Paludicola 5(4):242-254 June 2006

VERTEBRAL MORPHOLOGY OF *OPHTHALMOSAURUS NATANS* (REPTILIA: ICHTHYOSAURIA) FROM THE JURASSIC SUNDANCE FORMATION OF WYOMING.

Judy A. Massare[1], Emily A. Buchholtz[2], Jennifer M. Kenney[1], and Anne-Marie Chomat[2]

[1] Department of the Earth Sciences, SUNY College at Brockport, Brockport, NY 14420
[2] Department of Biology, Wellesley College, Wellesley, MA 02481

ABSTRACT

New ichthyosaur material, most likely *Ophthalmosaurus natans*, from the Sundance Formation of Natrona Co., WY preserves the posterior trunk and tail stock, allowing the construction of a composite vertebral column for the species. Although similar in body portions and count to the European species *O. icenicus*, shape differences in the vertebrae of the posterior trunk and anterior tail stock distinguish the two species. The column of the Sundance ichthyosaur displays much less regionalization than does that of *O. icenicus* and its vertebral profile suggests a locomotor style more similar to that of non-ophthalmosaurid parvipelvians than to that of *O. icenicus*. Characteristics of vertebral anatomy provide a morphological rationale for the taxonomic separation of *O. natans* and *O. icenicus*.

INTRODUCTION

Most of the Jurassic ichthyosaurs known from North America have been collected from the Sundance Formation of Wyoming, known as the "Sauranodon Beds" by early workers. The Sundance Formation is middle Bathonian to middle Oxfordian in age (Brenner and Peterson, 1994; Kvale et al., 2001: fig.5). The "Sauranodon" ichthyosaurs are most likely from the unit currently identified as the Redwater Shale, the upper member of the Sundance Formation. Imlay (1982) placed the Redwater Shale in the *Cardioceras cordatum* and *Perisphincties picatilis* zones, giving it a lower to middle Oxfordian age, although recent work indicates that the lower Redwater Shale has a late Callovian age (Kvale, et al., 2001). The Redwater Shale is situated between two regional unconformities: the J4 unconformity separates it from the underlying Pine Butte Sandstone member, and the J5 unconformity separates it from the Windy Hill Sandstone, the basal member of the Morrison Formation. (Pipiringos and O'Sullivan, 1978). The Redwater Shale was deposited during the Fourth Marine Cycle, the last major transgression of the Jurassic in this part of the western interior (Brenner and Peterson, 1994; Kvale et al., 2001: fig. 5).

Othniel Marsh (1879) gave the first ichthyosaur from the "Sauranodon Beds" the name *Sauranodon natans* (Marsh, 1879), but the generic name was preoccupied. A year later (1880a), he substituted the generic name *Baptanodon*. Early workers recognized its similarity to the British genus *Ophthalmosaurus* but argued it was different enough to merit its own genus (Knight, 1903; Gilmore, 1905). However, Andrews (1910), who studied *Ophthalmosaurus icenicus* from the Oxford Clay, considered the two genera identical and most subsequent workers have followed his lead (e.g., McGowan, 1976, 1978). In contrast, Appleby (1956) compared reconstructed occipital anatomy of *Ophthalmosaurus* with that of *Baptanodon*, arguing for recognition at the generic level. One of the specimens of '*Baptanodon'* used in his analysis, although preserved in three dimensions, is somewhat deformed. Moreover, *O. icenicus* lacks a complete three-dimensional skull, making cranial comparisons difficult. Kirton (1983) and McGowan and Motani (2003) have both questioned Appleby's (1956) reconstruction. The current consensus places the Wyoming ichthyosaurs within the genus *Ophthalmosaurus* (Maisch and Matzke, 2000; McGowan and Motani, 2003).

Early workers described five species of *Baptanodon*: *B. natans* (Marsh, 1879), *B. discus* (Marsh, 1880b), *B. marshi* (Knight, 1903), *B. robustus* (Gilmore, 1906), and *B. reedi* (Gilmore, 1907). Most of these specimens were collected from northern Albany County and northeastern Carbon County, Wyoming. The larger specimens, *B. robustus* and *B. reedi* were collected from eastern Fremont County and northern Johnson County, respectively. Recently several specimens have also been collected from northern Natrona County (JAM and others).

Baptanodon reedi, *B. robustus*, and *B. marshi* are known only from incomplete type specimens. The species diagnoses focused on small differences in the forelimbs, pectoral girdle and atlas-axis, as well as the overall size of the specimens. Gilmore himself (1905) recognized that the differences were minor ones, and all of the names except *B. discus* subsequently disappeared from the literature after Gilmore's work (e.g., McGowan, 1976). Mehl (1928) collected a specimen that he named *Apatodontosaurus grayi* from the Sundance Formation of Freemont County, but the genus and species are not recognized as valid (McGowan and Motani, 2003). Recent analysis of ichthyosaur taxa by Maisch and Matzke (2000) and by McGowan and Motani (2003) have assigned all of the North American Jurassic material to a single species, *Ophthalmosaurus natans* (Marsh, 1879), largely on the basis of geography. No diagnostic characteristics have been proposed to distinguish *O. natans* from the European species *O. icenicus*, the type species for the genus (McGowan and Motani, 2003).

New material collected by one of us (JAM) allows both the reconstruction and description of a complete vertebral series for a Sundance ichthyosaur and a detailed comparison of this column with that of *O icenicus* for the first time. Motani (1999) identified short (relative to height) dorsal centra as a diagnostic vertebral characteristic of *O. icenicus*. We therefore focus on centrum shape in our comparison. Many authors have used variations in centrum morphology and shape to identify ichthyosaur column subunits, typically neck, dorsum (trunk), anterior tail (tail stock) and fluke. Buchholtz (2001b) also recognized anterior and posterior subdivisions of the tail stock in some taxa with highly regionalized columns. Centrum dimensions have also been used as indicators of vertebral column flexibility (Buchholtz, 2001a; 2001b) and may therefore also be of value in the prediction of locomotor style and ecological preference.

Abbreviations—BMNH, British Museum of Natural History, London; GPIT, Institut und Museum für Geologie und Palaeontologie der Universität Tübingen, Tübingen; LEIUG, University of Leicester, Department of Geology, Leicester; PMAG, Peterborough Museum and Art Gallery, Peterborough; SMNS, Staatliches Museum für Naturkunde, Stuttgart; UW, University of Wyoming, Laramie.

