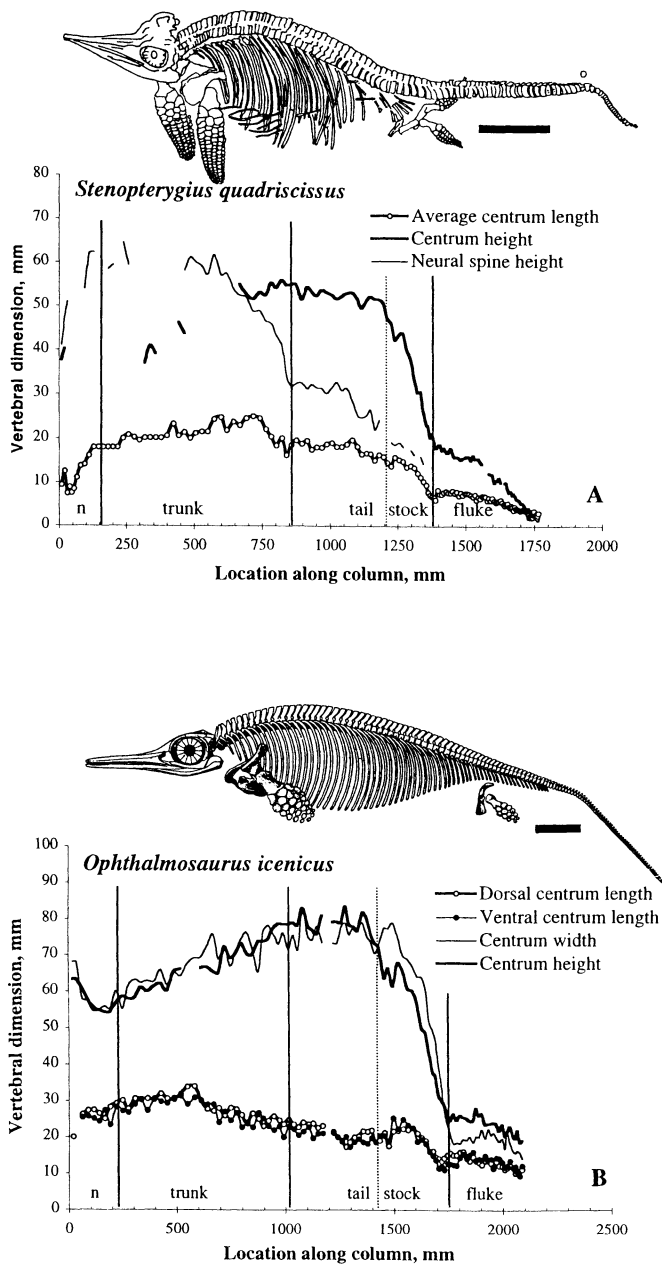


FIGURE 3. Centrum dimensions of (A) *Stenopterygius quadriscissus* (FSF R4154) and (B) *Ophthalmosaurus icenicus* (PMAG R340). Skeletal outline of *S. quadriscissus* was traced and reduced from a photograph originally published in Urlichs et al. (1994:76) and reversed for consistency of presentation. Skeletal outline of *O. icenicus* was taken directly from Andrews (1920: text-fig. 42). Skeletons differ in size, as indicated by dimensions on axes and scale bars, which are 25 cm in length. **Abbreviation n**, neck.

Ophthalmosaurus icenicus

Ophthalmosaurus was a mid-sized, large-eyed and small-toothed ichthyosaur (Fig. 3B). Numerous examples of 3-dimensionally preserved partial specimens of *O. icenicus* have been collected over the past one hundred years from the Oxford Clay of England. The mode of preservation makes these specimens invaluable for the documentation of centrum dimensions, but introduces complications. Identification of the sacral vertebra is difficult because ribs and pelvic bones are rarely preserved in-

tact or in situ, and both neural spines and caudal tail vertebrae are often dispersed or absent. The measurements of a large and nearly complete but undescribed specimen collected by and housed in the Peterborough Museum and Art Gallery, PMAG R340, are used here.

PMAG R340 has 101 vertebrae that run without gaps from the atlas to the mid fluke. The estimated precaudal count of 39 is based on variations in neural canal width that help to locate the hind limb in other specimens of the species (Buchholtz, unpublished data), but is much less confidently known than for other species surveyed. There are 34 tail stock vertebrae and 28 preserved fluke vertebrae, although the original fluke count was certainly somewhat greater. Atlas and axis are fused. The transition from bicipital to unicipital ribs occurs after vertebra 43, although individuals are known in which the transition occurs after vertebra 37 (Andrews, 1910) and after vertebra 27 (Appleby, 1956). The longest preserved rib is 0.79 precaudal length, indicating that the animal had a very deep body. Gastralia are not known from this or other specimens of the species. The pectoral fin is estimated to have been 0.41 and the pelvic fin 0.20 precaudal length based on the partially reconstructed appendages. Pubis and ischium are fused. Relative fluke size was estimated from the published reconstruction of Andrews (1910), based on a composite specimen, at 0.56 precaudal length.

Three-dimensional preservation allows centrum dimensions to the mid fluke be almost completely reconstructed. Centrum length peaks in the mid trunk, far more anteriorly than in other surveyed species. As a result, posterior trunk vertebrae are highly discoidal (relative centrum length ≈ 0.35) and closely resemble those of the anterior tail stock. Centrum width and height reach maximal values at the sacral vertebra, and plateau at these levels throughout the anterior tail stock. The transition from anterior to posterior tail stock is particularly clear, as centrum height drops below centrum width, producing the characteristic dorsoventrally compressed vertebrae. The transition to laterally compressed vertebrae at the fluke base is also abrupt. A series of ten vertebrae (#71–80) around the fluke base are wedge-shaped, with greater dorsal than ventral centrum lengths. Centrum edges in this zone are also markedly rounded.

Neural spines are not preserved in this specimen, or in most specimens available for study. They are largely reconstructed in most mounted specimens. Some of the vertebrae of FSF R461, a previously mounted skeleton, have original neural spines. Their relative height exceeds 1.0 as far back as the mid tail stock, a more extreme pattern than for any other species in this study.

DISCUSSION

A general plan of vertebral column anatomy in Jurassic ichthyosaurs is presented below, followed by a discussion of the variations on this generalized plan presented by each of the six species of the study. Finally, possible variations in lifestyle and phylogenetic considerations are discussed.

Generalized Vertebral Column Anatomy and Function

Discontinuities in vertebral anatomy allow subdivision of the Jurassic ichthyosaurian vertebral column into neck, trunk, tail stock, and fluke units. Standardized dimensions for the ichthyosaur *Ophthalmosaurus icenicus* and the living common dolphin *Delphinus delphis* are presented (Fig. 4A, B) to demonstrate the characteristic dimensional patterns for each unit. *Ophthalmosaurus icenicus* was chosen for this presentation because its method of preservation ensured the most complete and least deformed data set. It is also interpreted as the most derived of the ichthyosaurs surveyed, and therefore differs from the

