

# A Middle Jurassic (Bajocian) ophthalmosaurid (Reptilia, Ichthyosauria) from the Tuxedni Formation, Alaska and the early diversification of the clade

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**Abstract** – Ophthalmosauridae is a clade of derived thunniform ichthyosaurs that are best known from Callovian (late Middle Jurassic) to Cenomanian-aged (Late Cretaceous) deposits in both the Northern and Southern Hemispheres. Ophthalmosaurids arose prior to the Early–Middle Jurassic boundary, however, very little is known about their diversity and distribution in the earliest phase of their evolutionary history during the Aalenian–Bathonian (Middle Jurassic) interval. Here we describe new diagnostic ophthalmosaurid material from the Early Bajocian (Middle Jurassic) of Alaska. The specimen, UAMES 3411, is a partial disarticulated skull that was discovered in the Middle Jurassic Tuxedni Formation, which was deposited in shallow marine settings outboard of the then-accreting Wrangellia composite terrane. The new material is significant in that it is the first Jurassic ichthyosaur described from Alaska, one of the oldest ophthalmosaurids known and the only Middle Jurassic ophthalmosaurid described from the Northern Hemisphere. The new material adds to a rapidly growing data set on ophthalmosaurid diversity and suggests that the clade was geographically widespread by the Early Bajocian, very early in its evolutionary history.

Keywords: Talkeetna Mountains, Ophthalmosaurinae, palaeobiogeography, systematics.

## 1. Introduction

The Jurassic Period is generally regarded as the zenith of ichthyosaur (Reptilia: Ichthyopterygia) evolution. Early Jurassic deposits, particularly in England (Hettangian–Sinemurian) and Germany (early Toarcian), have yielded a great deal of material, both in diversity and sheer number of specimens (McGowan & Motani, 2003). Important intervals from the latter part of the Jurassic, such as the late Middle Jurassic Oxford Clay Formation (Callovian) and the Late Jurassic Kimmeridge Clay Formation (Kimmeridgian–Tithonian) and Agardhfjellet Formation (Tithonian) have also produced significant amounts of material (McGowan & Motani, 2003; Druckenmiller *et al.* 2012). However, the lack of deep-water Lagerstätten during the Aalenian to Bathonian interval creates a major gap in our understanding of ichthyosaur evolution (Benson & Butler, 2011). This gap represents a critical period in the evolutionary history of the clade in that it spans a period when more basal parvipelvians typical of the Toarcian coexisted with the first ophthalmosaurids (Fernández, 1994), which arose prior to the Aalenian–Bajocian boundary (Fernández, 2003) and subsequently become the only surviving clade of ichthyosaurs by the Callovian (McGowan & Motani, 2003). To date, only three valid ichthyosaur species have been named from the Aalenian–Bathonian interval. Two represent

more basal taxa, including *Stenopterygius aaleniensis* Maxwell, Fernández & Schoch, 2012 from the Aalenian of Germany and *Chacaicosaurus cayi* Fernández, 1994 from the Bajocian of Argentina (now also referred to *Stenopterygius* (Fernández, 2007a), but for a different opinion see Maisch & Matzke, 2000; Fischer *et al.* 2011, 2012). The only named ophthalmosaurid material from this interval is *Mollesaurus periallus* Fernández, 1999, a single partial skeleton from the early Bajocian of Argentina. Thus, our knowledge of ophthalmosaurid diversity during the Aalenian–Bathonian gap remains extremely sparse and diagnostic material from the northern hemisphere is entirely lacking. This gap ends at the Callovian, with the appearance of abundant material in the Oxford Clay Lagerstätte.

In 2001, a partial disarticulated skull of an ichthyosaur was discovered in the Middle Jurassic Tuxedni Formation in southern Alaska (Fig. 1). The specimen can be confidently referred to Ophthalmosauridae on the basis of its basioccipital morphology, and is significant in several regards. It is the first Jurassic ichthyosaur material described from Alaska and the only Middle Jurassic ichthyosaur material known from North America. It is the only Middle Jurassic ophthalmosaurid recognized from the Northern Hemisphere and one of the oldest diagnostic specimens of Ophthalmosauridae known. Although Ophthalmosauridae has historically been viewed as a taxonomically impoverished clade, studies on the taxonomy and diversity of this group are undergoing a renaissance. Since the publication of the

