SHORT COMMUNICATION

AN UPPER TRIASSIC (NORIAN) ICHTHYOSAUR (REPTILIA, ICHTHYOPTERYGIA) FROM NORTHERN ALASKA AND DIETARY INSIGHT BASED ON GUT CONTENTS

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

In 1950, the partial skeleton of a large vertebrate was discovered in the western Brooks Range of Alaska by a team of geologists mapping the U.S. Naval Petroleum Reserve No. 4 (now National Petroleum Reserve—Alaska). Because the preserved portion of the specimen was large (approximately 4 m in length) and found in an extremely remote location (Fig. 1), it was not collected at the time of discovery, although the site was subsequently revisited at later dates by geologists familiar with the find. A brief note mentioning the skeleton and its probable age was published 23 years later (Tailleur et al., 1973); however, the identity of the skeleton as an ichthyosaur, though suspected, was equivocal. In 2002, the specimen was relocated and collected by a team from the University of Alaska Museum, where it is now housed.

The skeleton, UAMES 2437, is significant in several regards. First, its identity as an ichthyosaurian is confirmed, making it the first ichthyosaur ever found in Alaska and also the largest and most complete specimen of this clade known from the state. The skeleton is one of only a handful of other identifiable ichthyosaurs known from Alaska (Druckenmiller and Maxwell, 2013) and represents the northernmost occurrence of any well-preserved Triassic ichthyosaur in North America. Given that the global record of ichthyosaur diversity from the Late Triassic—and particularly the Norian—is poor, the specimen helps to bridge the evolutionary gap between the much better known faunas from the Middle Triassic and Early Jurassic. The specimen is particularly remarkable in preserving a discrete mass of comminuted remains of vertebrates and invertebrates within the body cavity that are most easily interpreted as gut contents, thereby providing valuable insight into the diet and ecology of Late Triassic ichthyosaurs.

Institutional Abbreviations—Gmr, Geological Survey of Guizhou Province, Guiyang, People’s Republic of China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People’s Republic of China; UAMES, University of Alaska Museum, Fairbanks, U.S.A.

GEOLOGIC SETTING

In northern Alaska, Triassic marine rocks crop out across most of the northern front of the Brooks Range and extend into the North Slope subsurface. In the north-central and western Brooks Range, Lower Triassic–Lower Jurassic rocks make up the Otuk Formation (Mull et al., 1982) characterized by condensed, deeper-water facies of organic-rich mudrocks, bedded chert and limestone, all rich in bivalves and radiolarians (Bodnar, 1984; Blome et al., 1988; Kelly et al., 2007). The Otuk Formation (Fig. 2) contains the informally designated shale, chert, and limestone members (Patton and Tailleur, 1964) and the formally designated Blankenship Member (Mull et al., 1982; Bodnar, 1984; Blome et al., 1988). Biostratigraphically significant bivalves are rare in the Otuk shale member but become increasingly common in the middle to upper chert member and limestone member (Kelly et al., 2007). The Carnian–Norian boundary in the lower chert member is constrained by the stratigraphic position of Halobia ornatissima, H. beyrichi, and H. cordillerana (Fig. 2). The Triassic–Jurassic boundary is located at the top of the limestone member and is constrained by the stratigraphic position of Monotis subcircularis in the lower limestone member and Otapirota tailleuri in the overlying Blankenship Member (Kelly et al., 2007).

The ichthyosaur was collected at Cutaway Creek (Fig. 1) from the Otuk limestone member, which contains thin chert interbeds (Tailleur et al., 1973). Bivalve biostratigraphy indicates that the limestone member is late Norian in age (Kelly et al., 2007), and this is corroborated by recent work on a subsurface drill core that penetrated the Otuk Formation near the Red Dog massive sulfide deposit that documented late Norian radiolarians in the limestone member (Dumoulin et al., 2011). Kelly et al. (2007) interpreted the limestone member as the final portion of a late Norian progradational event. The lack of wave- or current-derived sedimentary structures and the trace and body fossils observed suggest deposition below storm wave base in an outer neritic to inner bathyal setting.