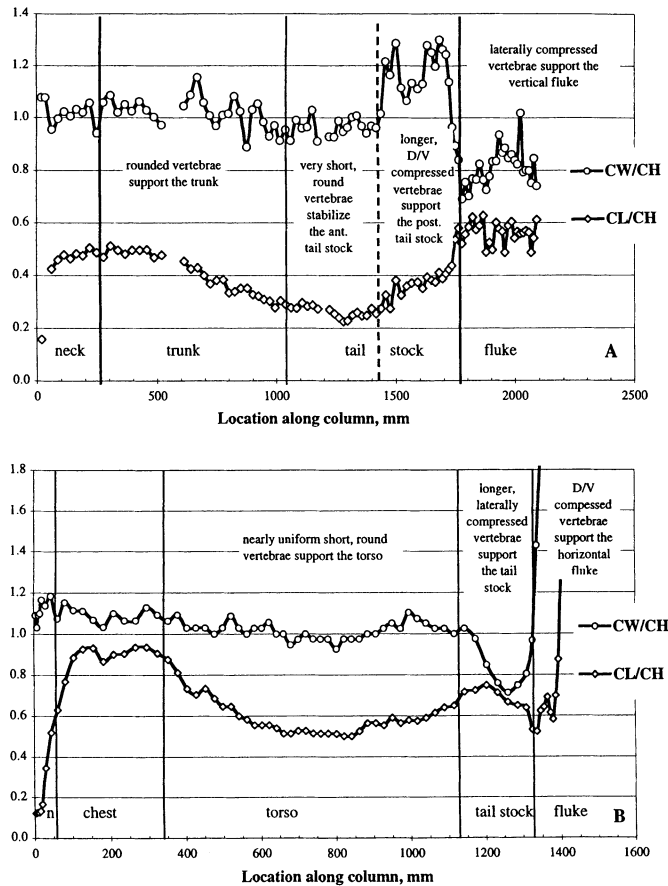


FIGURE 4. Relative centrum width and length in (A) the ichthyosaur *Ophthalmosaurus icenicus* (PMAG R340) and (B) the common dolphin *Delphinus delphis* (USNM 550868). Most of the body is supported and stabilized by foreshortened vertebrae with round cross sections in both species. Tail stock vertebrae are relatively lengthened. Vertebrae of the ichthyosaurian tail stock, which acts as a lateral cutwater, are dorsoventrally compressed; vertebrae of the fluke are laterally compressed. Vertebrae of the dolphin tail stock, which acts as a dorsoventral cutwater, are laterally compressed; vertebrae of the fluke are dorsoventrally compressed.

generalized pattern in several key characters, discussed below. Functional implications of each structural unit are suggested.

Neck—The neck extends from the atlas to the trunk. Although atlas and axis are clearly identifiable, subsequent vertebrae grade into trunk vertebrae in both shape and dimensions. As described by many authors (see e.g., Gilmore, 1905), anterior neck vertebrae are often broader than high, and presence of a ventral keel results in a shape classically defined as shield-like or cordiform. Rib facets are located high on the lateral surface, and diapophyseal facets are often but variably confluent with the base of the neural arch. Here the posterior end of the neck is called the neck base, and is somewhat arbitrarily defined at the beginning of the rapid increase in centrum width and height that identifies the trunk. This allocates somewhere between 9 and 13 vertebrae to the neck in the study specimens.

Neck vertebrae act to support and enable rotation of the head. Head stabilization and hydrodynamic shape are enhanced by relatively short cervical vertebrae in living posteriorly propelled secondary swimmers such as phocid seals, sirenians, and cetaceans (Fig. 4B). This reduction is most marked in species with rapid, cruising swimming styles (Buchholtz, in press). Neck vertebrae of Jurassic ichthyosaurs (Fig. 4A) are relatively short-

er than those of the remaining precaudal column, although only very modestly so. In this respect they differ markedly from these living analogs.

Trunk—The trunk runs from the neck base to (and including) the sacral vertebra. Despite the lack of an articulated pelvis, the identity of the sacral vertebra can be estimated in ichthyosaurs by the approximate location of the pelvic bones on slab mounts and/or by the abrupt shortening of the ribs that results in an “outline” of the body cavity. Precaudal (neck + trunk) count is relatively stable in Jurassic ichthyosaurs; almost all count variability is caudal. The stability in construction makes precaudal count and length useful standards for comparison of different species. Trunk vertebrae are nearly round (centrum width \approx centrum height). Their posteriorly increasing width, height and length are nearly proportional, so that trunk vertebrae are of remarkably similar shape. A plateau in centrum width and height identifies the beginning of the tail stock. Although the end of bicipital ribs, transition in neural spine shape, and peak in centrum length are also often typical of this location, these markers are moveable relative to the end of the trunk and are signals of functional differences among species.

The trunk has ancestral functions in the support and protection of the viscera and in support and movement of the limbs during locomotion. In the aquatic ichthyosaurs, as in living crocodylians (Manter, 1940), the tail was the major site of generation of propulsive force. The trunk presumably provided attachment sites for tail musculature. It will be argued below that the posterior trunk was stabilized to prevent undulation in more rigid species, or incorporated into the undulatory portion of the tail in more flexible species.

Tail Stock—The tail stock extends from the sacral vertebra to the fluke base. Two distinct (anterior and posterior) subunits are clearly recognizable in more rigid species, but are more subtly differentiated in more flexible species. The largest (highest and broadest) column centra are found in the anterior tail stock. They are also nearly round in cross section, suggesting that they supported a rounded body, and were not specialized for either lateral or vertical movement. Centrum length is typically reduced across the trunk-tail stock boundary, with the result that these are the most discoidal vertebrae in the column. In the posterior tail stock, centrum height decreases dramatically while centrum width decreases more modestly, producing dorsoventrally compressed vertebrae (Fig. 4A). They are of greater relative length than the vertebrae anterior to them. Shortly before the fluke base, centrum edges become progressively rounded. Such rounding increases the range of movement possible between adjacent centra, and indicates the site of greatest column flexion.

The function of the tail stock is key to the interpretation of swimming in ichthyosaurs. The large, round, discoidal vertebrae of the anterior unit are specialized for support by their size and for stiffness by their shape. The reduction in centrum length that typically occurs across the trunk-tail stock boundary occurs more anteriorly in those highly regionalized species, such as *Ophthalmosaurus icenicus*, in which the posterior trunk is also stabilized. The smaller, dorsoventrally compressed, and more elongate vertebrae of the posterior unit of the tail stock indicate the presence of a dorsoventrally compressed cutwater that displaced the fluke laterally, increasing its stride length. This was the undulatory unit. Its length and markers of relative stiffness vary considerable among the species considered.

Patterns of centrum shape in the laterally oscillating ichthyosaurs can be compared with those of the dorsoventrally oscillating cetaceans (Fig. 4A, B). Derived members of both groups stabilize the trunk with discoidal vertebrae of short relative centrum length, and enhance flexibility in the tail stock with more elongate vertebrae. Their relative centrum length curves are quite similar. In contrast, dimensions of the vertebrae of the tail

TABLE 1. Summary of postcranial dimensions in six Jurassic ichthyosaurs. Relative lengths of body units, ribs, and limbs are standardized to precaudal length; relative lengths of vertebral dimensions are standardized to centrum height. \diamond = measured on SMNS 50963; * = estimated from McGowan (1974), \ddagger = estimated from Andrews (1910).

Trait	Species					
	<i>Suevoleiathan disinteger</i> SMNS 15390	<i>Temnodontosaurus trigonodon</i> SMNA 15950	<i>Eurhinosaurus longirostris</i> GPIT 1025/18/1	<i>Ichthyosaurus communis</i> BRSMG Cb3578	<i>Stenopterygius quadriscissus</i> FSF R4154	<i>Ophthalmosaurus icenicus</i> PMAG R340
Column length, mm	3,011	5,414	3,368	—	1,764	2,090+
Precaudal length, mm	1,160	2,062	1,404	426	876	1,040
Relative length of tail stock	0.87	1.02	0.85	0.60	0.58	0.65
Relative length of fluke	0.73	0.61	0.56	0.38*	0.44	0.35 \ddagger
Relative length of longest rib	0.44	0.39	0.40	0.43*	0.62	0.79
Relative length of longest neural spine	1.36	1.47	1.38	1.42	1.71 \diamond	—
Least relative centrum length	0.36	0.31	0.33	0.35	0.29	0.23
Relative length of forelimb	0.51	0.47	0.44	0.41*	0.41	0.41
Relative length of hind limb	0.39	0.36	0.41	0.21*	0.22	0.20

stock, which acts as a cutwater, are reversed. They are dorsoventrally compressed in ichthyosaurs and laterally compressed in cetaceans.

