

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

PATRICK S. DRUCKENMILLER,^{*1,2} NEIL KELLEY,^{3,†} MICHAEL T. WHALEN,² CHRISTOPHER MCROBERTS,⁴ and JOSEPH G. CARTER⁵; ¹University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775, U.S.A., psdruckenmiller@alaska.edu; ²Department of Geosciences, University of Alaska Fairbanks, 900 Yukon Drive, Fairbanks, Alaska 99775, U.S.A., mtwhalen@gi.alaska.edu; ³Department of Geology, University of California, Davis, 1 Shields Avenue, Davis, California 95616, U.S.A., npkelley@ucdavis.edu; ⁴Geology Department, State University of New York at Cortland, P.O. Box 2000, Cortland, New York 13045, U.S.A., christopher.mcroberts@cortland.edu; ⁵Department of Geological Sciences, University of North Carolina at Chapel Hill, CB 3315, Chapel Hill, North Carolina 27599, U.S.A., clams@email.unc.edu

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 radiolaria (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 *Otapirina 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 radiolaria 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

*Corresponding author. †Current address: Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, District of Columbia 20013, U.S.A. kelleynp@si.edu

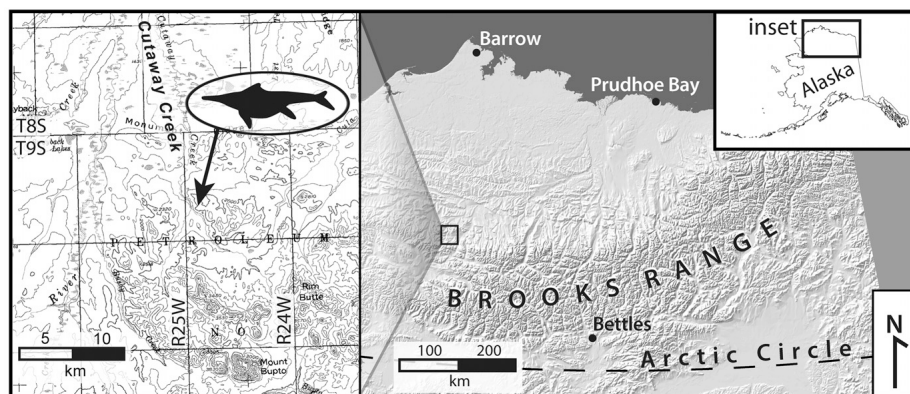


FIGURE 1. Study area in northern Alaska, western Brooks Range foothills. Digital shaded relief image modified from Riehle et al. (1997); inset map Howard Pass, Alaska, 1:250,000 (U.S. Geological Survey, 1956).

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 and 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*, *Guanlingsaurus 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 non-diagnostic (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* Nicholls and Manabe, 2004. The subrectangular morphology of the radius more closely resembles that seen in *Besanosaurus leptorhynchus* Dal Sasso and Pinna, 1996, *Himalayasaurus 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 *Guanlingsaurus 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 *Himalayasaurus*. 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 spine seen in *Cymbospondylus buchseri* (Sander, 1989).

In summary, UAMES 2437 broadly resembles other large Late Triassic merriamosaurs 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