MATERIALS AND METHODS

The specimen was mechanically prepared using an air abrasive and sodium bicarbonate powder in order to remove an encrusting layer of lichen. Due to the extreme hardness of the matrix, a hammer and chisel were selectively used to remove pieces of matrix, particularly in the forefin area. Measurements less than 10 cm were made with dial calipers. A skeletal map (Supplementary Data, Fig. S1) was derived from a digital photomontage made in Adobe Photoshop CS3 and verified through examination of the actual specimen. Petrographic thin sections were prepared from the rock surrounding the skeleton. Small pieces (<2.0 cm long) of matrix and macerated organic material from the probable gut contents were also removed from the block in

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order to examine the microstructure of the nacreous remains. The specimens were embedded in Epon 815 epoxy resin, sectioned, etched in a 10% hydrochloric acid solution for 15 seconds, semi-polished, rinsed in tap water, and air dried. Acetate peels (2.0 mm slabs) were prepared and examined by light microscopy. Scanning electron microscopy (SEM) was used to examine matrix from the area of the gut contents and to determine elemental abundances of individual fragments.

DESCRIPTION AND COMPARISONS

UAMES 2437 is a partial skeleton of a large ichthyosaur including fragments of the skull, numerous dorsal ribs and gastralia, badly weathered portions of the pectoral and pelvic girdles, a partial forefin, a single femur, and numerous poorly preserved fragments. Most of the skull and the entire caudal region are missing, as are the majority of the paddle elements. The specimen was found lying on its right side in a semi-articulated state (Supplementary Data, Fig. S1). Although most of the dorsal ribs lie nearly in life position, no complete vertebrae are preserved, although a few partial vertebral impressions are visible. The gastralia are largely distributed in three discrete clusters located at the anterior, middle, and posterior regions of the torso. The specimen was collected as a single block measuring 3.5 m long and averaging 0.9 m wide. Given that the torso (as measured from the preserved portions of the forefin to the femur) is reasonably well articulated, and assuming the body proportions are roughly equivalent to that of a nearly complete articulated skeleton of _Guizhouichthyosaurus tangae_ (IVPP V 11853; Shang and Li, 2009), then UAMES 2437 had an estimated body length of 7.3 m.

Due to the limited degree of taxonomically informative material preserved on UAMES 2437, the following description summarizes the taxonomically important features of the specimen, primarily those of the appendicular skeleton. Comparisons are made with other large (greater than 3 m body length) ichthyosaurs from the Middle–Late Triassic. We follow the recent work of Ji et al. (2013) in retaining _Shastasaurus pacificus_, _Guizhouichthyosaurus tangae_, _Guanlingosaurus liangae_, _Shonisaurus popularis_, and _Shonisaurus sikanniensis_ as distinct and valid taxa for the sake of clarity in the comparisons made in this paper. A complete description of the specimen is provided in Supplementary Data (Figs. S1, S2).

Three possible fragments may be cranial in origin, but are nondiagnostic (Fig. S1). The vertebrae are largely missing, and a presacral count is not possible. The morphology of the pectoral girdle and humerus cannot be discerned; however, three proximal limb elements were found in the anterior portion of the skeleton, the most proximal of which is interpreted to be the radius (Fig. S2). Two smaller and more distal elements are interpreted as the radiale and ulnare, but no other portions of the forelimb are preserved. Assuming the preserved forelimb elements are correctly identified as the radius and proximal mesopodials, they differ markedly from the strongly notched preaxial and postaxial margins of _Cymbospondylus piscosus_ Leidy, 1868, and the anteriorly convex margin of _Shonisaurus sikanniensis_ Nichols and Manabe, 2004. The subrectangular morphology of the radius more closely resembles that seen in _Besanosaurus leptorhynchus_ Dal Sasso and Pinna, 1996, _Himalayassaurus tibetensis_ Dong, 1972, and _Shonisaurus popularis_ Camp, 1976; however, in so far as can be discerned, the radius of UAMES 2437 lacks the conspicuous preaxial notch of _Besanosaurus_ and _Guanlingosaurus liangae_ (Yin et al., 2000) and is notably longer than wide compared with that of _Guizhouichthyosaurus tangae_ (Yin et al., 2000; Shang and Li, 2009) and _Himalayassaurus_. The preserved mesopodial elements, including the possible radiale, lack any indication of notching and thus differ from _Shastasaurus pacificus_ Merriam, 1895, and more closely resemble the discoidal morphology of _Guizhouichthyosaurus tangae_ and _Shonisaurus popularis_; however, the ulnare of UAMES 2437 lacks the prominent articular peg seen in the latter taxon (McGowan and Motani, 1999). Among hind limb elements, only comparisons with the femur are possible (Fig. S1). The femur most closely resembles that of _Shastasaurus pacificus_, _Shonisaurus_, and _G. tangae_ in overall proportions and morphology. In comparison, the femur of _Besanosaurus_ is shorter and broader, whereas that of _Cymbospondylus_ is notably more elongate. The distal ends of the mid-dorsal ribs of UAMES 2437 are not expanded into swollen knobs as depicted for both _Shonisaurus popularis_ (Camp, 1980) and _Shonisaurus sikanniensis_ (Nicholls and Manabe, 2004). The median elements of the gastralia clearly lack the prominent anterior spinne seen in _Cymbospondylus buchseri_ (Sander, 1989).