MATERIAL AND METHODS

Two large, similarly sized, and presumably adult vertebral series were used to construct a composite vertebral column of the Sundance ichthyosaur. UW 24205, designated the type specimen of *Baptanodon reedi* when it was originally described by Gilmore (1907), presently comprises 57 articulated vertebrae starting with what we interpret as the fused atlas-axis. The posterior tail stock and fluke are absent. The specimen also includes some limb material, and portions of neural arches are attached to some vertebrae. Gilmore (1907), however, indicated that the specimen had a total of 153 articulated vertebrae, as well as half of a skull and many other skeletal elements. This additional material has apparently been lost.

A second specimen, UW 34786 was collected recently from the Alcova Reservoir area, Natrona County, WY (UW locality VP- 2005-007). This specimen includes 44 articulated vertebrae from the posterior dorsal region to just posterior to the tail bend. A few isolated fluke vertebrae were also collected, but these were not articulated with the rest of the column and are not included in this analysis. In addition, many ribs and some incomplete neural arches are preserved.

Centrum length (CL), width (CW), and height (CH) were measured to the nearest tenth of a millimeter on UW 24205 and UW 34786 (Appendix). When possible, both dorsal and ventral centrum lengths were measured and then averaged to give the centrum length. When this was not possible, the centrum length was measured midway between dorsal and ventral margins. Centrum dimensions for each specimen were graphed against relative column position, scaling the precaudal region to a length of 1.0. A 3-term moving average was employed to smooth the variation and make the patterns in the data easier to see. Because some vertebrae were not separated from adjacent ones or were badly fractured, it was not possible to get all three dimensions on every centrum. When only one or two consecutive centra lacked measurements, the missing dimensions were interpolated from those of the centra immediately posterior and anterior to them. The interpolated dimensions were used only in the moving averages.

A composite column was constructed by overlapping the two incomplete specimens, using the transition from a separated diapophysis and parapophysis to a single rib facet as a means of estimating equivalence of column position. The 30 vertebrae in the overlapping portions of the two specimens are very similar in centrum dimensions (Table 1), so the specimens were not scaled relative to each other in constructing the composite. The total centrum length of the composite is about 280 cm, excluding intervertebral spacing, extending from the atlas-axis to the second fluke vertebra.

The composite specimen was compared to *Ophthalmosaurus icenicus* from the Callovian Oxford Clay of England as well as to other parvipelvians. Preference in the choice of comparison specimens was given to those with complete precaudal and anterior caudal columns. *Ophthalmosaurus icenicus* (PMAG R340) includes a nearly complete vertebral column from the atlas-axis into the partial tail fluke, 101 centra in all, making it one of the most complete specimens known. However, it displays some distortion and compression. *Suevoleviathan disinteger* (SMNS 15390), *Stenopterygius quadriscissus* (SMNS 50963), and *Eurhinosaurus longirostris* (GPIT 1025/18/1) are completely articulated skeletons from the Toarcian Posidonia Shale of Holzmaden. All are slab mounts, so centrum width could not be measured on most centra. Total preserved centrum length and vertebral counts of these specimens are compared in Table 2. As with the composite, centrum dimensions were measured to the nearest tenth of a millimeter. These specimens vary significantly in size, and their comparison was facilitated by the use of a shape index, centrum height / centrum length (CH/CL), instead of raw measurements. This ratio was calculated for each vertebra and plotted against centrum position in the column, again scaled to a precaudal length of 1.0.

TABLE 1. Average centrum dimensions (in mm) for the region of overlap between UW 24205 and UW 34786, based on the position of the last vertebra with bicipital ribs. The region of overlap is the 28th to 57th vertebrae of the composite. "diff" is the percent difference in dimension between the two specimens.

	UW 24205	UW34786	diff
length	43.5	41.7	- 4.1%
height	107.5	104.6	-2.7%
width	98.6	104.2	+ 5.7%

VERTEBRAL COLUMN OF THE SUNDANCE ICHTHYOSAUR

Description of UW 34786—UW 34786 (Figure 1B) is composed of 44 articulated vertebrae, most separated by 'intervertebral disks' of sediment that preserve the spacing of the vertebrae. The transition from separate parapophysis and diapophysis to a single facet on the centrum occurs between the 8th (two facets) and 9th (one elongated facet) vertebrae. This transition is used here not only to align the two partial columns (see below) but also to mark the precaudal / caudal transition. Thus the first eight vertebrae of UW 34786 are identified here as posterior dorsals and the 9th vertebra marks the transition from trunk to tail stock. The average length, width, and height of the first eight centra are 47.8 mm, 108 mm, and 104.4 mm respectively, typical of ichthyosaur vertebrae in general in that they are much wider and higher than they are long, and of immediately precaudal vertebrae in particular in that centrum width is greater than centrum height.

Coinciding with the transition from trunk to tail stock is a change in centrum length. Length decreases gradually from the 9th until about the 30th vertebra, posterior to which the decrease in centrum length is much more rapid. Vertebral shape also changes across the trunk / tail stock transition. The 9th vertebra has approximately equal CW and CH. Centrum height exceeds width posterior to the 9th vertebra, until at least the 25th vertebra. Posterior to that, measurements of width were not possible in the present state of preparation of the specimen. Thus the 9th vertebra marks the change in shape from CW>CH to CW<CH.

The decrease in height and length becomes much steeper between adjacent centra beginning at about the 30th vertebra, in the posterior part of the tail stock. The last fourteen vertebrae (31st to 44th) were prepared within the plaster jacket, and individual centra have not been removed because most of them are badly fractured (Figure 2A). This limits the measurements to height and length only, and those for the 38th through 43rd vertebrae are approximations.

The 25° bend in the vertebral column at about the 36th vertebra is unlikely to represent the anatomical tail bend or "knick" at the tail stock / fluke transition (Figure 2A). We locate the tail bend instead at the 40th, 41st, and 42nd centra. These centra are distinctive in that centrum margins lack the crisp edge or lip found in other vertebrae. Instead, these vertebrae are rounded in lateral view, with the maximum anterior-posterior dimension midway along the centrum height (Figure 2B). The vertebrae immediately posterior and anterior to these three, although also poorly preserved, show a more typical shape in lateral view, so it is unlikely that this feature is an artifact of preservation. We interpret the three unusual centra as the apical centra and the last two vertebrae (43rd and 44th) with dorsoventrally elongated shape, as fluke vertebrae.

The spacing between centra in ichthyosaur vertebral columns is rarely reported, although "intervertebral disks" of sediment are often present between centra in articulated specimens. In UW 34786, spacing between adjacent centra changes along the vertebral column. In the trunk, the sediment disks are about 15 mm in length. At the beginning of the tail stock, length decreases abruptly to about 10 mm. Throughout the tail stock, the intervertebral spacing increases posteriorly, even as centrum length decreases. Intervertebral spacing ranges from 10-11 mm at the start of the tail stock (from the 9th to 18th vertebra) to about 22 mm in the mid tail stock (from the 34th to 37th centra). Posterior to that, the intercentrum spacing decreases abruptly to about l0-12 mm for the remainder of the tail stock. If the general pattern is not an artifact of preservation, it suggests that

TABLE 2. Specimens of parvipelvian ichthyosaurs used in comparison of vertebral dimensions and shape. Total centrum length (CL) is rounded to the nearest 5 cm and omits intervertebral spacing. Total CL for the Sundance ichthyosaur is based on the composite constructed from the specimens listed. + indicates tail fluke is incomplete; ++ indicates specimen is incomplete.