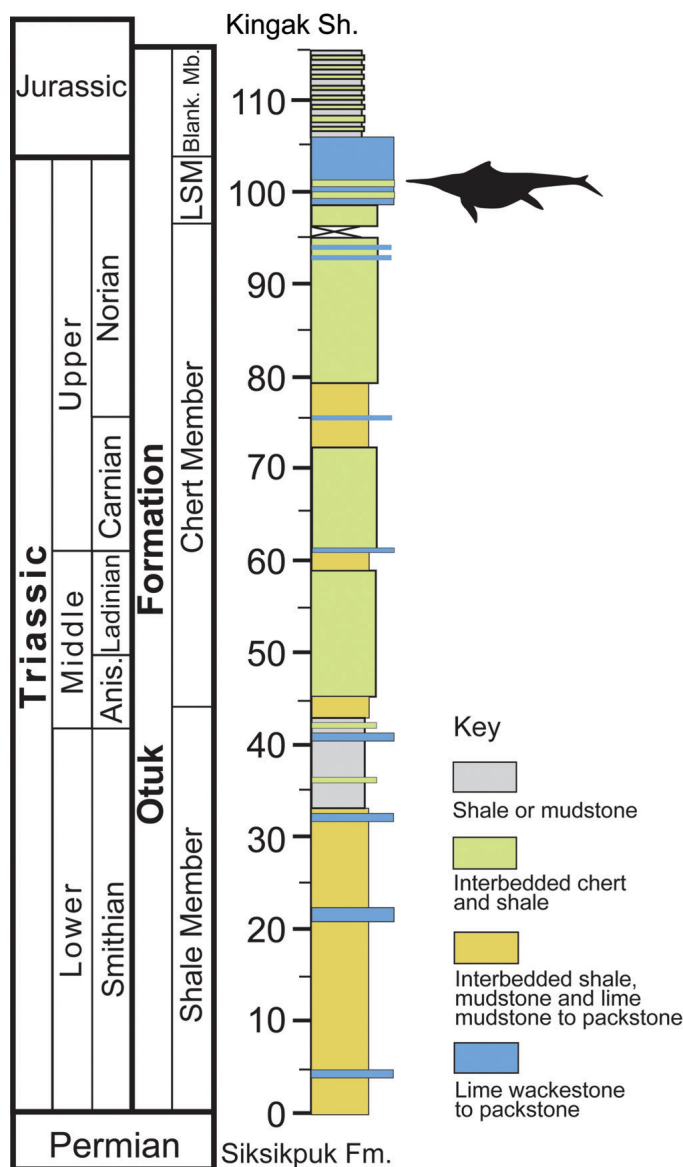


FIGURE 2. Stratigraphy of the Otuk Formation, reference section, Tigrlukpuk Creek, central Brooks Range (after Bodnar, 1984; Kelly et al., 2007). Stratigraphic column illustrates geologic age, lithostratigraphic units, lithology, and average grain size. Vertical scale shown in meters. Tigrlukpuk Creek 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 Otuk 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.

well defined, with the fragmented remains grading rapidly from an area of high density into clean matrix devoid of remains over a space of approximately 5 cm. All of the individual fragments are smaller than 1.0 cm in maximum dimension, and the vast majority are less than 0.3 cm in size. Interestingly, a small number of cephalopod hooklets (less than 10) were found in association with the specimen, but were widely dispersed in the matrix surrounding the skeleton. A detailed inspection did not reveal the presence of any hooklets within the gastric mass region.

Two types of organic remains dominate the mass. The first consists of blue to bluish-white flecks that stand out most conspicuously on weathered surfaces, where they contrast to the reddish-brown to brownish-gray matrix (Fig. 3C, F). On freshly broken surfaces, the fragments are nearly black (Fig. 3D, E). 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 osteichthyans. 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 fragmented 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 evidence for columnar stacking of the nacre tablets found in gastropods (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 comminuted remains is interpreted as incompletely digested remains within the alimentary canal, referred to here simply as gut contents. The most commonly preserved gut contents in ichthyosaurs 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 ichthyosaur species were specialist predators on cephalopods (Massare, 1987). Less frequently, the remains of fish (Buckland, 1836; Pollard, 1968; Keller, 1976; Bürgin, 2000) and other vertebrate prey, including other ichthyosaurs (Massare, 1987; Böttcher, 1989; Kear et al., 2003), have been reported in the gut contents of ichthyosaurs, 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 phosphatic residue interpreted as osteichthyan bones and scales, together with cephalopod shell fragments. Although vertebrate remains have been reported among the gut contents of other ichthyosaurs, the presence of mollusk shell is unusual. Interestingly, a Late Triassic (Carnian) ichthyosaur fossil from China (Cheng and Chen, 2007) referred to the genus *Panjiangsaurus* (likely a subjective junior synonym of *Guizhouichthyosaurus 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 *Guizhouichthyosaurus tangae* and UAMES 2437, a generalist/opportunistic feeding ecology encompassing vertebrate and shelled invertebrate prey might be characteristic of a group of closely related