Fluke—The fluke extends from the fluke base to the tail tip. The anterior limit is recognized by the dimensional reversal in centrum shape from the vertical compression of the tail stock to the lateral compression of the fluke. There is also a distinct plateau of centrum width, height, and length in the anterior fluke, all of which again decrease gradually after mid-fluke. A variable zone of wedge-shaped vertebrae (dorsal centrum length greater than ventral centrum length) on either side of the fluke base indicates a ventral tail bend, and has been described by several authors (Seeley, 1908; McGowan 1989). In some species there is also a slight trend in the opposite direction in the anterior tail, suggesting that the column recurved slightly upward within the ventral lobe of the fluke.

The fluke is interpreted as the propulsive surface of the animal. Its laterally compressed vertebrae supported the laterally compressed fluke surface. Again, this pattern is the reverse of that seen in whales, where dorsoventrally compressed fluke vertebrae support the dorsoventrally compressed fluke.

Relative length of the fluke varies among the species studied, and is standardized to precaudal length in the analysis below (total length of fluke vertebrae/total length of precaudal vertebrae). In living vertebrates aspect ratios of tails are calculated as S^2/A , where S = fluke span and A = planform area (Fish, 1998). Span/length is used as an approximation when area is unavailable. Unfortunately, span is also unavailable or highly suspect for most ichthyosaurian specimens. As a general rule of thumb, however, an increase in relative fluke length will indicate a decrease in fluke aspect ratio. High aspect ratio hydrofoils are characteristic of fast swimmers (Fish, 1998).

Summary of Inferred Swimming Style—Structural discontinuities between units of the column strongly suggest functional differences during locomotion. It is proposed here that Jurassic ichthyosaurs were axial swimmers that used a laterally oscillating, laterally compressed caudal fluke as the propulsor. Fluke displacement was accomplished by undulation of the dorsoventrally compressed posterior tail stock, which increased stride length of the propulsor. The anterior tail stock acted as a reinforced, stable base on which this undulation occurred. The trunk was largely uninvolved in locomotion; forelimbs and to a lesser extent hind limbs were used as rudders in steering.

Variations on the Generalized Plan

Despite remarkable similarity in body plan, Jurassic ichthyosaurs present variations on the general pattern of postcranial axial anatomy presented above. Many of these variations are

associated with different types of axial movement and swimming style in living vertebrates. Each character is discussed separately below, although of course all traits of a given species interacted to produce a unique suite of adaptations in the living animal. A discussion of implications for variations in life style among the ichthyosaurian species follows.

Body Shape—A continuum of body shapes and related swimming styles in fish has been recognized for many years (Breder, 1926; Nursall, 1958; Lindsey, 1978). Long, slender fish are often described as anguilliform or eel-like. They typically have flexible bodies and swim with body undulations of wavelength shorter than body length at relatively low speeds. In contrast, short, deep-bodied animals are termed thunniform, or tuna-like. They have stiff bodies, swim with body wavelengths longer than body length, and are capable of sustained cruising. Increase in wave frequency is associated with an increase in swimming velocity in all groups. Differences in body shape and stiffness are also associated with caudal fin design and lifestyle (Webb and Blake, 1985; Webb, 1988). More elongate, flexible fish typically possess lower aspect ratio caudal fins only subtly set off from the body; they are specialized for maneuverability. Shorter, more fusiform fish have higher aspect ratio caudal fins set off distinctly from the body at a narrow neck; they are specialized for speed. They often possess deep trunks and/or dorsal fins that increase the inertia of the anterior part of the body, minimizing the recoil that results from side forces generated by the tail. Such damping of inertial recoil has been shown to be more critical to swimming power requirements than the increased drag produced by the enlarged surface area (Webb, 1992). Webb and Blake (1985) summarized traits associated with maximum swimming speed in fish, including a tail with high aspect ratio (large span but small area), a narrow caudal peduncle, small total caudal area, stabilization of the anterior of the body with an anterior median fin, and a stiff, streamlined body.

None of the ichthyosaurs studied here can be placed at either extreme of the shape/flexibility continuum. All had flukes set off distinctly from the body, and all probably belong closer to the thunniform, than to the anguilliform, end of the continuum. Body size and proportions can be used to subdivide the six species into larger, more elongate, more flexible, and smaller, deeper-bodied, less flexible subgroups. *Suevoleiathan disinteger*, *Temnodontosaurus trigonodon*, and *Eurhinosaurus longirostris*, with total column lengths greater than 3,000 mm may be predicted to be more flexible than *Ichthyosaurus communis*, *Stenopterygius quadriscissus*, and *Ophthalmosaurus icenicus* with column lengths less than 3,000 mm (Table 1). The larger animals also have relatively longer tail stocks and relatively

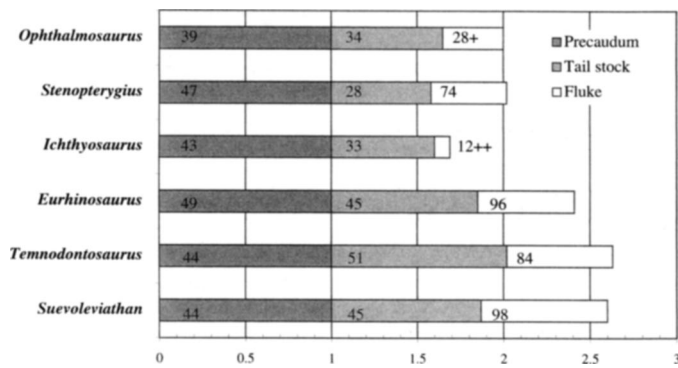


FIGURE 5. Vertebral counts and proportional lengths of postcranial units in six Jurassic ichthyosaurs. The data for each genus is standardized to the length of the precaudum (=1.0).

longer flukes, indicators of lower aspect ratio flukes and less extreme specialization for maximizing speed. Body regionalization and differentiation between anterior and posterior tail-stocks is most clearly marked in *S. quadriscissus* and *O. icenicus*.

Vertebral Count and Fusion—An increase of vertebral count, and thus of intervertebral joint count, must increase the flexibility of the column when other factors are held constant. This relationship was noted by Nursall (1958) who observed that vertebral counts are much higher in eels and other anguilliform fish than in tunas and other thunniform fish. More recently, Brainerd and Patek (1998) reported that lower vertebral numbers are correlated with lower curvature in the escape maneuvers in four species of tropical marine fishes. Long and Nipper (1996) tested the relationship between vertebral count and propulsive wavelength across taxa (fish, amphibians, and reptiles). They found that 21% of wavelength variation could be explained by vertebral count variation. Other sources of passive body stiffness include the skin, connective tissue, and axial skeleton (Long et al., 1994).

Counteracting intervertebral flexibility, intervertebral joints may be stiffened, fused, or constrained by extremes of vertebral shape. Hildebrand (1982) noted the role of enveloping neural and haemal spines, and of broad transverse processes in limiting intervertebral movement anterior to the narrow base of the caudal fin in the tuna. The neck is a frequent site of stabilization via vertebral fusion. Fusion of cervical vertebrae also occurs in many cetacean species, and appears to progress with ontogenetic age (Slijper, 1936; DeSmet, 1977). Fusion, and even reduction of cervical count, occurs in Sirenia (Kaiser, 1974). Very short, discoidal vertebrae (see below) permit very little intervertebral movement. Examples are found in the cervical series of many whales, where count is held constant at seven, and in the lumbar series of delphinid cetaceans, where count in more rigid animals is actually higher than in more flexible animals (Buchholtz, 2001).