Taxon	Specimen	precaudal count	tail stock count	total CL cm
Sundance ichthyosaur	UW 24250	35	22++	245+
Sundance ichthyosaur	UW 34786	8++	34	160++
Ophthalmosaurus icenicus	PMAG R340	39	34	210+
Suevoleviathan disinteger	SMNS 15390	44	45	300
Stenopterygius quadriscissus	SMNS 50963	46	35	175+
Eurhinosaurus longirostris	GPIT 1025/18/1	49	45	335

soft tissue variation along the column may have been extensive, especially in the tail stock, and therefore potentially important to the interpretation of regional flexibility. Whether this is unique to this species or whether it is the usual pattern among ophthalmosaurids or among parvipelvians in general requires further study.

Composite Vertebral Column—Alignment of UW 34786 and UW 24205 allows the reconstruction of the vertebral column of the Sundance ichthyosaur from the atlas-axis to the anterior end of the tail fluke. Figure 1 graphs a 3-term moving average of centrum dimensions against the relative position of the centrum along the vertebral column for each of the specimens. On UW 24205, the posteriormost double rib head occurs on vertebra 35 (labeled DB36 on the specimen). On UW 34786, the last double rib head occurs on vertebra 8. This transition was assumed to occur at the same anterior-posterior position on both specimens, indicated by the vertical line on Figure 1A and B. Other morphological transitions identify this as the trunk / tail transition as well. At about this same position on each specimen, the centrum dimensions change from CW>CH to CW<CH. Furthermore, both specimens display the same decrease in centrum length beginning at about this position in the vertebral column. Although the position of the transition from double head to single head rib is somewhat variable within a species (Motani and McGowan, 2003), the coincidence of multiple morphological transitions at this point increases our confidence in our chosen point of overlap. We therefore estimate that UW 34786 preserves vertebra 28-71.

In constructing the composite of the Sundance ichthyosaur (Figure 3A), we averaged each centrum dimension on corresponding vertebrae in the region of overlap between the two specimens to obtain the centrum dimensions for the composite. Anterior to the 28th vertebra, centrum dimensions are those of UW 24205. Posterior to the 57th vertebra, the dimensions are those of UW 34786. The total centrum length of the composite, neglecting intervertebral spacing, is about 280 cm, and includes 35 neck and trunk vertebrae, 34 tail stock vertebrae, and two fluke vertebrae.

DISCUSSION

Comparison of the Composite Column to that of *O. icenicus*—As noted above, *O. icenicus* has long been viewed as the closest relative of the Sundance ichthyosaur. After an extensive discussion, McGowan and Motani (2003) followed the "conservative course", recognizing these European and North American ichthyosaurs as two species within the genus *Ophthalmosaurus*. They noted that the only apparent differences between the two are geographic and stratigraphic. We follow their lead, but also argue that characteristics of the vertebral column document distinguishing differences and provide a morphological rationale in support of their taxonomic separation.

The number of vertebrae in the precaudal and prefluke regions has frequently been used in species diagnoses (e.g., McGowan, 1979). This regional division is more difficult to recognize in some taxa than others, and is particularly difficult to recognize in *Ophthalmosaurus icenicus*. Various authors have suggested precaudal / caudal transitions in *O. icenicus* as anterior as vertebra 27 (Appleby 1956) and as posterior as vertebra 42 (Kirton, 1983). This difficulty highlights a major morphological difference between *O. icenicus* and *O. natans* (see below): in *O. icenicus*, posterior torso vertebrae mimic those of the anterior tail stock in both shape and size. Here we use the value of 39 suggested by Buchholtz (2001b) for PMAG R340 on the basis of enlargement in neural canal size, which serves as an alternative method of locating the hind limb. The remaining count of 34 tail stock vertebrae is identical to that of the composite *O. natans.* Total prefluke counts are thus 69 and 73 respectively (Table 2), well within the range for a single species (McGowan, 1979). Moreover, the construction of the