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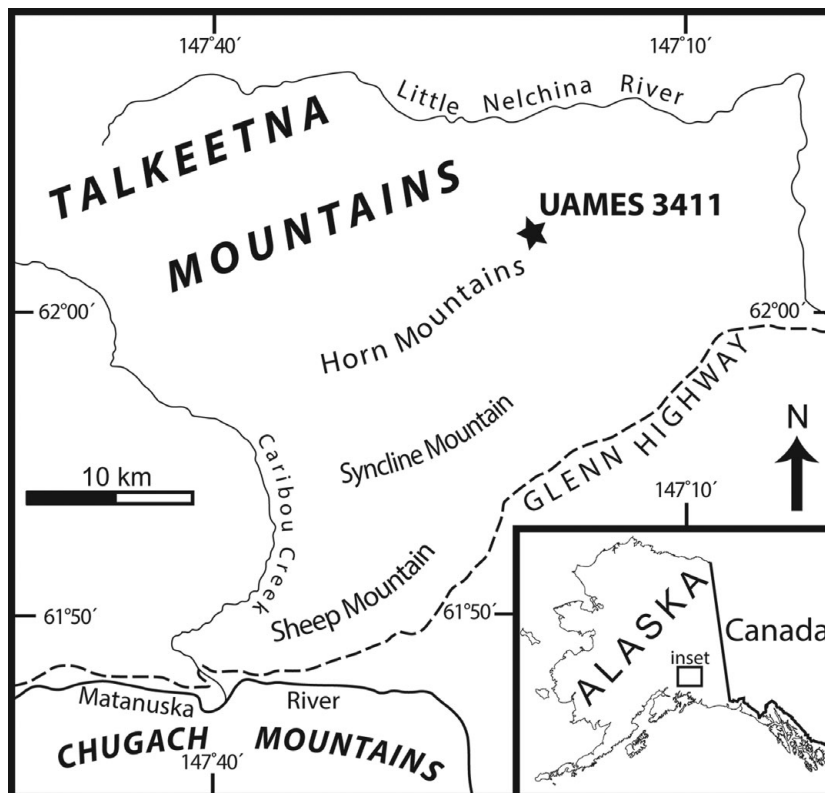


Figure 1. Discovery site of ichthyosaur UAMES 3411 in the southeastern Talkeetna Mountains, Alaska.

*Handbook of Paleoherpertology* (McGowan & Motani, 2003), the number of named genera has doubled, from 8 to 16 (Maxwell & Caldwell, 2006; Maxwell, 2010; Druckenmiller & Maxwell, 2010; Fischer *et al.* 2011, 2012, 2013; Druckenmiller *et al.* 2012). However, the early history of this important group remains poorly understood, making the current contribution extremely timely and relevant.

*Institutional abbreviations.* UAMES, University of Alaska Museum, Fairbanks; USGS, United States Geological Survey.

## 2. Geological setting

UAMES 3411 was discovered by an amateur palaeontologist in the Tuxedni Formation, where it crops out in the southeastern portion of the Talkeetna Mountains in south-central Alaska (Fig. 1). The Tuxedni Formation is part of the Wrangellia composite terrane, a massive crustal fragment that was translated northward and accreted to the western margin of North America during Jurassic and Cretaceous times (Plafker & Berg, 1994; Trop & Ridgway, 2007). In the Talkeetna Mountains, the Tuxedni Formation is approximately 300–400 m thick (Winkler, 1992) and consists entirely of shallow-marine sandstone, siltstone and shale that was deposited on a marine shelf in a forearc setting outboard (south) of a Jurassic arc pluton (Trop *et al.* 2005; Trop & Ridgway, 2007). The Tuxedni Formation is Middle Jurassic in age and in the study area lies

unconformably on Early Jurassic sediments of the Talkeetna Formation and is unconformably overlain by the Chinitna Formation, which is Bathonian to Callovian in age (Fig. 2; Imlay, 1964; Trop *et al.* 2005). The Tuxedni Formation consists of six named units in the Cook Region to the south (Detterman, 1963; Detterman & Reed, 1980), but is only subdivided in the Talkeetna Mountains into two informal units; a lower thin- to thick-bedded sandstone and an upper thin- to medium-bedded siltstone (Imlay, 1964; Winkler, 1992). The ichthyosaur was found in the lower portion of the unnamed upper siltstone unit of the Tuxedni Formation (Imlay, 1964).

The age of the UAMES 3411 is well constrained on the basis of a rich ammonite fauna associated with the specimen. Ammonoids collected from the discovery site in the course of this study are referred to several taxa also recognized by Imlay (1964) from the same locale (USGS Mesozoic locality 24113; Imlay, 1961, 1964). Notable members of this assemblage include *Parabigotites crassicosatus* Imlay, 1961, *Stephanoceras obesum* Imlay, 1964, *Witchellia adnata* Imlay, 1964, *Bradfordia costidensa* Imlay, 1964, and *Otoites* cf. *O. pauper* Westermann, 1954 (for a comprehensive list, see Imlay, 1964). Collectively, Imlay (1964) considered this assemblage equivalent to the European *Emileia* (formerly *Otoites*) *sauzei* Zone, equivalent to the northern *Sonninia propinquans* Zone (Gradstein, Ogg & Smith, 2004), which is currently recognized as middle Early Bajocian in age (Gradstein *et al.* 2012).