Despite great variation in body size, vertebral count of the precaudal column in the ichthyosaurs under study is relatively stable (Fig. 5). Five of the six species have precaudal counts between 44 and 49; *Ophthalmosaurus icenicus* is tentatively estimated to have 39. This stability of precaudal count and the relatively large and apparently functional hind limbs suggest that the precaudal column was not actively involved in swimming. The tail stock is more variable (28–51) than the precaudum in count. The tail stock exceeds the precaudum in count in *Suevoleiathan disinteger* and *Temnodontosaurus trigonodon*, and in length in *T. trigonodon*. Fluke counts are highest in animals with the highest tail stock counts and the greatest inferred flexibility.

Stabilization of the neck and enhancement of hydrodynamic shape by fusion of atlas and axis occurs in *Stenopterygius quadriscissus* and *Ophthalmosaurus icenicus*. These vertebrae also closely abut in the *Eurhinosaurus longirostris* and *Ichthyosaurus communis* specimens examined, although it was impossible to determine if they were actually fused. Fusion occurs in at least one large specimen of *Temnodontosaurus*. It is likely that, as in living vertebrates, fusion progressed with ontogeny in ichthyosaurs.

Ribs and Gastralria—Ribs support and protect the viscera, and also stabilize the thorax (mammals) or dorsum (reptiles). Slijper (1936) documented reduction in rib count and the replacement of sternal and bicipital ribs by floating and uncipital ribs during the early evolution of whales. He associated the increased thoracic flexibility that resulted with the extensive chest movements needed for swimming and diving. Ichthyosaurs retain ribs on all dorsal vertebrae. As in whales, rib attachments are bicipital anteriorly and uncipital posteriorly. It seems likely that bicipital ribs had less freedom of movement without disarticulation than uncipital ones, and the transition point is interpreted here as marking a transition from a more rigid to a more flexible body region. Transition from bicipital to uncipital ribs is somewhat variable between individuals of the same species, so exact vertebral location is less informative than general body region. Uncipital ribs first appear in the mid trunk of *Suevoleiathan disinteger*, the posterior trunk of *Eurhinosaurus longirostris*, at or near the sacral region of *Temnodontosaurus trigonodon* and *Stenopterygius quadriscissus*, and in the anterior tail stock of *Ichthyosaurus communis* and *Ophthalmosaurus icenicus*, predicting an increase in anterior body stiffness in that order.

Ribs, when complete, can provide information on body depth. Animals with relatively long ribs have deep bodies, associated with body stiffness, high swimming speeds, and the minimization of recoil (Webb and Blake, 1985; see above). The relatively long ribs of *Stenopterygius quadriscissus* and *Ophthalmosaurus icenicus* are interpreted to have enhanced both resistance to recoil and body stiffness.

Gastralia are dermal ossifications located within the ventral body wall. As contributors to the bony skeleton, they increase support, protection, and rigidity of the trunk. Unfortunately, they may be lost before preservation and/or overlooked or sacrificed during specimen preparation. Their absence today does not assure their absence in life. Gastralia are unknown today in *Suevoleiathan disinteger* and *Temnodontosaurus trigonodon*, but are present and must have contributed to body stiffness in *Ichthyosaurus communis*, *Eurhinosaurus longirostris*, and *Stenopterygius quadriscissus*. Their presence is also unknown in *O. icenicus*, although its mode of preservation makes the discovery of these small, free bones highly unlikely.

Vertebral Process Size and Shape—The neural processes of ichthyosaurs change in height, shape, orientation, and articulation along the column. High neural spines add depth to the body, providing enhanced surface area for the attachment of the axial musculature. In living sunfish, Long et al. (1994) found that in addition to contraction, axial musculature was a major contributor to body stiffness. Similar findings were reported for largemouth bass (Johnson et al., 1994), and may be extended by analogy to other axial locomotors. The relative size of neural processes can be quantified by reference to centrum height.

Neural spines in all six species decrease in height posteriorly from a maximum in the anterior trunk. In *Suevoleiathan disinteger*, *Temnodontosaurus trigonodon* and *Eurhinosaurus longirostris*, the decrease in height begins immediately after its peak. In contrast, the neural spine heights of *Ichthyosaurus communis* and *Stenopterygius quadriscissus* plateau throughout most of the trunk, gradually decreasing in the posterior trunk and anterior tail stock. Posterior retention of tall neural spines

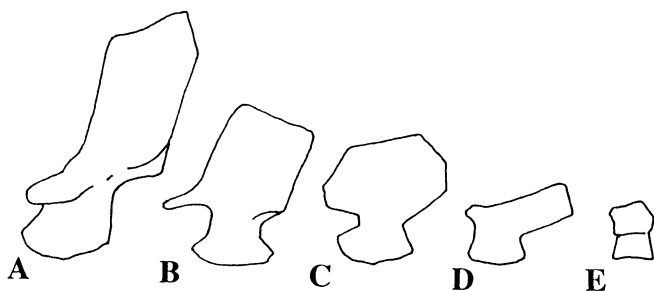


FIGURE 6. Generalized neural spine shape sequence from anterior to posterior in Jurassic ichthyosaurs, traced from video images of *Stenopterygius quadriscissus* SMNS 50963. Vertebrae with high, rectangular spines (A) always occur in the anterior trunk, and may extend as far back as the anterior tail stock in species with rigid torsos. They are succeeded by vertebrae with square (B) and irregularly polygonal (C) spines. Posteriorly inclined rod-shaped neural spines (D) always occur in the posterior tail stock, and small upright spines (E) in the anterior fluke.

is particularly marked in *S. quadriscissus* (Table 1). An even more extreme pattern occurs in reconstructed (e.g., BM(NH) R 3702, R 3893 and R 4124, which together comprise a composite display specimen) and partial (e.g., FSF R461) specimens of *Ophthalmosaurus icenicus*, where neural spine height is greater than centrum height as far back as the mid-tail stock. The high spines increase the body depth and recoil resistance, and indicate the presence of a muscle mass that must have contributed to body stiffness.

The same general sequence of neural spine shapes occurs along the column of all ichthyosaurs in this study. From anterior to posterior, neural spines are in sequence roughly rectangular, square, obliquely polygonal, and rod-shaped (Fig. 6). Maisch (1998a) diagrammed this sequence for *Suevoleiathan disinteger*. Transition points between neural spine shapes occur at different places along the column in different ichthyosaurian species and correspond with changes in neural spine height. The high neural spines of the *Ichthyosaurus communis*, *Stenopterygius quadriscissus*, and *Ophthalmosaurus icenicus* trunks reflect the retention of the upright, rectangular spine shape into the posterior trunk and even into the tail stock. Similarly, the low neural spines of *Suevoleiathan disinteger* trunk reflect the anterior position of the transition from rectangular and square spine shape to polygonal spine shape. Neural spines of the posterior tail stock are similar in all species.

Changes in neural spine orientation accompany changes in shape. Anterior neural spines stand upright; caudal deflection increases posteriorly, and is most marked in vertebrae just anterior to the fluke. Neural spines of the fluke, when (rarely) observed, are again upright. By reference to the work of Videler (1993) with fish, inclined neural spines, when connected by a dorsal ligament, act as springs. They pull a flexed vertebral column back toward the median plane, and potentially save energy during rhythmic bending movements.

Shape also plays an important role in determining the extent of contact between adjacent neural spines. Rectangular and square-shaped spines of adjacent vertebrae are typically in contact through all or most of their height. Their contact and the occasional presence of shallow tongue and groove articulations between adjacent spines presumably enhanced body stiffness. Polygonal and rod-shaped spines have minimal contact or lack contact completely.