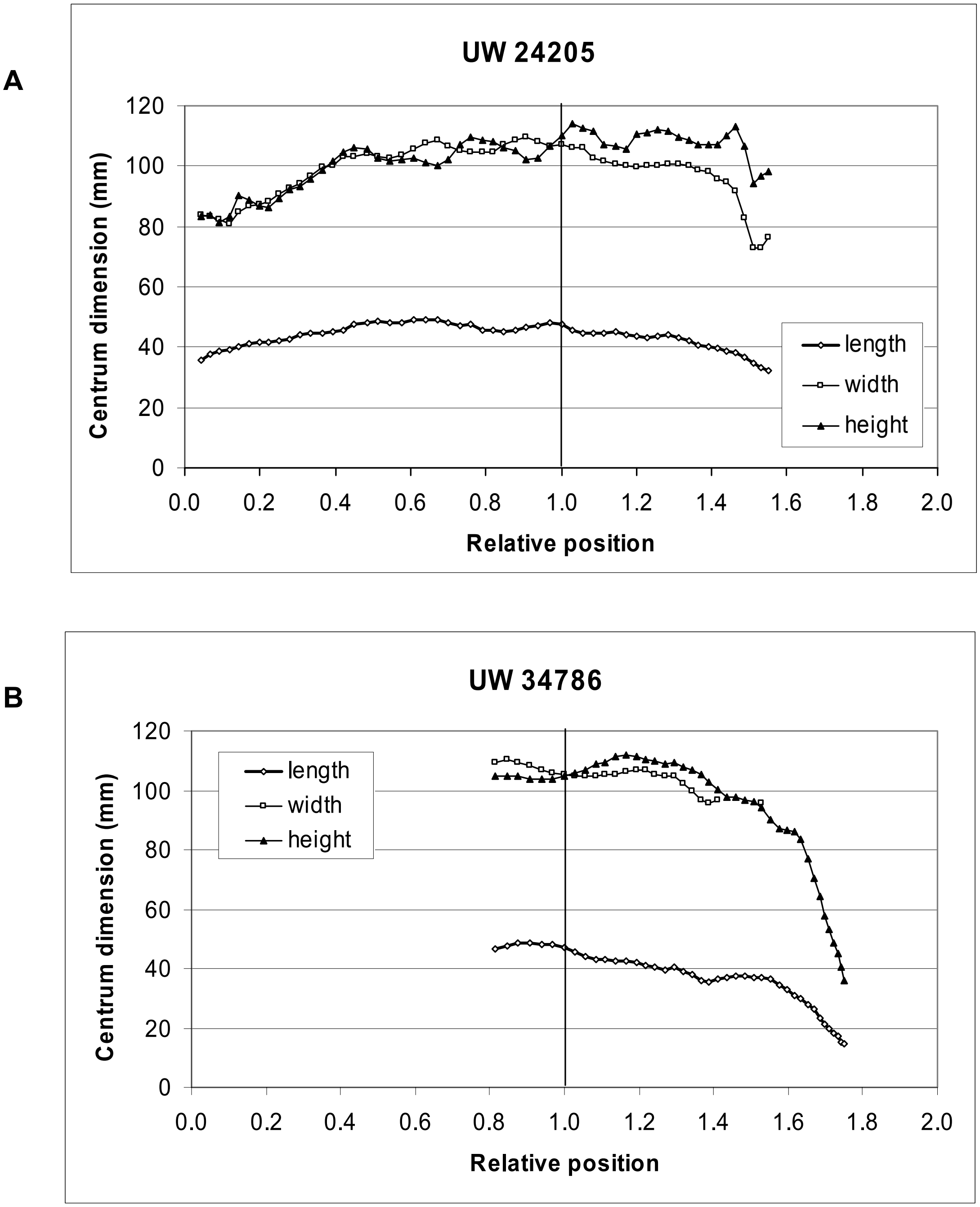

FIGURE 1. Three-term moving average of centrum dimensions plotted against the relative position along the vertebral column for two specimens of *Ophthalmosaurus natans*. Position was scaled to a precaudal length of 1.0. The transition from trunk to tail stock was taken as the change from bicipital to unicipital ribs.

composite may have introduced a small amount of error. Thus, vertebral counts do not distinguish *O. natans* from *O. icenicus*. Body proportions are also similar. In both species, the tail stock, one of the more variable features among genera (Buchholtz, 2001b), is about 0.8 the length of the precaudum.

Centrum dimensions, however, suggest that *Ophthalmosaurus icenicus* and *O. natans* represent variations on a common theme of parvipelvian postcranial morphology (Figure 3A, B). In both species, centrum height and width increase gradually throughout the trunk, reach a plateau in the posterior

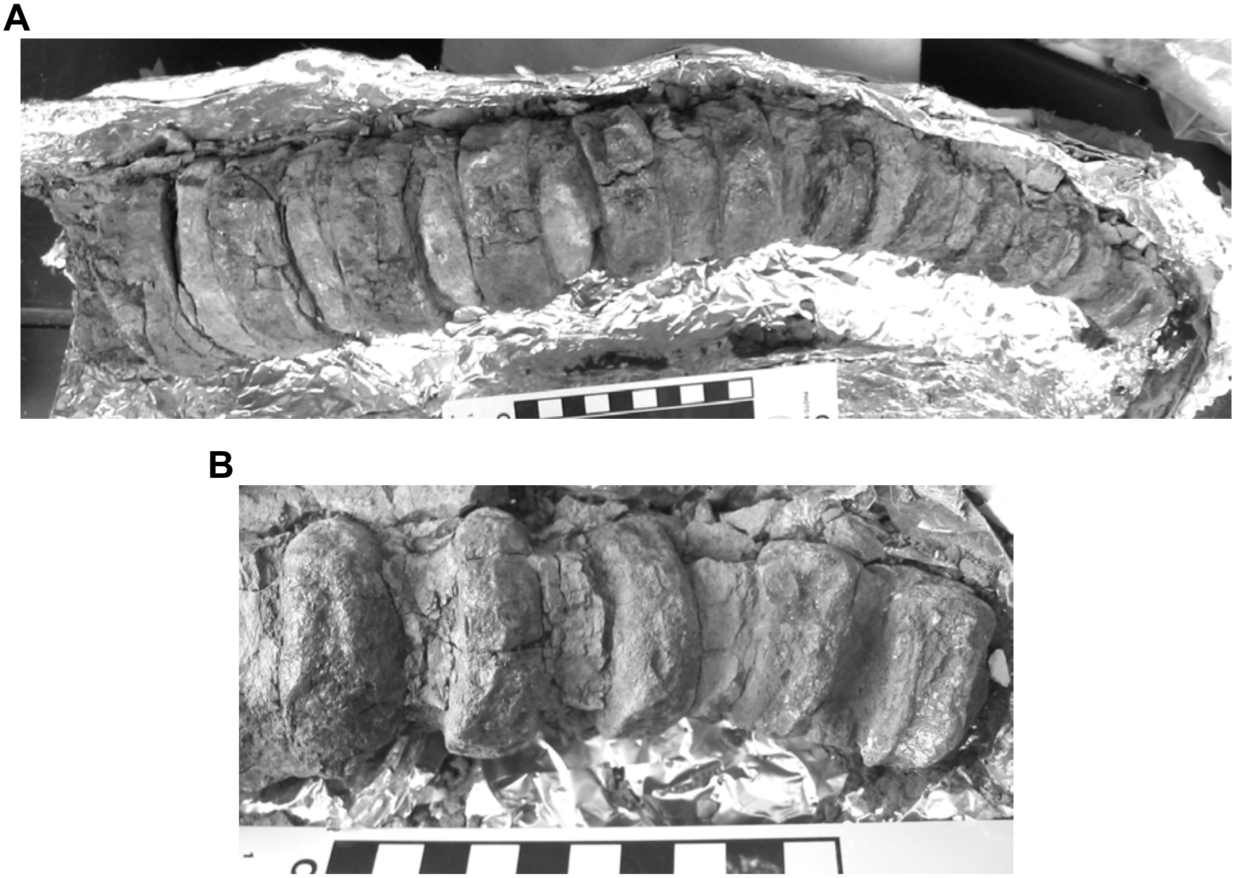

FIGURE 2. A, Posterior portion of UW 34786, from vertebra #32 to #44, showing the spacing between adjacent centra. Black bar indicates position of the apical vertebra. The tail bends downward (as shown) and also inward in the photo, foreshortening the posterior portion. B, Closer view of the last five vertebrae #40-44, showing the three apical vertebrae and two fluke vertebrae. Note the rounded shape and lack of crisp edges on the apical centra. Scale in cm.

tail stock, and then decrease fairly rapidly beyond relative position 1.5 (about 2/3 of the length of the tail stock). The pattern of centrum length, however, is different. In both species, centrum length increases until about the middle of the trunk. In *O. icenicus*, it decreases from there into the tail stock, reaching a plateau at about the middle of the anterior tail stock before decreasing again in the posterior tail stock. In *O. natans*, however, the length is fairly constant in the posterior trunk, and the gradual decrease in length occurs throughout the entire tail stock, with a slightly faster decrease in the posterior tail stock. Thus the decrease in length begins more anteriorly, in the trunk itself, in *O. icenicus* compared to *O. natans*.