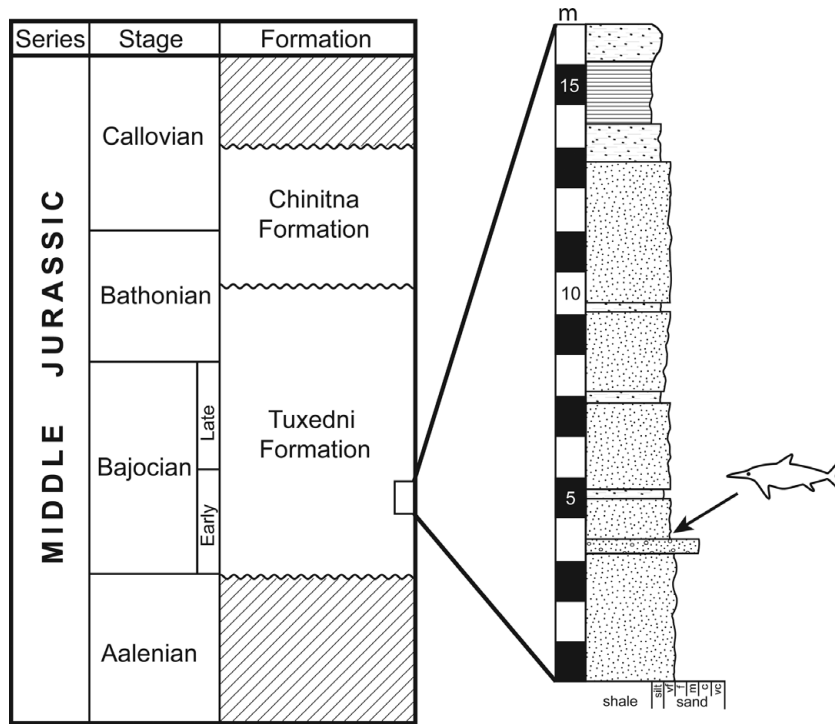


Figure 2. Stratigraphic relationships of the Tuxedni Formation in the Talkeetna Mountains, southern Alaska and the position of UAMES 3411 in a measured section at the discovery site. Stratigraphy derived from Imlay (1964), Winkler (1992) and Schaff & Gilbert (1987).

**3. Systematic palaeontology**

Order ICHTHYOSAURIA de Blainville, 1835  
 PARVIPELVIA Motani, 1999  
 Family OPTHALMOSAURIDAE Baur, 1887  
 Subfamily OPTHALMOSAURINAE Baur, 1887  
 Ophthalmosaurinae indet.  
 Figures 3–6

*Referred material.* UAMES 3411, a partial disarticulated skull including the basioccipital, stapes, quadrates, partial supratemporal and isolated fragments.

*Locality.* Approximately 2.4 km north of the mouth of Albert Creek, southeastern Talkeetna Mountains, south-central Alaska; 62° 01.698' N, 147° 17.654' W (NAD 27).

*Age and horizon.* Lower portion of unnamed siltstone member, Tuxedni Formation; middle Early Bajocian (Imlay, 1964).

**3.a. Description**

*Basioccipital.* The basioccipital (Fig. 3) is a robust element, and has suffered little taphonomic distortion (length = 44 mm; width = 77 mm; height = 40 mm). The anterior surface of the basioccipital is pitted and has a deep dorsoventrally-oriented furrow along the midline that is most conspicuous dorsally where it creates a prominent notch on the anterodorsal surface. There is no trace of a basioccipital peg or a notochordal pit on the anterior surface. In dorsal view, the basioccipital is mediolaterally broader than anteroposteriorly long, being broadest at the level of the opisthotic facets. Two large, ventrally depressed exoccipital facets occupy most of the dorsal surface but are

separated by a well-defined anteroposterior ridge that forms the floor of the neural canal. The anterolateral surface bears a prominent stapedia facet, which is taller than broad, slightly concave and faces ventrolaterally and slightly anteriorly. Immediately dorsal to this is a much smaller dorsally oriented opisthotic facet. Lying between the stapedia facet and the occipital condyle is the extracondylar area that consists of a prominent concave surface of smooth, finished bone. The extracondylar area is clearly visible in posterior view, where the lateral portions of the basioccipital projects beyond the occipital condyle (Fig. 3a, b). Ventrally, the extracondylar areas of the left and right surfaces are separated by a ridge along the midline. The occipital condyle is broadly convex posteriorly and faces somewhat ventrally in lateral view. The condyle is mediolaterally broadest in its dorsal half and bears a notochordal pit in the centre of the articular surface.