Zygapophyses guide and limit the range of movement between adjacent vertebrae. In whales, zygapophyses exist on anterior vertebrae, but not in posterior, more flexible parts of the

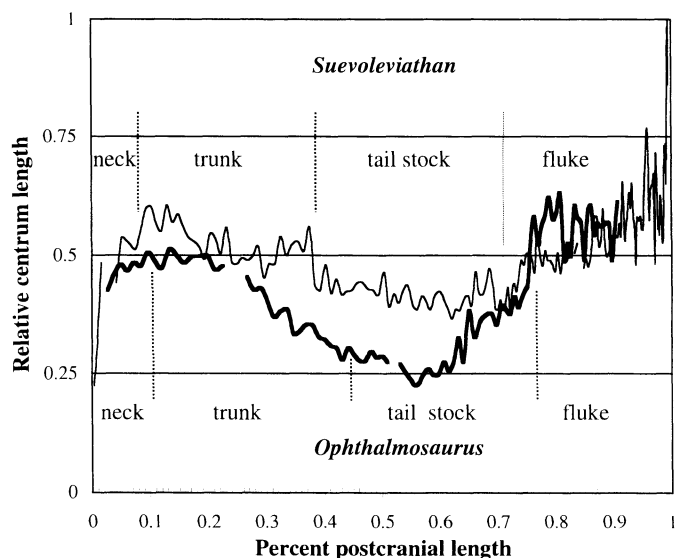


FIGURE 7. Relative centrum lengths of *Suevoleiathan disinteger* (SMNS 15390) and *Ophthalmosaurus icenicus* (PMAG R340). Note variation in relative lengths of functional units as well as in vertebral dimensions. *Suevoleiathan disinteger* is interpreted as occurring at the more flexible/slower swimming end, and *O. icenicus* at the more rigid/faster swimming end of a continuum of swimming styles in Jurassic ichthyosaurs.

column (Slijper, 1936; DeSmet, 1977). Robustness and size of zygapophyses also decreases posteriorly in ichthyosaurs, enhancing the flexibility of the posterior column.

Ichthyosaurs lack transverse processes on their vertebrae.

Centrum Width, Height, and Length—Vertebral shape significantly affects intervertebral movement, and thus body stiffness. By simple geometry, disk-shaped vertebral centra with relatively great width and height relative to length will have large anterior and posterior areas of contact, and minimal angular deflection will be possible before adjacent vertebrae obstruct one another. Conversely, spool-shaped centra with relatively small areas of intervertebral contact will have a greater range of motion. Variations in shape may be represented numerically as relative centrum length, or centrum length/centrum height. Among cetaceans, the most thunniform and rigid species (dolphins and porpoises) have extremely discoidal trunk centra, while those of more flexible species (river dolphins and delphinopterids) are more cylindrical (Buchholtz, 1998a, b, 2001). Variations in centrum shape along a single column also correspond closely with regional flexibility. The same general principles must apply to ichthyosaurs as well.

All Jurassic ichthyosaurs have disc-shaped vertebrae throughout the entire length of the column, with the exception of the extreme fluke tip. Nevertheless, the strength of trait expression is more extreme in some parts of the column than others, and in some species than others. A comparison of relative centrum length in *Suevoleiathan disinteger* and *Ophthalmosaurus icenicus* (Fig. 7), at opposite ends of the morphological continuum, is used to show the range of trait expression. Variation in relative centrum length in *S. disinteger* is subtle. Vertebrae of the tail stock are modestly more discoidal than those of the trunk or the tail, reflecting their function in support of the oscillatory tail. There is little distinction between anterior and posterior tail stock, and little between tail stock and the fluke. At least some undulation must have occurred throughout all of the tail, and probably throughout the postcranium.

In contrast, vertebrae of *Ophthalmosaurus icenicus* are much

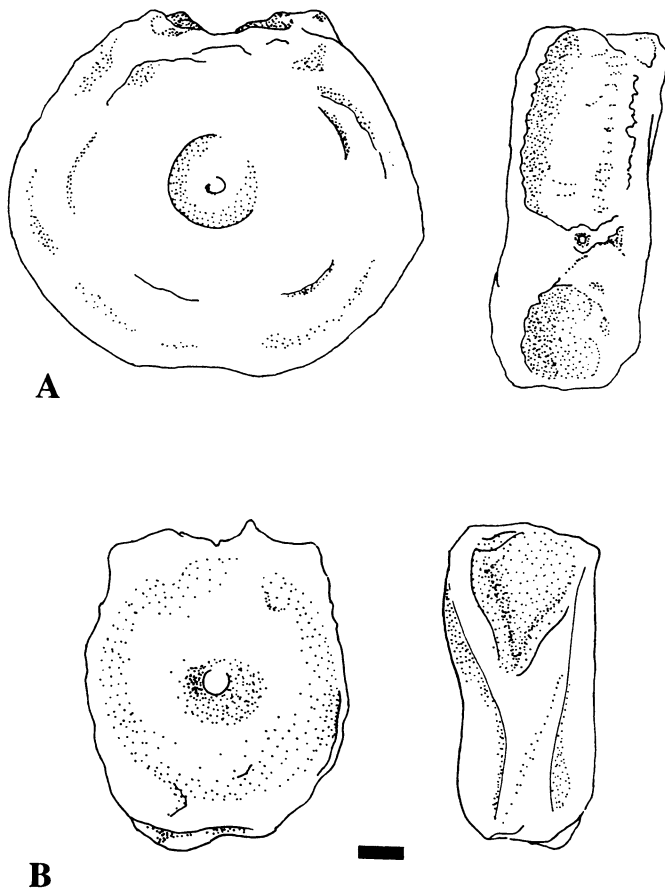


FIGURE 8. Posterior (left) and lateral (right) views of caudal vertebrae of *Ophthalmosaurus icenicus* (BMNH 2169), an incomplete specimen with exceptional 3-dimensional preservation. **A**, posterior tail stock vertebra, estimated to have been the fourth pre-tailbend vertebra. Centrum width exceeds height and centrum margins are modestly rounded; **B**, anterior fluke vertebra estimated to have been the second post-tailbend vertebra. Centrum height modestly exceeds width, and centrum margins are markedly rounded. Scale bar equals 5 mm.

more extremely regionalized anatomically. Vertebrae of the anterior tail stock are extremely discoidal, with heights more than 4 times their length. The posterior trunk is also stabilized by discoidal vertebrae, and can be interpreted as forming a single rigid unit with the anterior tail stock. The posterior tail stock shows an abrupt increase in relative centrum length, and the anterior fluke has even longer relative centrum length than *Suevoleviathan disinteger*. This was likely the restricted site of almost all column movement.

As noted above, a reversal of vertebral dimensions is characteristic of the tail stock-fluke boundary. Unfortunately, preservation of both width and height is rare in slab mounts, making comparison of compression difficult. It is dramatic however in *Ophthalmosaurus icenicus* (Fig. 8), where vertebrae of the posterior tail stock have centrum widths up to 1.3 times centrum height that supported the dorsoventrally compressed cutwater. They are succeeded by vertebrae with centrum widths as low as 0.7 times height that supported the laterally compressed fluke.