What appears to be a minor difference in the pattern of centrum length produces a major difference in centrum shape, specifically in CH/CL ratio (Figure 4). From the posterior trunk to the beginning of the posterior tail stock, the CH/CL ratio is much larger in *O. icenicus* than in *O. natans*. Examination of additional partial *O. icenicus* skeletons of comparable size (LEIUG 90986, Sedgwick Museum J63920-J64036, BMNH R2180) suggests that taphonomic compression of PMAG R340 centra has reduced its CL measurements, elevating CH/CL to some extent. These additional comparative specimens display the same pattern of centrum shape seen in PMAG R340, but have maximum CH/CL values of 3.9, 3.4, and 4.0 respectively. Motani (1999) identified a centrum height/length ratio of 3.0 or larger as diagnostic of the genus *Ophthalmosaurus*, although neither Maisch and Matkze (2000) nor McGowan and Motani (2003) included this in their later diagnoses. Our data suggest that a ratio of 3.0 or greater in the anterior tail stock can distinguish *O. icenicus* from *O. natans*, at least in adults. Even though this difference is best seen in a long, articulated segment of the vertebral column, it can also be recognized on isolated centra from the posterior trunk and anterior tail stock.

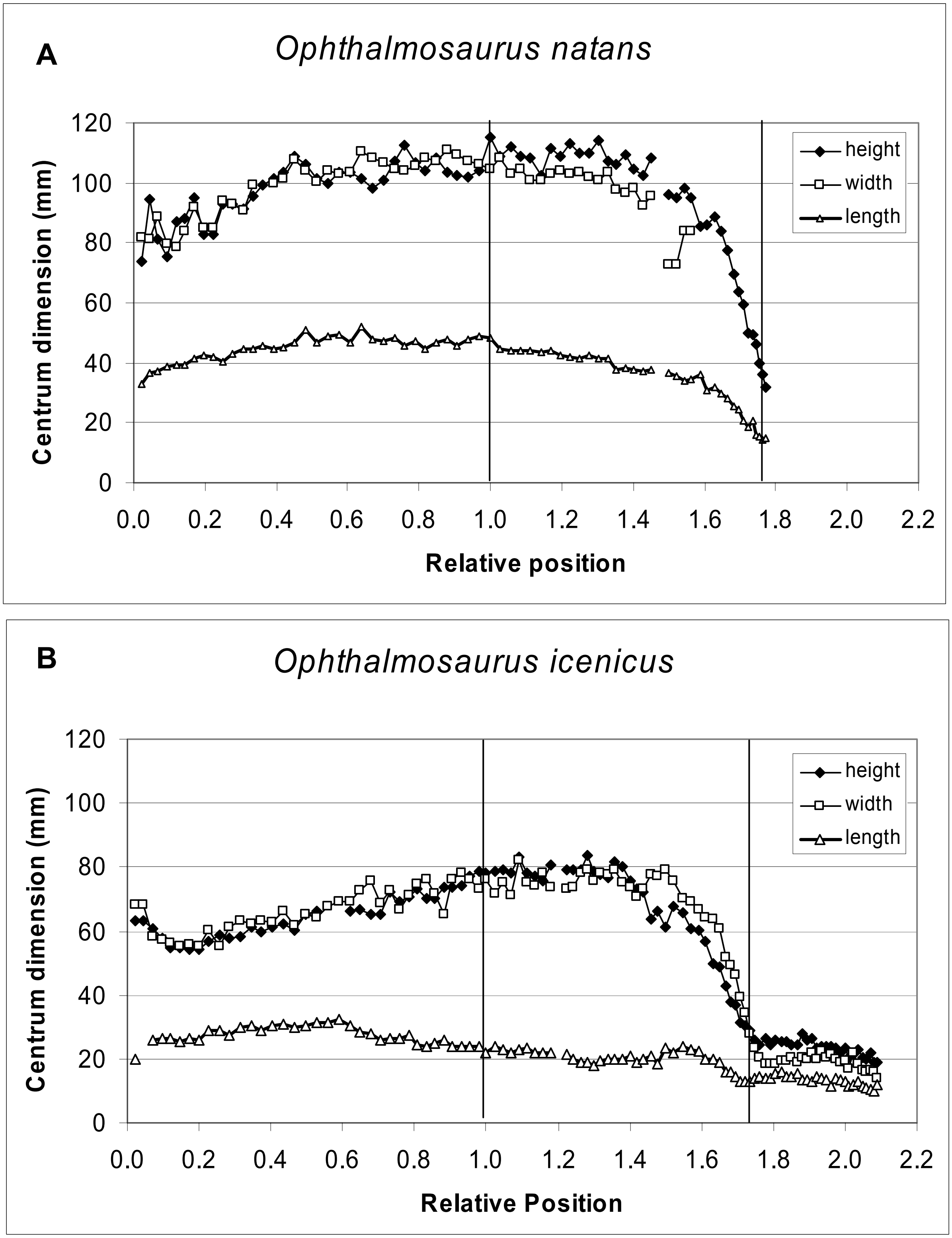

FIGURE 3. Centrum dimensions of *Ophthalmosaurus natans* (composite) and *O. icenicus* (PMAG R340). Position along the vertebral column is scaled to a precaudal length of 1.0. The vertical lines delimit the trunk, tail stock, and fluke.