*Stapes.* A single stapes, interpreted as the right, is preserved in UAMES 3411 (Fig. 4). The stapes is a short (length = 36 mm) and robust element, with a massively expanded medial end. The medial surface is convex and bears a large posterior facet for the basioccipital and a smaller, anteriorly situated basisphenoid facet. These two facets are separated by a shallow dorsoventrally oriented groove. The dorsomedial surface of the stapes bears a narrow roughened surface corresponding to the opisthotic facet, but this area is poorly defined. The stapedia shaft is short, anteroposteriorly broader than tall and unconstricted in dorsal or ventral view. The dorsal surface of the shaft is convex while the ventral surface is concave. The anterior surface of the stapedia shaft is relatively narrower than the broadly rounded posterior margin, forming a ridge. As seen in posterior view, the middle of the shaft connects to the medial portion of stapes at a height just dorsal of its dorsoventral midpoint. In ventral view, the facet for the pterygoid and possibly supratemporal

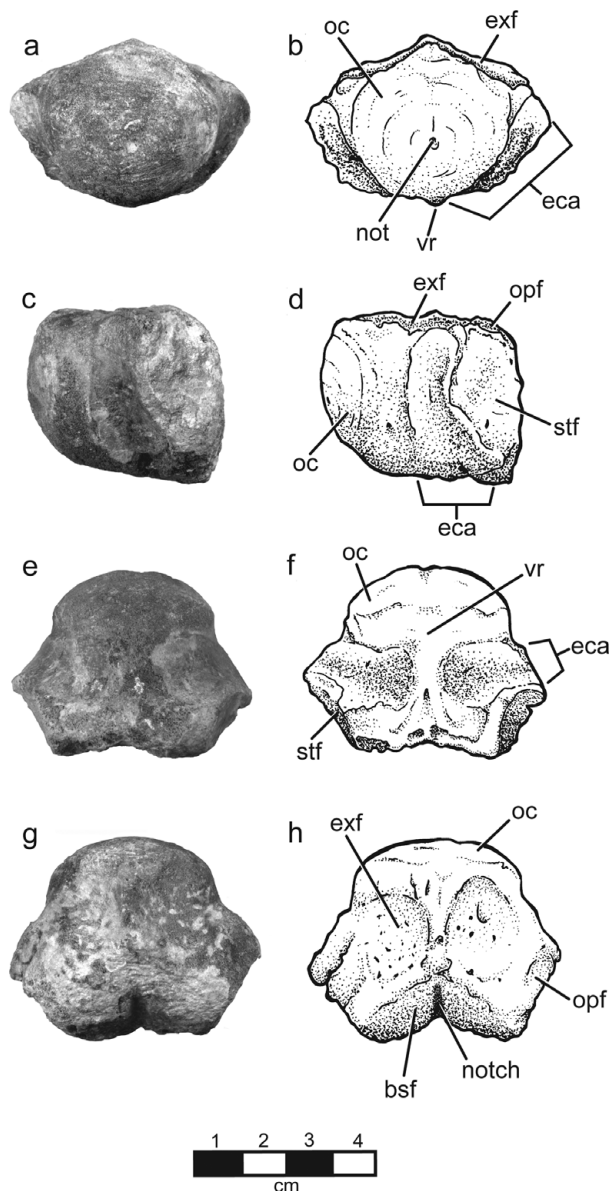


Figure 3. Photographs and interpretations of the basioccipital of UAMES 3411 in occipital (a, b), right lateral (c, d), ventral (e, f), and dorsal (g, h) views. Abbreviations: bsf, basisphenoid facet; exf, exoccipital facet; eca, extracondylar area; not, notochordal pit; oc, occipital condyle; opf, opisthotic facet; stf, stapedial facet; vr, ventral ridge.

(*sensu* Kirton, 1983) is small triangular area that lies along the anterolateral margin of the stapedial shaft. The lateral end of the stapes is not expanded and bears a small ventrolaterally-facing facet for the quadrate.