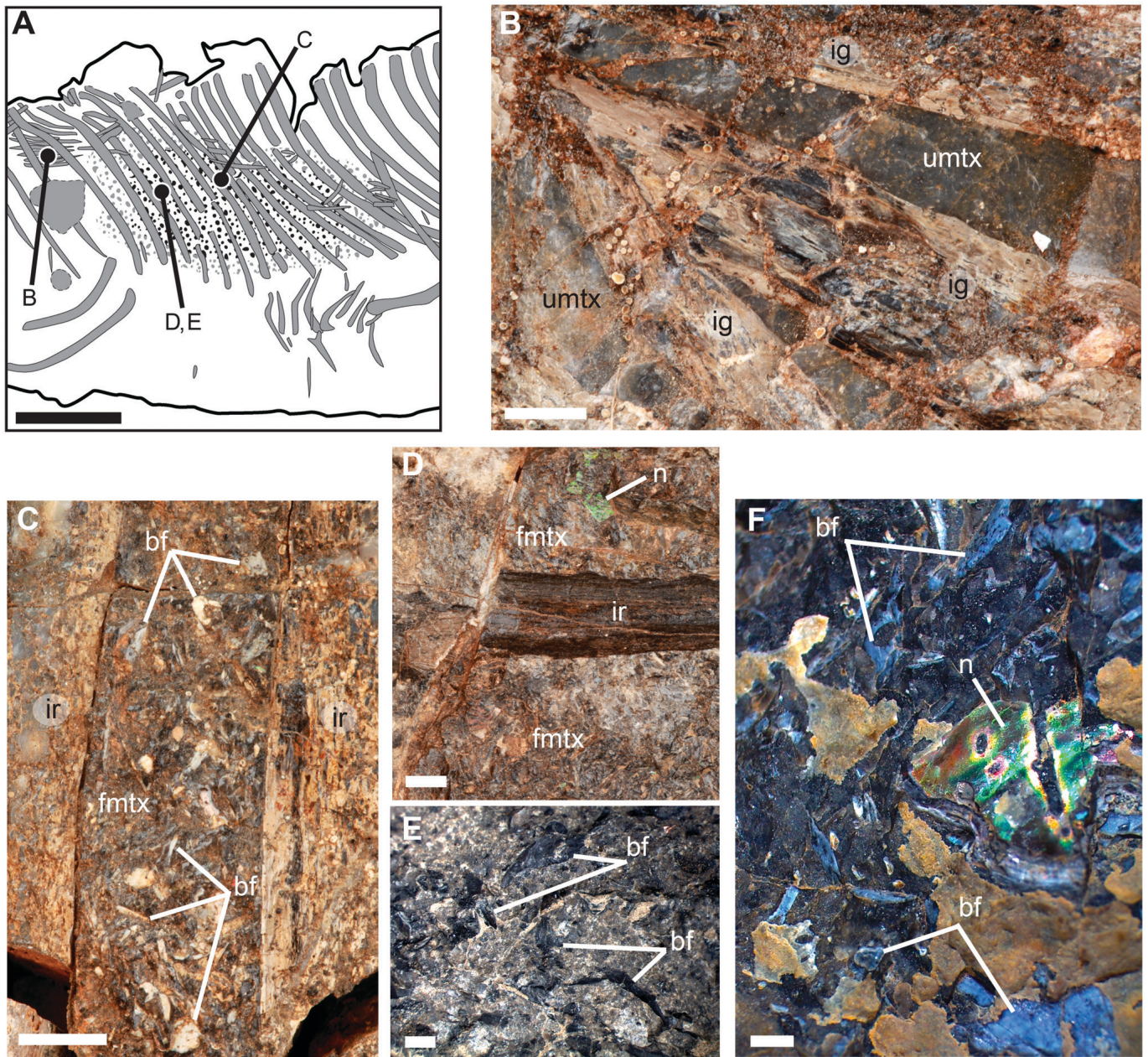


FIGURE 3. Detailed views of the gastric mass of UAMES 2437. **A**, location of images **B–E** (**F** is an isolated fragment from the gastric mass collected separately); **B**, unfossiliferous matrix from outside the gastric mass; **C**, macroscopic view of weathered fossiliferous matrix, showing numerous 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**.