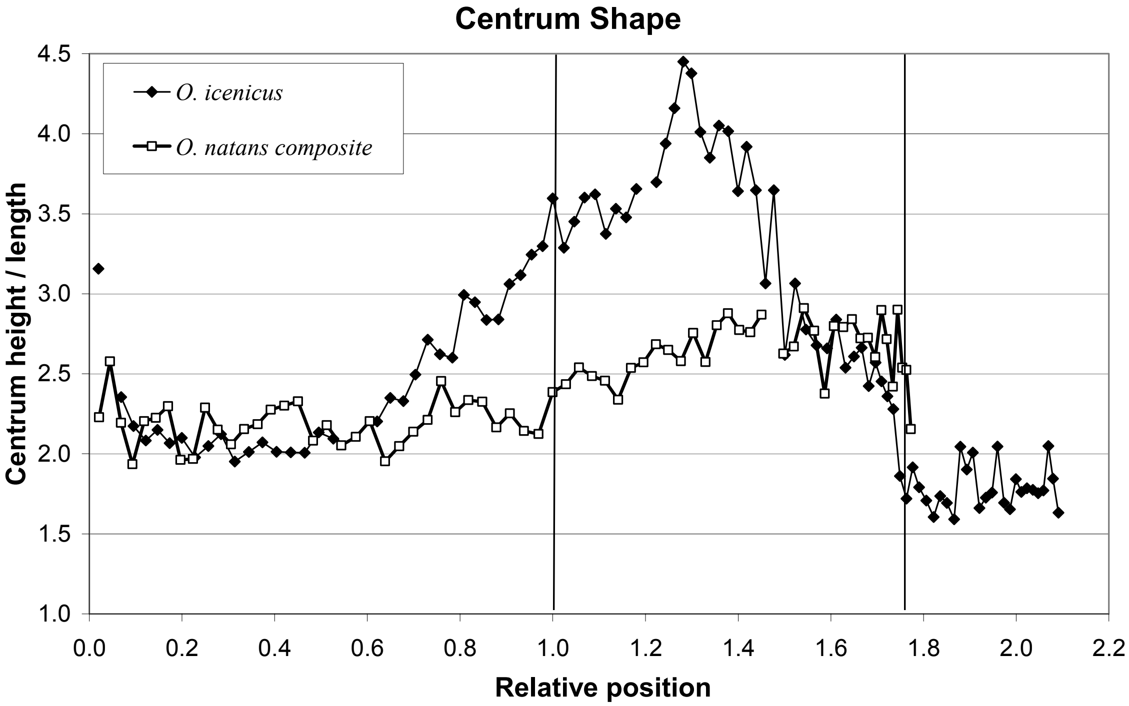

FIGURE 4. Centrum height/length ratio of *Ophthalmosaurus icenicus* (PMAG R340) and *O. natans* composite. Centrum relative position is scaled to a precaudal length of 1.0. Vertical lines delimit the trunk, tail stock, and fluke.

Parvipelvian Comparisons and Swimming Style—Buchholtz used centrum count and dimensions to predict column flexibility in living and fossil whales (2001a) and in ichthyosaurs (2001b). Discoidal vertebrae, with large CH relative to CL, are typical of column areas of reduced flexibility. The necks of cetaceans, where centrum length is greatly reduced and vertebrae may even fuse, are extreme examples. Conversely, more elongate vertebrae with low CH/CL ratios are typical of mobile column regions, typically anterior to the fluke in animals with axial locomotion.

Differences in the pattern of CH/CL between *Ophthalmosaurus icenicus* and *O. natans* indicate differences in the location and extent of column mobility. These differences are most marked in the posterior trunk and the anterior tail stock. In *O. icenicus*, the anterior trunk CH/CL ratio of 2.0 rises to 3.0 in the posterior trunk (position 0.9) and to nearly 4.5 in the anterior tail stock (position 1.3) indicating progressively more discoidal shape and less mobility in the column. The ratio then decreases rapidly across the posterior tail stock, signaling increased posterior flexibility. The column of *O icenicus* is therefore strongly regionalized, with anterior areas of limited mobility (posterior trunk and anterior tail stock) and posterior areas of enhanced mobility (posterior tail stock and fluke). The trunk / tail transition of terrestrial ancestors is barely recognizable.

In *Ophthalmosaurus natans*, variations in CH/CL ratios are much less extreme and much less regionalized. CH/CL varies minimally between 2.0 and 2.5 throughout the trunk. It increases modestly and gradually throughout the tail stock, from 2.5 to 3.0, before decreasing slightly to 2.5 at the base of the fluke. This would suggest only a minor decrease in mobility throughout the tail stock until near the base of the fluke. Thus *O. natans* lacks the marked regionalization seen in *O. icenicus*, and shows much less variation in the CH/CL ratio in the tail stock.

These differences can be put in context by comparing CH/CL ratios of these two taxa with those of the parvipelvian reference group. Two discretely different patterns of vertebral morphology are recognizable (Figure 5). *Suevoleviathan disinteger* and *Eurhinosaurus longirostris* are characterized by large vertebral count, long terminal flukes, long total column length (>2.4 times precaudal length) and minimal regionalization of centrum shape. Following Buchholtz (2001b), we interpret these elongate columns as highly mobile, and predict that these species swam with undulatory movements of the posterior trunk, tail stock, and fluke. They were likely

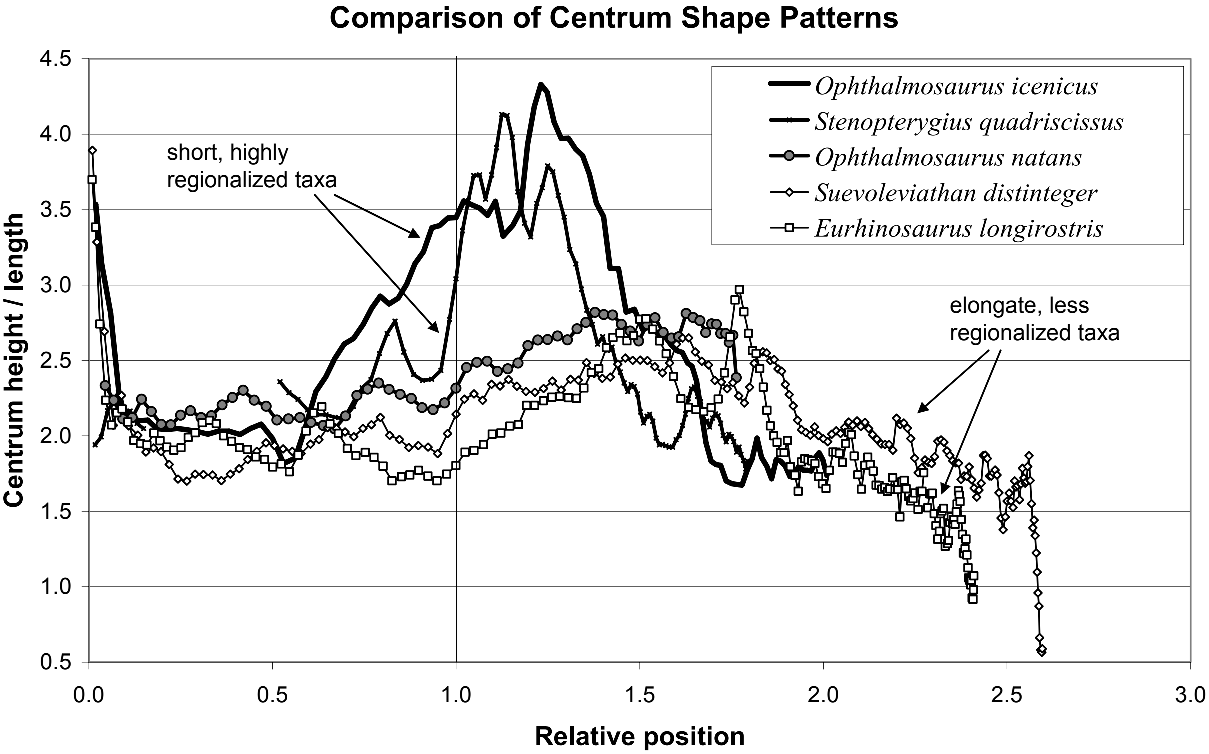

FIGURE 5. Patterns of body proportions and centrum shape (CH/CL) in parvipelvian ichthyosaurs. The column of *Ophthalmosaurus natans* shows similarities in body proportions to *O. icenicus* and *Stenopterygius quadriscissus* and similarities in centrum shape to *Eurhinosaurus longirostris* and *Suevoleviathan disinteger*.