Additional indications of the movement of one vertebra on the next occur on the bodies of the centra themselves. I am indebted to Ronald Böttcher for first pointing this out to me, and to Ryosuke Motani for providing a reference to the same observation by Seeley (1908). Rounding of the anterior and

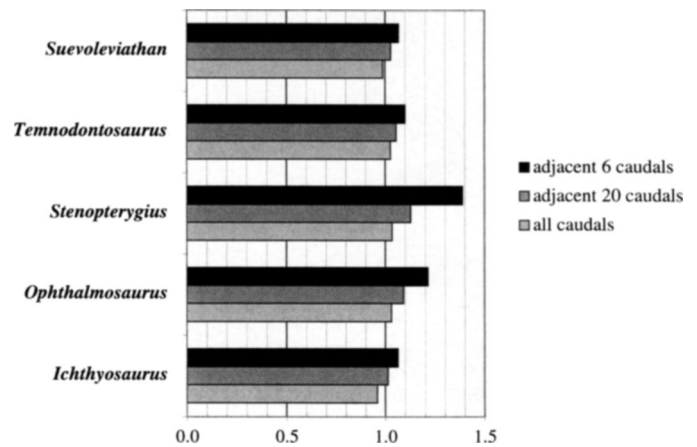


FIGURE 9. The ratio of dorsal centrum length to ventral centrum length in all caudals, the 20 caudals surrounding the fluke base, and the six caudals surrounding the fluke base in Jurassic ichthyosaurs. Data for *Eurhinosaurus longirostris* was not collected. One vertebra interpreted as showing extreme postdepositional deformation was excluded from the data set of *Suevoleviathan disinteger*.

posterior centrum edges occurs in the tail stock and anterior fluke. It is most extreme at the fluke base itself, with the result that these vertebrae are bun-shaped, and entirely lack the crisp edges of trunk or posterior fluke centra. This zone may be used to identify areas of the most dramatic column bending.

Centrum edges of *Suevoleviathan disinteger* are uniformly gently rounded, additional evidence that modest flexion must have occurred along the entire column. In contrast, the only zone of centra with rounded edges in *Ophthalmosaurus icenicus* occurs in the posterior tail stock and the first few fluke vertebrae. Most of the column must have been held rigid, with flexion largely restricted to the posterior tail stock and anterior fluke.

Ventral displacement of the vertebral column into the fluke at a "tail bend" undoubtedly occurred in many ichthyosaur specimens, but has unfortunately been artificially introduced into other specimens during preparation (Riess, 1986; McGowan, 1992). Its presence during life can be established by a comparison of dorsal and ventral centrum length (McGowan, 1990). By analogy with the pattern in sharks (Thomson, 1976; Thomson and Simanek, 1977), high angle tail bends in ichthyosaurs supported high aspect ratio caudal fins, and are therefore associated with animals adapted for speed and endurance. Because the vertebrae are often somewhat distorted, measurements of individual vertebrae can be unreliable. Ratios of dorsal centrum length to ventral centrum length are presented for all (preserved) caudals, for the twenty vertebrae adjacent to the fluke base, and for the six vertebrae adjacent to the fluke base in the five species for which both dorsal and ventral lengths were collected (Fig. 9). Data indicate the presence of only modest wedging and inferred tail bend in *Suevoleviathan disinteger*, *Temnodontosaurus trigonodon*, and *Ichthyosaurus communis*, and more extreme wedging and tail bend in *Stenopterygius quadriscissus* and *Ophthalmosaurus icenicus*, those species with the most extreme regionalization of the body. This data set was not collected for *Eurhinosaurus longirostris*, but the presence of a tail bend in this species has been confirmed by tomography by McGowan (1990).

In contrast to most tetrapods, ichthyosaurs have amphicoelous centra. By analogy to fish, their anterior and posterior central cavities were presumably filled with notochordally derived material. Elastic notochordal tissue housed in centrum cavities

TABLE 2. Summary and distribution of traits discussed in the text. (X) = variably present.

Trait	Species					
	<i>Suevoleviathan disinteger</i> SMNS 15390	<i>Temnodontosaurus trigonodon</i> SMNA 15950	<i>Eurhinosaurus longirostris</i> GPIT 1025/18/1	<i>Ichthyosaurus communis</i> BRSMG Cb3578	<i>Stenopterygius quadricissus</i> FSF R4154	<i>Ophthalmosaurus icenicus</i> PMAG R340
Caudal wedging/tail bend	X	X	X	X	X	X
Tail stock shorter than precaudum	X		X	X	X	X
Tail stock count < precaudal count			X	X	X	X
All precaudal ribs bicapital			X	X	X	X
Gastralia known to be present			X	X	X	(?)
Postcranial length < 3,000 mm				X	X	X
Fluke < 0.5 precaudal length				X	X	X
Hind limb length \ll forelimb length				X	X	X
Elongate neural spines in posterior trunk				X	X	X
Ischium and pubis fused		(X)	(X)	(X)	X	X
Atlas and axis fused		(X)	(X)	(X)	X	X
Longest ribs > 0.5 precaudal length					X	X
Reduced relative centrum length in posterior trunk					X	X

resists both compression and stretching in some teleost fish (Symmons, 1979), acting as a spring to return the axial skeleton to the midline. It is tempting to ascribe an analogous system to ichthyosaurs. The functional implications of the slight but consistent differences in size and shape between anterior and posterior centrum cavities in ichthyosaurs are unclear.

Limb Size and Attachment—Transitions from paraxial appendicular locomotion to axial locomotion are accompanied by a reduction in the size and function of the paired appendages. Degree of reduction may be used as a general guide to either the recentness or the completeness of the transition, or both. Reduction in size, loss of distal elements, and simplification of proximal elements of the limbs or girdles are typical of many reduction sequences (Lande, 1978). Structural reduction almost always proceeds in distal to proximal sequence. Although whales and seacows have completely lost external hind limbs, simplified and reduced pelvic and/or femoral elements still exist. The forelimb is retained as a steering mechanism in all Sirenia and Cetacea, and as a secondary locomotor organ in some slower species (e.g., river dolphins, seacows) that live in shallow water (Hartman, 1979; Klima et al., 1980; Benke, 1993). Fishes with powerful axial locomotion may also use appendicular swimming during low-power activities (Webb and Blake, 1985).

In parallel with other secondary axial swimmers, all six species of this study have smaller hind limbs than forelimbs (Table 1). The relatively large hind limbs of *Suevoleviathan disinteger*, *Temnodontosaurus trigonodon* and *Eurhinosaurus longirostris* suggest their use in steering and possibly even propulsion at slow speeds. In contrast, the hind limbs of *Ichthyosaurus communis*, *Stenopterygius quadricissus*, and *Ophthalmosaurus icenicus* are of approximately half this relative size, and it is unlikely that they were actively involved in either locomotion or steering. Use of the hind limbs as rudders in these animals was probably redundant because of limited body flexibility, and large limb size would have compromised hydrodynamic shape. Fusion of the ischium and pubis is not known in *S. disinteger*, is partial or occasional in *T. trigonodon*, *E. longirostris* and *I. communis*, and complete in *S. quadricissus* and *O. icenicus* (Motani, 1999b). It is here understood as an indicator of proximal simplification.

The forelimbs of the six species are less variable in relative size, and were probably involved in steering in all species. The large size and broad shape of the *Suevoleviathan disinteger*

forelimb suggests it may have had more extensive locomotor involvement.

Conclusions and Phylogenetic Implications

All Jurassic ichthyosaurs surveyed possessed a clearly defined caudal fluke and are interpreted here as swimming by its lateral oscillation on a flexible tail stock. An anatomical continuum (Table 2) suggests a functional continuum in swimming style among these animals. At the more anguilliform end of this continuum, *Suevoleviathan disinteger* and *Temnodontosaurus trigonodon* had highly flexible bodies. Both tail stock and fluke are long relative to precaudal length, and vertebral counts are very high. The anterior tail stock was not clearly demarcated from the posterior tail stock, and only very modestly specialized for support and strength by reduction of relative centrum length. The long, thin body shapes of both species suggest only modest regional differentiation, and the large limbs may have been used as aids in slow swimming as well as rudders during faster swimming. These animals were both slower and more agile than their contemporaries. Of the two species, *Suevoleviathan disinteger* has longer relative centrum length, limbs, and fluke, suggesting greater flexibility. Its smaller adult body size and tooth size must also have dictated smaller prey than that preferred by *Temnodontosaurus trigonodon*.