**Quadrate.** Both quadrates are preserved in UAMES 3411. The right quadrate is most complete (height = 64 mm) and is described here (Fig. 5). As seen in posterior view, the quadrate consists of a relatively narrow dorsal portion and a much wider and more robust ventral portion that includes the articular condyle with the mandible. The element is not 'C' shaped in posterior view, unlike the quadrates of many ichthyosaurs (e.g. *Ophthalmosaurus*; Kirton, 1983), due to the weakly developed lateral and medial portions of the occipital and pterygoid lamellae, respectively. The

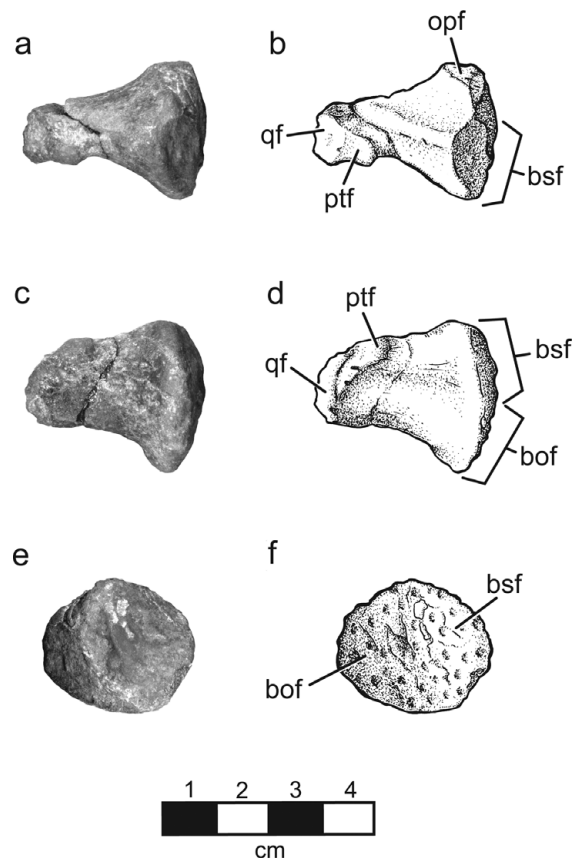


Figure 4. Photographs and interpretations of the right stapes of UAMES 3411 in anterior (a, b), ventral (c, d), and medial (e, f) views. Abbreviations: bof, basioccipital facet; bsf, basisphenoid facet; opf, opisthotic facet; ptf, pterygoid facet; qf, quadrate facet.

occipital and pterygoid lamellae are clearly separated by a dorsoventrally oriented ridge. The stapedial facet is a well-defined ovate depression located on the posterior surface of the element. Its lateral margin just contacts the ridge separating the occipital and pterygoid lamellae, forming a notch. In lateral view, the quadrate is concave; the occipital lamella is relatively thickened compared to the anteroposteriorly thin pterygoid lamella. An area of unfinished bone extends along most of the medial margin of the pterygoid lamella but ends ventrally and is not continuous with the mandibular facet. In dorsal view, the quadrate is roughly triangular in shape, with the apex of the triangle composed of the extremely thin dorsal portion of the pterygoid lamella. The dorsal surface is capped with an area of unfinished bone, presumably for articulation with the supratemporal. Ventrally, the articular condyle is largely located on the ventrolateral surface of the quadrate, and is mediolaterally wider than anteroposteriorly long. The surangular and articular facets are poorly differentiated from one another, being separated only by a broad ridge rather than a marked groove, as in *Ophthalmosaurus*.

**Supratemporal.** An incomplete supratemporal is associated with UAMES 3411, which is interpreted to be the right (Fig. 6). The lateral ramus has been lost but portions of both the medial and ventral rami are preserved three dimensionally. The medial ramus is a thickened bar of bone that forms the posterior margin of the supratemporal