to be agile, but capable of only moderate speeds. *Stenopterygius quadriscissus* and *O. icenicus* represent the other extreme, with much smaller counts, shorter flukes, shorter total column length (≤2.0 times precaudal length), and differentiated regions of more discoidal (posterior trunk, anterior tail stock) and more elongate (posterior tail stock) vertebrae. We interpret these columns as having reduced anterior and enhanced posterior mobility, and predict that these species had a less undulatory and more thunniform swimming style. They were likely among the fastest of the ichthyosaurs for their size. *Ophthalmosaurus natans* represents an intermediate between these extremes. It shares low count and a relatively short column with *O. icenicus* and *S. quadriscissus*, but has less extreme CH/CL ratios and minimal column regionalization, similar to *S. leviathan* and *E. longirostris*. We therefore predict that *O. natans* was a generalist in locomotor style, capable of high but not extreme speeds.

All Jurassic ichthyosaurs were fast, efficient swimmers in comparison to contemporaneous marine reptiles of the same size (Massare, 1994, 1988). As such, they likely employed pursuit, rather than ambush, predation. More subtle differences in swimming style, such as those suggested here, could have influenced the details of predation style, foraging strategy/habitat, and perhaps prey preference. The more undulatory style of *O. natans* probably sacrificed speed for maneuverability compared to *O. icenicus*. A difference in foraging habitat could take advantage of these differences: a clear, open water habitat for the faster species; a more physically complex, nearshore environment for the more maneuverable one. With regard to prey capture, *O. icenicus* may have sustained a longer, faster chase but *O. natans* would have been more successful with maneuverable prey. A difference in swimming style also has the potential to affect prey preference. Massare (1987) argued that tooth form suggested that *O. icenicus* preyed upon soft-bodied cephalopods and small fish. Interestingly, a recently discovered specimen of *O. natans* (UW 34653) from the Redwater Shale preserves gastric contents comprised of cephalopod hooklets (Massare and Young, 2005). It is unlikely then, that the general type of prey was substantially different.

CONCLUSIONS

The European species, *Ophthalmosaurus icenicus,* and the North American ichthyosaur, *O. natans*, share many cranial and postcranial similarities. They have been placed in separate species largely on the basis of stratigraphic and geographic differences. The discovery of a new specimen of *O. natans* allows an examination of its prefluke vertebral column, and provides the opportunity to compare details of vertebral anatomy. Despite similarity to *O. icenicus* in vertebral count and body proportions, characteristics of centrum shape clearly distinguish *O. natans* from the European species. These morphological differences support taxonomic separation at the specific level.

O. icenicus has a highly regionalized vertebral column, with tall, short, and therefore highly discoidal vertebrae in the posterior trunk and anterior tail stock, clearly differentiated from more equidimensional vertebrae in the posterior tail stock. In contrast, the posterior tail stock vertebrae of *O. natans* are less discoidal in shape and the tail stock shows much less regional differentiation.

Differences in centrum shape predict differences in the flexibility of the vertebral column and suggest that *Ophthalmosaurus icenicus* had a more rigid anterior column and more thunniform swimming style than did *O. natans*. Thunniform swimmers are more hydrodynamically efficient and may have faster sustained swimming speeds than non-thunniform swimmers of the same size (Massare, 1988, 1994). Swimming style thus may influence mode of predation, foraging strategy, or preferred habitat, and could indicate ecological differences between the two species as well.

ACKNOWLEDGMENTS

We dedicate this paper to Betsy Nicholls, a friend and colleague for many years. She is greatly missed. UW 34786 was excavated under permit # PA05-WY-130 to JAM from the Bureau of Land Management, and we thank the BLM staff in Casper and Cheyenne for making this research possible. The specimen was discovered by Steve Pfaff and Melissa Connely, Casper College, who generously called it to our attention. Claire Eiselen, Eshan Mitra, Melissa Connely, and Steve Pfaff assisted with the excavation. A Scholarly Incentive Grant from SUNY Brockport to JAM partially funded the excavation. Thank you to Ryan Grimm (SUNY Brockport) who prepared a major portion of UW 34786. We are also grateful to the staff of the Natural History Museum, London; Peterborough Museum and Art Gallery, Peterborough; Staatliches Museum für Naturkunde, Stuttgart; the University of Leicester Department of Geology, Leicester; the Sedgwick Museum, Cambridge; the Museum für Geologie und Paleontologie der Universität Tübingen, Tübingen; and the University of Wyoming, Laramie, for allowing access to their collections. Finally, we thank M. Fernández and R. Motani for their helpful reviews.

LITERATURE CITED

Andrews, C. W. 1910. A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay. Part I. 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.

Brenner, R. L. and J. A. Peterson. 1994. Jurassic sedimentary history of the northern portion of the Western Interior Seaway, USA, p. 217-232 in M.V. Caputo, J.A. Peterson, and K.J. Franczyk (eds.), Mesozoic Systems of the Rocky Mountain Region, USA. Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists, Special Publication.

Buchholtz, E. A. 2001a. Vertebral osteology and swimming style in living and fossil whales (Order: Cetacea). Journal of Zoology, London 253:175-190.

Buchholtz, E. A. 2001b. Swimming styles in Jurassic ichthyosaurs. Journal of Vertebrate Paleontology 21: 61-73.

Gilmore, C. W. 1905. Osteology of *Baptanodon* (Marsh). Memoirs of the Carnegie Museum 2 (2):77-129.

Gilmore, C. W. 1906. Notes on osteology of *Baptanodon*. With a description of a new species. Memoirs of the Carnegie Museum 2(9): 325-337.

Gilmore, C. W. 1907. A new species of *Baptanodon* from the Jurassic of Wyoming. American Journal of Science (4) 23:123-198.