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.

The majority of preserved ichthyosaurian 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; Buchy et al., 2004; Cheng and Chen, 2007; Buchy, 2010). The mix of vertebrate and mollusk shell fragments in the preserved gut contents of UAMES 2437 and previously reported for *Guizhouichthyosaurus tangae* (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; Buchy 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).

ACKNOWLEDGMENTS

We thank R. Gangloff, I. Tailleux, B. Kent, C. Benson, G. Mull, K. May, and D. Norton for information concerning the discovery, early history, and collection of the specimen. Assistance with the figures was provided by H. Foss. C. Ji and W.-L. Fu provided assistance with Chinese language references. A special thanks go to Sen. T. Stevens and Major L. Young and the CH-47 Chinook crew of the 'Sugar Bears,' B Company, 4th Battalion, 123rd Aviation Regiment, Fort Wainwright, Alaska, without whose support collection of the specimen would not have been possible. Logistical and administrative support was provided by the U.S. Bureau of Land Management. The specimen was collected under BLM Permits AA-83996 and AA-8270-930. SEM work was provided by K. Severin and the Advanced Instrumentation Laboratory at the University of Alaska Fairbanks.

LITERATURE CITED

- Blome, C. D., K. M. Reed, and I. L. Tailleux. 1988. Radiolarian biostratigraphy of the Otuk Formation in and near the National Petroleum Reserve in Alaska. U.S. Geological Survey Professional Paper 1399:725–776.
- Bodnar, D. A. 1984. Stratigraphy, age, depositional environments and hydrocarbon source rock evaluation of the Otuk Formation, north-central Brooks Range, Alaska. M.S. thesis, University of Alaska Fairbanks, Fairbanks, Alaska, 232 pp.
- Böttcher, R. 1989. Über die Nahrung eines *Leptopterygius* (Ichthyosauria, Reptilia) aus dem süddeutschen Posidonienschiefer (Unterer Jura) mit Bemerkungen über den Magen der Ichthyosaurier. Stuttgarter Beiträge für Naturkunde, Series B 155:1–19.
- Brinkmann, W. 2004. Mixosaurier (Reptilia, Ichthyosauria) mit Quetschzähnen aus der Grenzbitumenzone (Mitteltrias) des Monte San Giorgio (Schweiz, Kanton Tessin). Schweizerische Paläontologische Abhandlungen 124:1–84.
- Buchy, M.-C. 2010. Morphologie dentaire et régime alimentaire des reptiles marins du Mésozoïque: revue critique et réévaluation. *Oryctos* 9:49–82.
- Buchy, M.-C., P. Taugouroudeau, and P. Janvier. 2004. Stomach contents of a Lower Triassic ichthyosaur from Spitzbergen. *Oryctos* 5:47–55.
- Buckland, W. 1836. The Bridgewater Treatises, vol. 1: Geology and Mineralogy Considered with Reference to Natural Theology. W. Pickering, London, 599 pp.
- Bürgin, T. 2000. *Euthynotus* cf. *incognitos* (Actinopterygii, Pachycormidae) als Mageninhalt eines Fischesauriers aus dem Posidonienschiefer Süddeutschlands (unterer Jura, Lias Epsilon). *Eclogae Geologicae Helvetiae* 93:491–496.
- Callaway, J. M., and J. A. Massare. 1990. The affinities and ecology of Triassic ichthyosaurs. *Geological Society of America Bulletin* 102:409–416.
- Camp, C. L. 1976. Vorläufige Mitteilung über große Ichthyosaurier aus der oberen Trias von Nevada. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Abteilung I* 185:125–134.
- Camp, C. L. 1980. Large ichthyosaurs from the Upper Triassic of Nevada. *Palaeontographica, Abteilung A* 170:139–200.
- Carter, J. G. 1990. Shell microstructural data for the Bivalvia. Part I. Introduction; pp. 297–301 in J. G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends*, Volume 1. Von Nostrand Reinhold, New York.