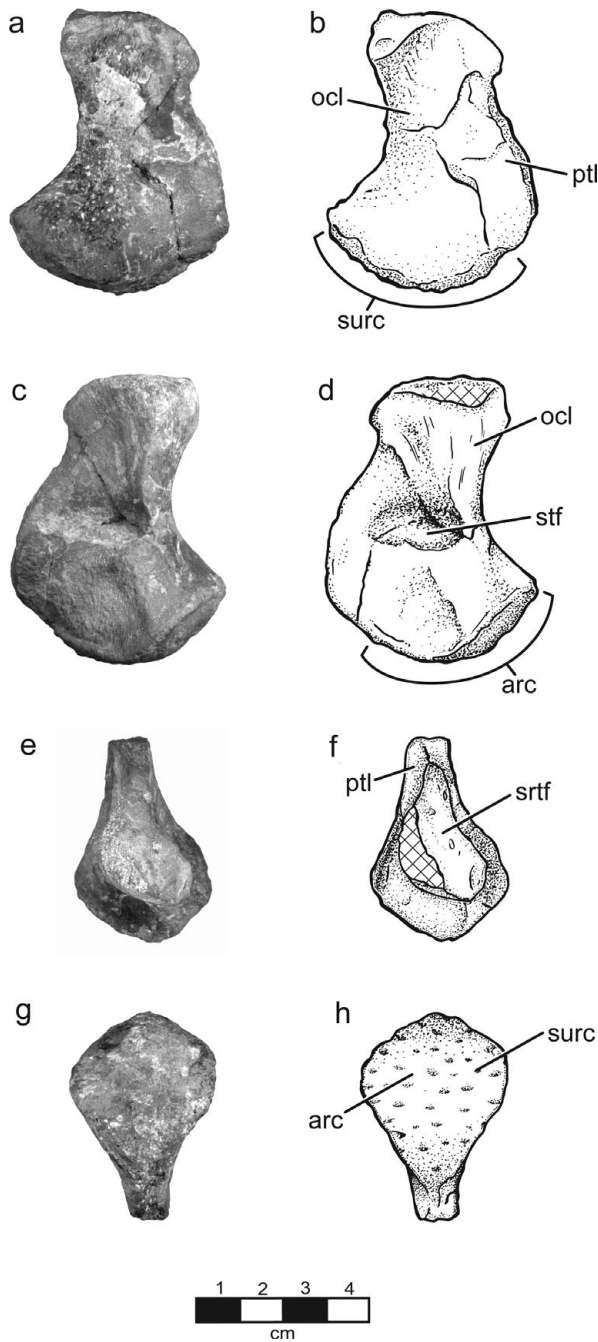


Figure 5. Photographs and interpretations of the right quadrate of UAMES 3411 in anterior (a, b), posterior (c, d), dorsal (e, f), and ventral (g, h) views. Cross-hatched areas represent damage. Abbreviations: arc, articular condyle; ocl, occipital lamella; ptl, pterygoid lamella; srtf, supratemporal facet; stf, stapedial facet; surc, surangular facet.

fenestra. Several horizontally oriented ridges and grooves are present along the anterior face of the medial ramus for articulation with the parietal. The ramus gradually tapers in size medially, but its medial-most end is not preserved. Two small tubercles are present along the occipital face of the supratemporal, near the junction of the medial, lateral and ventral rami, similar to that described by Kirton (1983) for *Ophthalmosaurus*. The bone fiber orientation on the occipital face of the supratemporal radiates outward from the tubercles and extends ventrally onto the ventral ramus. The occipital surface of the ventral ramus also bears broadly rounded

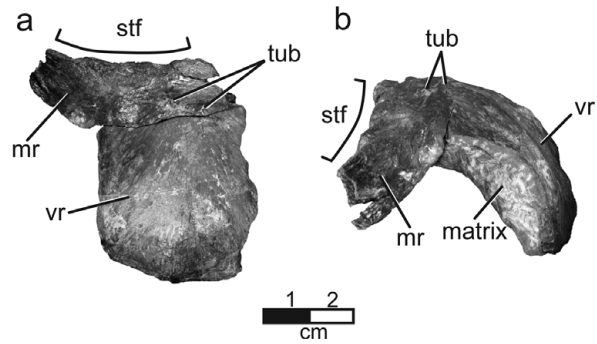


Figure 6. Photographs of the right supratemporal of UAMES 3411 in dorsal (a) and medial (b) views. Abbreviations: mr, medial ramus; stf, supratemporal fenestra; tub, tubercles; vr, ventral ramus.

ridges and swales that parallel the bone fiber orientation. The ventral ramus is a thin lamina of bone that curves nearly 90 degrees ventrally from the medial ramus. Other aspects of the morphology of the ramus are difficult to interpret as it is not complete and only partially prepared.

#### 4. Discussion

##### 4.a. Ophthalmosaurid affinities and comparison with Middle Jurassic ichthyosaurs

UAMES 3411 is referable to the Ophthalmosauridae, based on the absence of a basioccipital peg and a reduced extracondylar area (McGowan & Motani, 2003). However, the latter feature has been oversimplified and variably applied and thus requires redefinition. The extracondylar area represents portions of the lateral and ventral surfaces of the basioccipital anterior of the occipital condyle and posterior to the stapedial/opisthotic facets. Typically, the extracondylar area is surfaced in smooth periosteal bone. In basal parvipelvians (e.g. *Ichthyosaurus*) the extracondylar area is a wide sheet of bone both lateral and ventral of the occipital condyle; in posterior view, this large extracondylar area produces a basioccipital morphology that is almost square in outline, with the exception of a slight ventral notch. In lateral view, the extracondylar area projects ventrally and somewhat anteriorly so that the body of the basioccipital appears triangular (apex pointing ventrally) in outline (McGowan, 1973; McGowan & Motani, 2003). In more derived Lower Jurassic forms (e.g. *Stenopterygius*) the extracondylar area has been considerably reduced. In posterior view, the extracondylar area is partially hidden from view by the occipital condyle, and a ventral notch is absent (Maisch, 1998). When seen in lateral view, the anteroventral process is prominently visible, such that the ventral margin of the extracondylar area extends ventral to the ventral margin of the occipital condyle (Fernández, 1994; Maisch, 1998). In UAMES 3411, the extracondylar area is proportionately similar in anteroposterior length to that of *Stenopterygius*. However, in lateral view, the anteroventral process is absent and the ventral margin of the basioccipital is parallel to the floor of the