Imlay, R. W. 1982. Jurassic (Oxfordian and Late Callovian) ammonites from the Western Interior region of the United States. U.S. Geological Survey Professional Paper 1232, 44 pp. 26 pl.

Kirton, A. M. 1983. A review of British Upper Jurassic ichthyosaurs. Ph.D. thesis (thesis number D 47227), University of Newcastle-upon-Tyne, 239 pp.

Knight, W. C. 1903. Notes on the genus *Baptanodon*, with a description of a new species. American Journal of Science 15:76-871.

Kvale, E. P., G. D. Johnson, D. L. Mickelson, K. Keller, L. C. Furer, and A. W. Archer. 2001. Middle Jurassic (Bajocian and Bathonian) dinosaur megatracksites, Bighorn Basin, Wyoming, U.S.A. Palaios 16:233-254.

Maisch, M. W. and A. T. Matzke. 2000 .The Ichthyosauria. Stuttgarter Beiträge zur Naturkunde, Serie B 298:1-159.

Marsh, O. C. 1879. A new order of extinct reptiles (Sauranodonta) from the Jurassic Formation of the Rocky Mountains. American Journal of Science (3) 17:85-86,

Marsh, O. C. 1880a. Note on *Sauranodon.* American Journal of Science (3) 91:491.

Marsh, O. C. 1880b. On the limbs of *Sauranodon*, with notice of a new species. American Journal of Science, Series 3, 19:169-171.

Massare, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. Journal of Vertebrate Paleontology 7:121-137.

Massare, J. A. 1988. Swimming capabilities of Mesozoic marine reptiles: Implications for method of predation. Paleobiology 14:187-205.

Massare, J. A. 1994. 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, U.K.

Massare, J. A. and H. A. Young. 2005. Gastric contents of an ichthyosaur from the Sundance Formation (Jurassic) of central Wyoming, Paludicola 5:20-27.

McGowan, C. 1976. The description and phenetic relationships of a new ichthyosaur genus from the upper Jurassic of England. Canadian Journal of Earth Science 13:668-683.

McGowan, C. 1978. Further evidence for the wide geographical distribution of ichthyosaur taxa (Reptilia: Ichthyosauria). Journal of Paleontology 52:1155-1162.

McGowan, C. 1979. A revision of the Lower Jurassic ichthyosaurs of Germany with descriptions of two new species. Palaeontographica, A 166:93-135.

McGowan, C. and R. Motani. 2003. Ichthyopterygia, Part 8, in H. D. Sues (ed.) Handbook of Paleoherpetology, Verlag Dr. Friedrich Pfeil; München, 175pp.

Mehl, M. G. 1928. *Apatodonosaurus*, a new genus of ichthyosaurs from the Jurassic of Wyoming. Journal of the Scientific Laboratories, Denison University 23:111-126.

Motani, R. 1999. Phylogeny of the Ichthyopterygia. Journal of Vertebrate Paleontology 19:472-495.

Pipiringos, G. N. and R. B. O'Sullivan, 1978. Principal unconformities in Triassic and Jurassic rocks, Western Interior United States-a preliminary survey. U.S. Geological Survey Professional paper 1035-A, 29 pp, 1 pl.

APPENDIX

Centrum dimensions of the two specimens of *Opthalmosaurus natans* used in constructing the composite for the species. Measurements are to the nearest tenth of a millimeter.

* measurement uncertain or taken on fractured or deformed centrum

UW 24205			
vert #	centrum width	centrum height	centrum length
1	81.8*	73.9	33.2
2	81.3	94.5	36.7
3	88.5	81.1	37.0
4	79.6*	75.3	38.9
5	78.4	87.1	39.5
6	84.0	88.0	39.6
7	91.9	95.0	41.4
8	85.1	82.9	42.3
9	85.1	82.9	42.1
10	93.9	92.8	40.6
11	93.1	92.7	43.1
12	90.6	91.4	44.4
13	99.4	95.8	44.5
14		99.3	45.5
15	100.0	101.4	44.6
16	101.5*	103.8	45.1
17	107.6	108.7	46.7
18	104.3*	106.2	51.0
19	100.3	101.3	46.5
20	104.3	100.0	48.7
21	102.8	103.5	49.2
22	103.5	103.5	47.0
23	110.5	101.2	51.8
24	108.3	98.3*	48.0
25	106.8	101	47.3
26	104.8	107.4	48.6
27	103.9	112.4	45.8
28	104.6	108.9	48.1
29	105.1	105.1	43.6
30	104.7	110.2	44.6
31	111.5	102.4	47.1
32	109.4	102.5	45.5
33	108.5	100.9	47.1
34	106.4	104	49.5
35	104.5	115	47.9
36	111.1*	111.8	44.8
37	103.0	115.6	44.7
38	103.6	110.7	44.1
39	101.1	108.4	45.6

UW 34786			
vert #	centrum width	centrum height	centrum length
1	106	104.5	46.4
2	111	103.4	45.7
3	110	106.2	48.5
4	110	104.9	48.7
5			
6	106	103.2	48.2
7			48.4
8			48.5
9	105	105.5	44.5
10	104	108.1	43.4
11	105	107.5	43.7
12			42.7
13			42.9
14	106	113.5	42.7
15	108	111.7	42.2
16	107	109.6	41.0
17	106	109.8	39.2
18	104	109.5	41.0
19			38.6
20	106	110.4	41.7
21	96.6	105.4	36.0
22			35.5
23	96.5	105.3	35.7
24	93.7	97.5	35.4
25	99.2	98.6	37.8
26		97.4	37.6
27		96.9*	37.4*
28		96.3	37.2
29	95.5	95.9	36.9
30		89.9*	36.4*
31		85.3*	35.9*
32		86.2	30.8
33		88.5	31.7
34		84.1	29.6
35		77.3	28.4
36		69.5	25.5
37		63.8	24.5
38		59.4	20.5
39		50.0	18.4

UW 24205			
vert #	centrum width	centrum height	centrum length
40	100.9*	102.3	44.6
41	100.7	109.3	45.1
42	99.4	106.0*	42.5
43	99.5	116.5	43.2
44	101.8	110.0	43.8
45	99.6	110.3	44.2
46	101.0	114.2	44.3
47	101.0	104.1	41.7
48	98.4	107.2	39.9
49	96.4	109.6	40.7
50	100.0*	104.3*	39.9
51	91.4	107.6	38.9
52	92.4	118.2	37.8
53			
54	72.8*	95.1*	35.7
55	73.0*	93.6	33.9
56	72.3*	101.0	30.8
57	84.0*	100.5*	32.4

UW 34786			
vert #	centrum width	centrum height	centrum length
40		49.6	20.5
41		46.4	16.0
42		39.6	15.6
43		36.1	14.3
44		31.9	14.8