- Chateigner, D., C. Hedegaard, and H. R. Wenk. 2000. Mollusc shell microstructures and crystallographic textures. *Journal of Structural Geology* 22:1723–1735.
- Cheng, L., and X. Chen. 2007. Gut contents in the Triassic ichthyosaur *Panjiangsaurus* from the Guanling biota in Guizhou. *Geology in China* 34:61–65.
- Cheng, L., O. Wings, X. Chen, and P. M. Sander. 2006. Gastroliths in the Triassic ichthyosaur *Panjiangsaurus* from China. *Journal of Paleontology* 80:583–588.
- Dal Sasso, C., and G. Pinna. 1996. *Besanosaurus leptorhynchus* n. gen. n. sp., a new shastasaurid ichthyosaur from the Middle Triassic of Besano (Lombardy, N. Italy). *Palaeontologia Lombarda, Nuova Serie* 4:1–23.
- Dauphin, Y. 2006. Structure and composition of the septal nacreous layer of *Nautilus macromphalus* L. (Mollusca, Cephalopoda). *Zoology* 109:85–95.
- Dong, Z.-M. 1972. [An ichthyosaur fossil from the Qomalangma Feng region]; pp. 7–10 in Z.-J. Yang and Z.-M. Dong (eds.), *Aquatic Reptiles from the Triassic of China*. Memoir of the Institute of Vertebrate Paleontology and Paleoanthropology 9. [Chinese]
- Dumoulin, J. A., R. C. Burruss, and C. D. Blome. 2011. Lithofacies, age and geochemistry of the Otuk Formation (Triassic) in the Red Dog District, northwest Alaska. *American Association of Petroleum Geologists Pacific Section Annual Meeting, Search and Discovery Article* 90125.
- Druckenmiller, P. S., and E. E. Maxwell. 2013. A Middle Jurassic ophthalmosaurid (Reptilia, Ichthyosauria) from the Tuxedni Formation (Bajocian), Alaska and the early diversification of the clade. *Geological Magazine* 151:41–48.
- Fröbisch, N. B., J. Fröbisch, P. M. Sander, L. Schmitz, and O. Rieppel. 2013. Macropredatory ichthyosaur from the Middle Triassic and the origin of modern trophic networks. *Proceedings of the National Academy of Sciences of the United States of America* 110:1393–1397.
- Ji, C. D.-Y. Jiang, R. Motani, H. Wei-Cheng, Z.-Y. Sun, and T. Cai. 2013. A new juvenile specimen of *Guanlingsaurus* (Ichthyosauria, Shastasauridae) from the Upper Triassic of southwestern China. *Journal of Vertebrate Paleontology* 33:340–348.
- Kear, B. P., W. E. Boles, and E. T. Smith. 2003. Unusual gut contents in a Cretaceous ichthyosaur. *Proceedings of the Royal Society of London B* 270(Supplement):S206–S208.
- Keller, T. 1976. Magen- und Darminhalte von Ichthyosauriern des süddeutschen Posidonienschiefers. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1976:266–283.
- Kelly, L. N., M. T. Whalen, C. A. McRoberts, E. Hopkin, and C. S. Tomsich. 2007. Sequence stratigraphy and geochemistry of the upper Lower to upper Triassic of northern Alaska: implications for paleo-redox history, source rock accumulation, and paleoceanography. *Alaska Division of Geological and Geophysical Surveys Report of Investigation* 2007-1:1–50.
- Leidy, J. 1868. Notice of some reptilian remains from Nevada. *Proceedings of the Academy of Natural Sciences Philadelphia* 20:177–178.
- Lomax, D. R. 2010. An *Ichthyosaurus* (Reptilia: Ichthyosauria) with gastric contents from Charmouth, England: first report of the genus from the Pliensbachian. *Paludicola* 8:22–36.
- Massare, J. A. 1987. Tooth morphology and prey preference in Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7:121–137.
- 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., and R. Motani. 1999. A reinterpretation of the Upper Triassic ichthyosaur *Shonisaurus*. *Journal of Vertebrate Paleontology* 19:42–49.