In contrast, *Stenopterygius quadricissus* and *Ophthalmosaurus icenicus* had sharply regionalized bodies that place them toward the thunniform end of the continuum. Both tail stock and fluke were short relative to precaudal length. The anterior tail stock and even posterior portions of the trunk were stabilized with highly discoidal vertebrae against the action of the short posterior tail stock, which was dorsoventrally compressed and flexible. Fusion of axis and atlas stabilized the neck; deeply wedged vertebrae at the fluke base indicate significant tail bends and support an interpretation of high aspect ratio flukes. Trunk depth was enhanced with high neural spines and long ribs to resist the recoil generated by the flexion that was limited to the area around the fluke base. The small forelimbs were most likely used only for steering. The small size of the hind limbs and fusion of pelvic elements suggests that they were in the process of reduction and loss. These animals must have been capable of rapid and sustained swimming, and may have chased their prey over long distances. Of the two, *Ophthalmosaurus icenicus* shows the more extreme expression of almost every anatomical trait associated with body regionalization and rigidity. In this

respect, it was an analog to living porpoises that have highly rigid bodies, while *Stenopterygius quadriscissus* was an analog to the more flexible dolphins (Curren et al., 1994). These species were not contemporaries, so no direct competition occurred.

Eurhinosaurus longirostris and *Ichthyosaurus communis* fall between these extremes. *Eurhinosaurus longirostris* was much larger than *I. communis*, had relatively longer limbs and fluke, and lacked the elongated ribs and neural spines that are indicators of a rigid body. However, its sharply defined posterior tail stock is typical of smaller, more rigid animals. Conversely, the smaller *I. communis* had most of the indicators of body rigidity, but a tail stock that was less distinctly differentiated into support and undulatory subunits. Their enormous differences in body size must have dictated different prey species and eliminated direct competition.

Because pre-Jurassic ichthyosaurs were typically elongate and lacked adaptations for extreme speed, it is probably safe to assume that traits associated with body rigidity are derived among Jurassic species. The common presence of a tail bend in all species surveyed identifies it as primitive to the group. The distribution of derived traits allows predictions of the order of acquisition of traits associated with thunniform swimming style and of phylogeny. Reductions of vertebral length and count and the posterior extension of bicipital ribs throughout the trunk preceded reductions of limb and body size, and of the modification of neural spines. Only the most extremely modified species possess the deep body shape, fusion of vertebral and girdle elements, and the modification of the posterior trunk that minimized trunk movement during fluke oscillation. Although the possibility of multiple, convergent origins of these traits cannot be ignored, the relationships inferred for these six taxa on the basis of only postcranial traits is highly congruent with those proposed on the basis of an anatomically and taxonomically much wider study by Motani (1999b). The only area of disagreement is the location of the genus *Stenopterygius*, which Motani (1999b) placed outside a clade including *Ichthyosaurus* and *Ophthalmosaurus*. The shared modifications of the posterior trunk present in both *Stenopterygius* and *Ophthalmosaurus* suggest in contrast that these two genera are the most derived with respect to locomotor style and share a more recent common ancestry than either does with *Ichthyosaurus*. The possibility of such a relationship has been entertained by both Godefroit (1993) and Motani (1999b).

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LITERATURE CITED

- Andrews, C. W. 1910. A descriptive catalog of the marine reptiles of the Oxford Clay, Part I. Printed for the British Museum, London, 205 pp.
- Appleby, R. M. 1956. The osteology and taxonomy of the fossil reptile *Ophthalmosaurus*. Proceedings of the Zoological Society of London 126:403–447.
- . 1979. The affinities of Liassic and later ichthyosaurs. Palaeontology 22:921–946.
- Benke, H. 1993. Investigations on the osteology and the functional morphology of the flipper of whales and dolphins (Cetacea). Investigations on Cetacea 24:9–252.
- Besmer, A. 1947. Beiträge zur Kenntnis des Ichthyosauriergebisses. Schweizerische Palaeontologische Abhandlungen 65:1–21.
- Brainerd, E. L., and S. N. Patek. 1998. Vertebral column morphology, C-start curvature, and the evolution of mechanical defenses in tetraodontiform fishes. Copeia 1998:971–984.
- Breder, C. M., Jr. 1926. The locomotion of fishes. Zoologica 4:159–312.
- Buchholtz, E. A. 1998a. Implications of vertebral morphology for locomotor evolution in early Cetacea; pp. 325–351 in J. G. M. Thiewissen (ed.), The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea. Plenum Press, New York.
- . 1998b. Whales: correlation of Slijper's 'Stufen' with centrum dimensions. Journal of Vertebrate Paleontology 18 (3, suppl.):30A.
- . 2001. Vertebral osteology and swimming style in living and fossil whales (Order: Cetacea). Journal of Zoology, London 253: 175–190.
- Caldwell, M. W. 1996. Ichthyosauria: A preliminary phylogenetic analysis of diapsid affinities. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 200:361–386.
- Curren, K., N. Bose, and J. Lien. 1994. Swimming kinematics of a harbour porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*). Marine Mammal Science 10: 485–492.
- DeSmet, W. M. A. 1977. The regions of the cetacean vertebral column; pp. 58–80 in J. Harrison (ed.), Functional Anatomy of Marine Mammals, volume 3. Academic Press, New York.
- Fish, F. E. 1998. Biomechanical perspective on the origin of cetacean flukes, pp. 303–324 in J. G. M. Thiewissen (ed.), The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea. Plenum Press, New York.
- Gilmore, C. W. 1905. Osteology of *Baptanodon* (Marsh). Memoirs of the Carnegie Museum 2:77–129.
- Godefroit, P. 1993. The skull of *Stenopterygius longifrons* (Owen, 1881). Revue de Paléobiologie, Genève, Vol. Spéciale 7:67–84.
- . 1994. Les reptiles marins du Toarcien (Jurassique inférieur) belgo-luxembourgeois. Mémoires pour servir à l'explication des cartes géologiques et minières de la Belgique 39:1–98.
- Hartman, D. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. The American Society of Mammalogists Special Publication No. 5, 150 pp.
- Hauff, B. 1953. Das Holzmadenbuch. Verlag der Hohenlohe'schen Buchhandlung; Öhringen, 54 pp.
- Hildebrand, M. 1982. Analysis of Vertebrate Structure, 2nd ed. John Wiley and Sons, New York, 654 pp.
- Huene, F. von. 1922. Die Ichthyosaurier des Lias und ihre Zusammenhänge. 4. Jahresversammlung der palaeontologischen Gesellschaft. Verlag Bornträger, Berlin, 114 pp.
- . 1926. Neue Ichthyosaurierfunde aus dem schwäbischen Lias. Neues Jahrbuch für Mineralogie, Beilage-Band 55(B): 66–86.
- . 1951. Eine neue Ichthyosaurier-Gattung der mittleren Trias. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 94: 80–92.
- Hungerbühler, A., M. W. Maisch, F. Westphal, T. Lingham-Soliar, and F. Stein. 1989. Schwimmsaurier. Ausstellungskataloge der Universität Tübingen 24:1–89.
- Johnson, T. P., D. A. Syme, B. C. Jayne, G. V. Lauder, and A. F. Bennett.