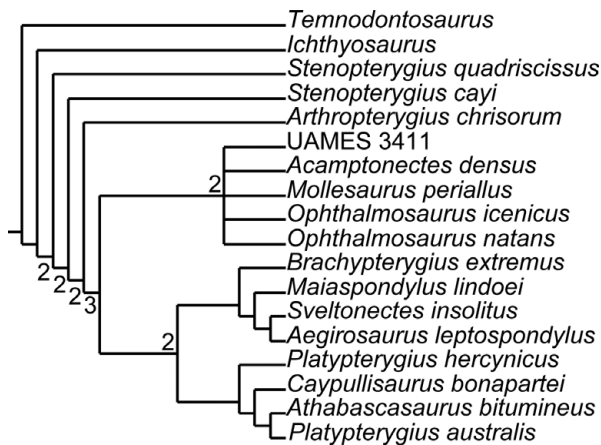


Figure 7. Phylogenetic position of UAMES 3411 and corresponding Bremer support values based on a reanalysis of the matrix of Fischer *et al.* (2012).

foramen magnum. Thus, the basioccipital of UAMES 3411 appears square to rectangular in lateral view rather than triangular, which is the typical morphology of ophthalmosaurids (McGowan, 1976; Fischer *et al.* 2011; Druckenmiller *et al.* 2012; Fischer *et al.* 2012). Similarly, in posterior view the extracondylar area has been reduced ventrolaterally so that the basioccipital no longer appears square to rectangular in outline, rather it approaches the hexagonal outline seen in *Ophthalmosaurus* and other ophthalmosaurids (Kirton, 1983). Based on the character optimization proposed by Fischer *et al.* (2012), the absence of the basioccipital peg suggests that this specimen is not from a basal ophthalmosaurid (e.g. *Arthropterygius*; Maxwell, 2010). The extracondylar area in UAMES 3411 is not as reduced as in most platypterygiines, and shows slightly less lateral reduction than ophthalmosaurine ophthalmosaurids (*sensu* Fischer *et al.* 2012). Even though the Alaskan specimen lacks a ventral notch on the basioccipital, an ophthalmosaurine synapomorphy, reanalysis of the Fischer *et al.* (2012) matrix places UAMES 3411 within the ophthalmosaurines (scorings: 17.1, 18.1, 19.1; Fig. 7), with the clade receiving the same Bremer support as in the original analysis.

Unlike the isolated forefin material described by Fernández (2003), the braincase elements described herein are clearly diagnostic beyond the level of Ophthalmosauridae. The specimen differs from other Middle Jurassic ophthalmosaurines (i.e. *Ophthalmosaurus icenicus* and *Mollesaurus periallus*) based on the morphology of all three braincase elements (Kirton, 1983; Fernández, 1999). Unlike UAMES 3411, the basioccipital of *Ophthalmosaurus* bears a notochordal pit and incipient basioccipital peg on its anterior surface. In addition to the features discussed above, the stapedial facets of UAMES 3411 do not extend as far ventrally as in *Ophthalmosaurus* and *Mollesaurus* and the opisthotic facet of *Ophthalmosaurus* is more laterally directed. In the Alaskan specimen the occipital condyle is better defined and more clearly offset from

the body of the basioccipital. In overall size relative to the basioccipital, the stapes of UAMES 3411 is relatively less massive compared to *Ophthalmosaurus* and *Mollesaurus*. Medially, the opisthotic facet of the stapes of UAMES 3411 is much less prominent than other Middle Jurassic ophthalmosaurids, and the stapedial shaft is also proportionately shorter and more dorsoventrally compressed (Kirton, 1983; Fernández, 1999). The quadrate of UAMES 3411 differs from that of *Ophthalmosaurus* in the reduction of the anterodorsal portion of the pterygoid lamella. Similarly, the dorsal portion of the occipital lamella is reduced in its posterolateral extent, so that the portion of the quadrate that forms the medial border of the quadrate foramen is less 'C' shaped than that of *Ophthalmosaurus*. Finally, the surangular and articular facets of UAMES 3411 are not as clearly separated as in *Ophthalmosaurus* (Appleby, 1956; Kirton, 1983). The Late Jurassic – Early Cretaceous genera *Caypullisaurus* and *Acamptonectes* have been described as showing a similar basioccipital morphology to *Ophthalmosaurus*, and hence to UAMES 3411, however, these genera differ dramatically in quadrate (Fernández, 2007b; Fischer *et al.* 2012) and stapedial (Fischer *et al.* 2012) morphology. Specifically, the quadrate in *Caypullisaurus* is very reduced, being dorsoventrally about as tall as the occipital condyle is wide, and is strongly 'C' shaped, as in *Ophthalmosaurus* (Fernández, 2007b). In *Acamptonectes*, the quadratojugal and surangular facets of the quadrate are much more strongly developed than in UAMES 3411. The stapes of *Acamptonectes* also has a proportionately longer, more slender shaft, and a more strongly developed medial head than in the Alaskan material (Fischer *et al.* 2012).