In summary, UAMES 2437 broadly resembles other large Late Triassic merriamasaur in overall size and in the morphology of the forelimb. Further, the apparent absence of triradiate posterior gastralia is also consistent with our identification of it as a merriamosaur (McGowan and Motani, 2003). However, a lack of well-preserved diagnostic material precludes its referral to any known species, nor is it sufficiently different to warrant the erection of a new taxon. Given the available material, we thereby consider it to be a basal merriamosaurian with probable affinities to _Shastasaurus_, _Shonisaurus_, and/or _Guizhouichthyosaurus_.

Gastric Mass

A discrete mass of comminuted organic fragments occurs in the anterior half of the rib cage (Figs. 3, S1). The mass is ovoid in shape and has a maximum length of 58 cm and a maximum width of 29 cm. The remains are visible between the ribs and are densely concentrated in the matrix. The margins of the mass are...
the presence of any hooklets within the gastric mass region. A detailed inspection did not reveal
surrounding the skeleton. Many of these fragments are thin and scale-like. SEM elemental
analysis of the fragments show peaks of calcium and phosphorus, whereas the surrounding matrix is dominantly silica, most likely
derived from radiolarians that were noted in abundance in thin
sections. Based on their color, texture, composition, and shape, these remains are interpreted as bony tissue and most likely
scales and broken bones of osteichthysans. No fish teeth or other
identifiable skeletal elements were observed.

A second conspicuous type of remains, although not as abundant
as the first, consists of thin fragments of red and green iridescent
material with a nacreous luster, which stand out conspicuously in reflected light, especially on freshly broken,
dark surfaces (Fig. 3D, F). These remains are interpreted as frag-
mented nacreous mollusk shell. Acetate peels of the nacre reveal
some relict microstructure, but it is poorly preserved. There is no
evidence for any well-defined prismatic outer shell layer typical
of a Triassic bivalve (Carter, 1990). Likewise, there is little evi-
dence for columnar stacking of the nacre tablets found in gastro-
pods (Chateigner et al., 2000; Dauphin, 2006). The thinness of the
fragments, their lack of a strong prismatic outer shell layer,
and the curvature suggest that they are most likely derived from
cephalopod shells.

**DISCUSSION**

**Gut Contents**

Given its size, location, and distribution, the mass of commi-
nuted remains is interpreted as incompletely digested remains
within the alimentary canal, referred to here simply as gut con-
tents. The most commonly preserved gut contents in ichthyo-
saurs consist of dense concentrations of dibranchiate cephalopod
hooklets (Moore, 1856; Pollard, 1968; Rieber, 1970; Keller, 1976;
Böttcher, 1989; Brinkmann, 2004; Buchy et al., 2004; Massare
and Young, 2005; Lomax, 2010), reinforcing a view that many
ichthysaur species were specialist predators on cephalopods
(Massare, 1987). Less frequently, the remains of fish (Buckland,
1836; Pollard, 1968; Keller, 1976; Böttcher, 1989; Kear et al., 2003),
have been reported in the gut contents of ichthysaurs, whereas phosphatic nodules have been
interpreted as partially digested bone (Kear et al., 2003). Rare
occurrences of non-prey items, such as wood (Keller, 1976),
sand, and pebbles (Cheng et al., 2006), were presumably ingested accidentally.

The preserved gut contents in this specimen consist of phos-
phatic residue interpreted as osteichthyan bones and scales,
together with cephalopod shell fragments. Although vertebrate
remains have been reported among the gut contents of other ich-
thyosaurs, the presence of mollusk shell is unusual. Interestingly,
a Late Triassic (Carnian) ichthysaur fossil from China (Cheng
and Chen, 2007) referred to the genus *Panjiangsaurus* (likely a subjective junior synonym of *Guizhouchiyousaurus tangae*
(Wang et al., 2008; Shang and Li, 2009)) also contains preserved
gut contents comprising vertebrate bone fragments and mollusk shell, similar to the specimen reported here. However, these
fragments were interpreted as bivalve remains, not cephalopod. Similarly, Camp (1980) reported a mixture of vertebrate remains
and mollusk shell in the gastric contents of *Shonisaurus popularis*.