1994. Modeling red muscle power output during steady and unsteady swimming in largemouth bass. *American Journal of Physiology* 267:R481–R488.
- Kaiser, H. E. 1974. Morphology of the Sirenia. S. Karger, Basel, 75 pp.
- Klima, M. 1992. Schwimmbewegungen und Auftauchmodus bei Walen und bei Ichthyosauriern. II. Vergleich des Auftauchmodus. *Natur und Museum* 122:73–89.
- , M., H. Oelschläger, and D. Wunsch. 1980. Morphology of the pectoral girdle in the Amazon dolphin *Inia geoffrensis* with special reference to the shoulder joint and the movements of the flippers. *Zeitschrift für Säugetierkunde* 45:288–309.
- Lande, R. 1978. Evolutionary mechanisms of limb loss in tetrapods. *Evolution* 32:73–92.
- Lindsey, C. C. 1978. Form, function and locomotory habits in fish; pp. 1–100 in W. S. Hoar and D. J. Randall (eds.), *Fish Physiology*. Academic Press, New York.
- Lingham-Soliar, T., and W.-E. Reif. 1998. Taphonomic evidence for fast tuna-like swimming in Jurassic and Cretaceous ichthyosaurs. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 207:171–183.
- Long, J. H., Jr., and K. S. Nipper. 1996. The importance of body stiffness in undulatory propulsion. *American Zoologist* 36:678–694.
- , M. J. McHenry, and N. C. Boetticher. 1994. Undulatory swimming: how traveling waves are produced and modulated in sunfish (*Lepomis gibbosus*). *Journal of Experimental Biology* 192:129–145.
- Maisch, M. W. 1997. A case against a diapsid origin of the Ichthyosauria. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 205:111–127.
- 1998a. A new ichthyosaur genus from the Posidonia Shale (Lower Toarcian, Jurassic) of Holzmaden, SW-Germany with comments on the phylogeny of post-Triassic ichthyosaurs. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 209:47–78.
- 1998b. The temporal region of the Middle Jurassic ichthyosaur *Ophthalmosaurus*—further evidence for the non-diapsid architecture of the Ichthyosauria. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1998:401–414.
- 1998c. Kurze Übersicht der Ichthyosaurier des Posidonienschiefers mit Bemerkungen zur Taxonomie der Stenopterygiidae und Temnodontosauridae. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 109:401–431.
- Manter, J. T. 1940. The mechanics of swimming in the alligator. *Journal of Experimental Zoology* 83:345–358.
- Martill, D. M. 1987. A taphonomic and diagenetic case study of a partially articulated ichthyosaur. *Palaeontology* 30:543–555.
- , J. Hudson, and K. Page. 1991. Introduction, pp. 11–34 in D. Martill and J. Hudson (eds.), *Fossils of the Oxford Clay*. The Palaeontological Association, London.
- Massare, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7:121–137.
- 1988. Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. *Paleobiology* 14:187–205.
- 1995. Swimming capabilities of extinct marine reptiles: a review; pp. 133–149 in L. Maddock, Q. Bone, and J. M. V. Rayner (eds.), *Mechanics and Physiology of Animal Swimming*. Cambridge University Press, Cambridge.
- 1997. Introduction to behavior, faunas, and evolution; pp. 401–421 in J. M. Callaway and E. L. Nicholls (eds.), *Ancient Marine Reptiles*. Academic Press, New York.
- , and J. Faulkner. 1997. Sharks as morphological analogs for ichthyosaurs. *Paludicola* 1:117–125.
- McGowan, C. 1973. Differential growth in three ichthyosaurs: *Ichthyosaurus communis*, *I. breviceps*, and *Stenopterygius quadriscissus* (Reptilia, Ichthyosauria). *Life Science Contributions, Royal Ontario Museum* 93:1–21.
- 1974a. A revision of the longipinnate ichthyosaurs of the Lower Jurassic of England, with descriptions of two new species (Reptilia: Ichthyosauria). *Life Science Contributions, Royal Ontario Museum* 97:1–37.
- 1974b. A revision of the latipinnate ichthyosaurs of the Lower Jurassic of England (Reptilia: Ichthyosauria). *Life Science Contributions, Royal Ontario Museum* 100:1–30.
- 1978. Further evidence for the wide geographical distribution of ichthyosaur taxa (Reptilia: Ichthyosauria). *Journal of Palaeontology* 52:1155–1162.
- 1979. A revision of the Lower Jurassic ichthyosaurs of Germany with descriptions of two new species. *Palaeontographica A* 166:93–135.
- 1989. The ichthyosaur tail: a verification problem facilitated by computed tomography. *Paleobiology* 15:429–436.
- 1990. Computed tomography reveals that *Eurhinosaurus* (Reptilia: Ichthyosauria) does have a tail. *Canadian Journal of Earth Sciences* 27:1541–1545.
- 1992. The ichthyosaur tail: sharks do not provide an appropriate analogue. *Palaeontology* 35:555–570.
- 1996. Giant ichthyosaurs of the Early Jurassic. *Canadian Journal of Earth Sciences* 33:1011–1021.
- Motani, R. 1997. Temporal and spatial distribution of tooth implantation in ichthyosaurs; pp. 81–103 in J. M. Callaway and E. L. Nicholls (eds.), *Ancient Marine Reptiles*. Academic Press, London and New York.
- 1998. Ichthyosaur swimming revisited: implications from the vertebral column and phylogeny. *Journal of Vertebrate Paleontology* 18 (3, suppl.):65A.
- 1999a. On the evolution and homologies of ichthyopterygian forefins. *Journal of Vertebrate Paleontology* 19:28–41.
- 1999b. Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology* 19:473–496.
- , H. You, and C. McGowan. 1996. Eel-like swimming in the earliest ichthyosaurs. *Nature* 382:347–348.
- Nursall, J. R. 1958. The caudal fin as a hydrofoil. *Evolution* 12:116–120.
- Riess, J. 1986. Fortbewegungsweise, Schwimmbiophysik und Phylogenie der Ichthyosaurier. *Palaeontographica A* 192:93–155.
- Seeley, H. G. 1908. On the extremity of the tail in Ichthyosauria. *Annals and Magazine of Natural History* 8:436–441.
- Slijper, E. J. 1936. Die Cetaceen. *Vergleichen-antomisch und Systematisch. Capita Zoologica* 6–7:1–590.
- 1948. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. *Verhandlungen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde, Tweede Reeks* 42:1–128.
- Symmons, S. 1979. Notochordal and elastic components of the axial skeleton of fishes and their functions in locomotion. *Journal of Zoology, London* 189:157–206.
- Taylor, M. A. 1987. Reinterpretation of ichthyosaur swimming and buoyancy. *Palaeontology* 30:531–535.
- Thomson, K. 1976. On the heterocercal tail in sharks. *Paleobiology* 2:19–38.
- , and D. Simanek. 1977. Body form and locomotion in sharks. *American Zoologist* 17:343–354.
- Urlichs, M., R. Wild, and B. Ziegler. 1994. Der Posidonien-Schiefer des unteren Juras und seine Fossilien. *Stuttgarter Beiträge zur Naturkunde, Series C* 36:1–95.
- Videler, J. J. 1993. *Fish Swimming*. Chapman & Hall, London, 260 pp.
- Webb, P. W. 1988. 'Steady' swimming kinematics of tiger muskey, an esociform accelerator, and rainbow trout, a generalist cruiser. *Journal of Experimental Biology* 138:51–69.
- 1992. Is the high cost of body/caudal fin undulatory swimming due to increased friction drag or inertial recoil? *Journal of Experimental Biology* 162:157–166.
- , and R. W. Blake. 1985. Swimming; pp. 110–128 in M. Hildebrand, D. M. Bramble, K. R. Liem, and D. B. Wake (eds.), *Functional Vertebrate Morphology*. Harvard University Press, Cambridge.
- Worthington, R. D., and D. B. Wake. 1972. Patterns of regional variation in the vertebral column of terrestrial salamanders. *Journal of Morphology* 137:257–277.

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