Unfortunately, few studies have described the posterior braincase elements of *Stenopterygius*, the proposed sister taxon to Ophthalmosauridae (Fischer *et al.* 2012). However, in *Stenopterygius cayi*, from the Bajocian of Argentina and other species of the genus, the basioccipital possesses an expanded extracondylar area as described above. The stapes bears a prominent posterodorsal notch, as described for *Ichthyosaurus*, and is hypothesized to carry the stapedial artery (McGowan, 1973). The stapedial shaft is far less dorsoventrally compressed, and more slender. The quadrate of *Stenopterygius* has never been figured in detail, and three-dimensional material of this taxon is rare.

While some authors believe that the braincase changed slowly among ichthyosaurs (McGowan, 1972), recent results have emphasized the taxonomic utility of many different aspects of braincase morphology within ophthalmosaurids (Maxwell, 2010; Fischer *et al.* 2011, 2012). There is also evidence that braincase morphology may vary substantially between closely related species (Appleby, 1956), suggesting relatively rapid rates of morphological evolution. Although UAMES 3411 can be distinguished from other ophthalmosaurids based on the material preserved, we

refrain from erecting a new taxon based solely on the supratemporal and three braincase elements.

#### 4.b. Evolutionary and palaeobiogeographical implications

Diagnostic material of Middle Jurassic ichthyosaurs is relatively rare, with only three localities producing diagnostic material known worldwide: the Aalenian Opalinuston Formation of Germany (Maxwell, Fernández, & Schoch, 2012); the Bajocian Los Molles Formation of Argentina (Fernández, 1994, 1999); and the well known Callovian Oxford Clay Formation of England (Appleby, 1956; Kirton, 1983). Although ichthyosaurian remains are not rare in the Oxford Clay, only a single genus and species is currently considered to be present: *Ophthalmosaurus icenicus* (Kirton, 1983; McGowan & Motani, 2003). The Alaskan specimen represents the first diagnostic evidence of Ophthalmosauridae in the Middle Jurassic of North America, and also significantly extends the temporal distribution of the clade backward from Oxfordian-aged material (*Ophthalmosaurus natans*) in the Redwater Shale Member of the Sundance Formation of Wyoming (McGowan & Motani, 2003). (Note that a latest-Callovian age has been proposed for the lower part of the Redwater Shale; see Massare *et al.* 2006 for a summary.) The occurrence of ophthalmosaurine material in Alaska also suggests that this subclade had achieved a widespread distribution by the Early Bajocian, within approximately one million years after the first occurrence of Ophthalmosauridae at the Aalenian–Bajocian boundary (Fernández, 2003). Apart from the Argentinian material, Bajocian ichthyosaur remains are also reported from Germany and Chile, although these constitute isolated vertebrae and other fragments (Quenstedt, 1856–1858; Fraas, 1891; Huene, 1922; Fernández, 2007a) and are not diagnostic at the family level.

In spite of some limitations imposed by the fragmentary nature of the material, it can be stated with confidence that the Alaskan specimen cannot be referred to any known Middle Jurassic ichthyosaur, including *Stenopterygius* spp., or the ophthalmosaurids *Ophthalmosaurus* and *Mollesaurus*. Given the paucity of material from the Aalenian–Bathonian interval, the specimen considerably enhances our knowledge of ichthyosaur diversity in the Middle Jurassic by doubling the number of diagnostic ophthalmosaurids present in the Bajocian (from one to two), and increases to five the total number of forms from the entire Aalenian–Callovian interval. UAMES 3411 also indicates that ophthalmosaurids were widespread and present in both the Northern and Southern hemispheres early in their history. Marine reptile diversity estimates are low for the Bajocian (Bardet, 1994), with the eastern Pacific (Argentina and Chile) representing one of the only regions producing diagnostic material from this time interval (Gasparini & Fernández, 2006). However, globally, the number of fossiliferous marine formations of Bajocian age is relatively high (Benson *et al.*

2010). The present study emphasizes the importance of reconnaissance field work in formations not previously known to produce vertebrate material and sampling outside of known localities (i.e. Neuquén Basin and the Oxford Clay) to improve our understanding of the radiation and dispersal of new clades.

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