Given the potential phylogenetic affinity between *Guizhouchiyousaurus tangae* and UAMES 2437, a generalist/opportunistic
feeding ecology encompassing vertebrate and shelled inverte-
brate prey might be characteristic of a group of closely related

**FIGURE 2.** Stratigraphy of the Otuk Formation, reference section, Tigliukpuk Creek, central Brooks Range (after Bodnar, 1984; Kelly et al., 2007). Stratigraphic column illustrates geologic age, lithostratigraphic units, lithology, and average grain size. Vertical scale shown in meters. Tigliukpuk Creek is approximately 240 km to the east and much thicker than the more distal Cutaway Creek Section. Stratigraphic sections closer to Cutaway Creek are significantly thinner (total Otuk Formation at Tiglukpuk Creek = ~45 m, shale member = 10 m, chert member = 17 m, limestone member = 10 m, Blankenship Member = 8 m; Mull et al., 1982). Abbreviations: Anis., Anisian; Blank. Mb., Blankenship Member; LSM, limestone member.
Triassic ichthyosaurs. However, the mollusk fragments reported from *G. tangae* were identified as bivalve shell, creating an apparent disparity between the inferred dietary mode of *G. tangae*, which seemingly included benthic and pelagic prey, and that of UAMES 2437, which apparently fed on pelagic shelled cephalopods and fish. Given that microstructural analysis is necessary to identify taxa that produce nacreous shell and that the reasons for the identification of the mollusk fragments in *G. tangae* were not fully explained (Cheng and Chen, 2007), a reexamination of the mollusk fragments associated with *G. tangae* is warranted.

Other Late Triassic ichthyosaurs, including *Shonisaurus* and *Shastasaurus*, have been interpreted as specialist predators of cephalopods based on reduced dentition and other purported similarities with teuthophagous whales (McGowan and Motani, 1999; Nicholls and Manabe, 2004; Sander et al., 2011), although this interpretation has been challenged (Motani et al., 2013; Ji et al., 2013). Unfortunately the condition of this specimen precludes comparison of its dentition or skull morphology with the direct evidence of diet recorded by the gut contents.

FIGURE 3. Detailed views of the gastric mass of UAMES 2437. A, location of images B–E (*F* is an isolated fragment from the gastric mass collected separately): B, unfossiliferous matrix from outside the gastric mass; C, macroscopic view of weathered fossiliferous matrix, showing numerous light colored fragments of bone lying between dorsal ribs; D, unweathered fossiliferous matrix found between the dorsal ribs showing a large fragment of cephalopod nacre and concentrated bone fragments; E, magnified view of black, unweathered bone fragments; F, magnified view of bluish, weathered bone fragments and iridescent cephalopod nacre. *Abbreviations:* bf, bone fragment; fmtx, fossiliferous matrix; ig, ichthyosaur gastralium; ir, ichthyosaur dorsal rib; n, nacre; umtx, unfossiliferous matrix. Scale bars equal 25 cm in A, 5 mm in B–D, and 1 mm in E–F.
The majority of preserved ichthyosauarian gut contents are reported from Jurassic or Cretaceous fossils and thus represent a relatively advanced stage of ichthyosaur evolution. Gastric residues from Triassic ichthyosaurs are comparatively rare—although they have been reported from several specimens (Rieber, 1970; Camp, 1980; Brinkmann, 2004; Bucky et al., 2004; Cheng and Chen, 2007; Bucky, 2010). The mix of vertebrate and mollusk shell fragments in the preserved gut contents of UAMES 2437 and previously reported for Guizhouchiichthyosaurus tunganensis (Cheng and Chen, 2007) and Shonisaurus popularis (Camp, 1980) suggests that Triassic shastasaurians fed on a variety of prey. In contrast, gut contents reported for other Triassic ichthyosaurs consist of cephalopod hooklets (Rieber, 1970; Brinkmann, 2004; Bucky et al., 2004), more typical of Jurassic and later ichthyosaurs. Triassic ichthyosaurs occupied a range of predatory guilds, as indicated by substantial variation in dentition and body size, possibly more than their Jurassic and Cretaceous counterparts (Callaway and Massare, 1990), and probably played an important role in Triassic marine food webs as apex predators that fed upon multiple trophic tiers (Fröbisch et al., 2013).

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