- McGowan, C., and R. Motani. 2003. Handbook of Paleoherpptology, Part 8. Ichthyopterygia. Verlag Dr. Friedrich Pfeil, Munich, 175 pp.
- Merriam, J. C. 1895. On some reptilian remains from the Triassic of northern California. *American Journal of Science* 50:55–57.
- Moore, C. 1856. On the skin and food of ichthyosauri and teleosauri. Reports of the British Association for the Advancement of Science 1856:69–70.
- Motani, R., C. Ji, T. Tomita, N. Kelley, E. Maxwell, D.-Y. Jiang, and P. M. Sander. 2013. Absence of suction feeding ichthyosaurs and its implications for Triassic mesopelagic paleoecology. *PLoS ONE* 8: e66075. doi: 10.1371/journal.pone.0066075.
- Mull, C. G., I. L. TAILLEUR, C. F. Mayfield, I. Ellersieck, and S. Curtis. 1982. New upper Paleozoic and lower Mesozoic stratigraphic units, central and western Brooks Range, Alaska. *American Association of Petroleum Geologists Bulletin* 66:348–362.
- Nicholls, E. M., and M. Manabe. 2004. Giant ichthyosaurs of the Triassic—a new species of *Shonisaurus* from the Pardonet Formation (Norian, Late Triassic) of British Columbia. *Journal of Vertebrate Paleontology* 24:838–849.
- Patton, W. W., and I. L. TAILLEUR. 1964. Geology of the Upper Killik-Itkillik region, Alaska. U.S. Geological Survey Professional Paper 303-G:409–499.
- Pollard, J. E. 1968. The gastric contents of an ichthyosaur from the Lower Lias of Lyme Regis, Dorset. *Palaeontology* 11:376–388.
- Rieber, H. 1970. *Phragmoteuthis? ticinensis* sp. nov., ein Coeloidea-Rest aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kanton Tessin, Schweiz) *Paläontologische Zeitschrift* 44:32–40.
- Riehle, J. R., M. D. Fleming, B. F. Molnia, J. H. Dover, J. S. Kelley, M. L. Miller, W. J. Nokleberg, G. Plafker, and A. B. Till. 1997. Digital shaded relief image of Alaska. U.S. Geological Survey. Geological Investigations Series I-2585.
- Sander, P. M. 1989. The large ichthyosaur *Cymbospondylus buchseri*, sp. nov., from the Middle Triassic of Monte San Giorgio (Switzerland), with a survey of the genus in Europe. *Journal of Vertebrate Paleontology* 9:163–173.
- Sander, P. M., X. Chen, L. Cheng, and X. Wang. 2011. Short-snouted toothless ichthyosaur from China suggests Late Triassic diversification of suction feeding ichthyosaurs. *PLoS ONE* 6:e19480. doi: 10.1371/journal.pone.0019480.
- Shang, Q.-H., and C. Li. 2009. On the occurrence of the ichthyosaur *Shashtasaurus* in the Guanling biota (Late Triassic), Guizhou, China. *Vertebrata Palasiatica* 47:178–193.
- Tailleur, I. L., C. G. Mull, and H. A. Tourtelot. 1973. A skeleton in Triassic rocks in the Brooks Range foothills. *Arctic* 26:79–81.
- U.S. Geological Survey. 1956. Howard Pass, Alaska. 1:250,000. U.S. Geological Survey.
- Wang, X., G. H. Bachmann, H. Hagdorn, P. M. Sander, G. Cuny, X. Chen, C. Wang, L. Chen, L. Cheng, F. Meng, and G. Xu. 2008. The Late Triassic black shales of the Guanling area, Guizhou Province, southwest China: a unique marine reptile and pelagic crinoid fossil Lagerstätte. *Palaeontology* 51:27–61.
- Yin, G., X. Zhou, Z. Cao, Y. Yu, and Y. Luo. 2000. A preliminary study on the early Late Triassic marine reptiles from Guanling, Guizhou, China. *Geology-Geochemistry* 28:1–23. [Chinese with English summary]

Submitted March 26, 2013; revisions received October 8, 2013;

accepted November 13, 2013.

Handling editor: Robin O'Keefe.