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Description of an Unusual Cervical Vertebral Column of a Plesiosaur from the Kiowa Shale

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DESCRIPTION OF AN UNUSUAL CERVICAL VERTEBRAL

COLUMN OF A PLESIOSAUR FROM

THE KIOWA SHALE

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by

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PREFACE

This manuscript has been formatted in the style of the Journal of Vertebrate Paleontology.

Keywords: plesiosaur, polycotylid, cervical vertebrae, *Dolichorhynchops*, *Trinacromerum*

ABSTRACT

The Early Cretaceous (Albian) Kiowa Shale of Clark County, Kansas consists mainly of dark gray shale with occasional limestone deposits that represent a near shore environment. Faunal lists have been published based on fragmentary materials; however, few individual specimens have been described in the last 100 years. Here an unusual plesiosaur specimen (KUVP 16375) is described. The specimen consists of 17 cervical vertebrae: 10 articulated and 7 disarticulated. Some of the vertebrae are uniquely preserved with an atypical ventral excavation not present in known plesiosaur vertebrae. It is not clear whether or not this character is of phylogenetic or diagnostic significance. Many vertebrae lack distinct rib facets. Neural spines are absent from all elements of the specimen. A number of elements possess well-defined zygapophyses and neural canals. Foramina subcentralia are present in the ventral surface of plesiosaur cervical vertebrae but appear to be absent in many of the vertebrae of KUVP 16375.

The specimen is described and interpreted as a polycotylid. The specimen is then compared to other plesiosaurs including other polycotylids and its phylogenetic position is analyzed. Character matrices and the physical description allowed referral of the specimen to the Polycotylidae. This family consists of short-necked, large-headed plesiosaurs and is represented by small sample sizes from the Kiowa Shale. Determination of the genus and species is not made at this time.

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INTRODUCTION

Plesiosaurs are an extinct lineage of aquatic reptiles from the Mesozoic era. Their distribution was global in oceans of the Cretaceous including areas in what is now Kansas. Plesiosaurs were adapted for life in aquatic environments and evolved from nothosaurs (O'Keefe, 2001; Druckenmiller and Russell, 2008). Nothosaurs were semi-terrestrial reptiles with long necks, small heads, and webbed feet on both forelimb and hindlimb. The Plesiosauria are first recognized as an evolutionarily distinct order near the Triassic – Jurassic time boundary (O'Keefe, 2001).

The Plesiosauria included short and long-necked forms originally hypothesized to possess divergent evolutionary histories. Short-necked plesiosaurs were originally placed in the Pliosauroidea whereas long-necked plesiosaurs were placed in the Plesiosauroidea (Welles, 1952). Dedicated swimming paddles evolved from nothosaurian webbed feet (Carroll, 1988). They also possess short tails, some of which are hypothesized to exhibit features of a caudal fin expansion (Dames, 1895; Wilhelm, 2010).

Typical plesiosaur cervical vertebrae possess narrow width neural spines and lateral rib facets; two rib facets in more primitive plesiosaurs, typically Triassic and Jurassic aged plesiosaurs, and a single facet in more derived plesiosaurs, typically Jurassic and Cretaceous aged plesiosaurs (Romer, 1956; O'Keefe, 2001). These ribs articulated on the centrum via short parapophyses (Storrs, 1991). Two foramina, called foramina subcentralia, are present in the ventral surface of known plesiosaur cervical

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vertebrae (Storrs, 1991; Williston, 1903). Centra vary between species with platycoelus and amphicoelus morphologies found within the Plesiosauria.

The vertebrae are typically short ventral to dorsal and elongate anteroposteriorly (Romer, 1956; Storrs, 1991). The cervical series range from subcircular and flattened or ventrally and dorsally crushed in the anterior vertebrae to spool shaped in the posterior-most region of the cervicals (Smith, 2007; O'Keefe and Street, 2009). Neural arches of plesiosaur vertebrae are formed by the dorsal spinous processes, consisting of the zygapophyses and neural spine, and the dorsal surface of the centrum (Owen, 1849).

Numerous plesiosaur remains recovered from the Kiowa Shale throughout Kansas are housed in either the Natural History Museum at the University of Kansas (KUVP) or the Sternberg Museum of Natural History (FHSM) at Fort Hays State University. These materials date from the late 19th century (the earliest collected by C. N. Gould in 1893) to the late 20th century (the latest collected by J. D. Stewart and J. A. Chorn in 1983). Many of the plesiosaur fossils from the Kiowa Shale are undescribed (personal observation). Collected materials are housed at the University of Kansas Natural History Museum and account for a significant portion of the collection of Kiowa Shale plesiosaur materials.

The Kiowa Shale is exposed throughout southern and central Kansas where it is associated with the Red Hills and Smoky Hills regions. The majority of Kiowa Shale plesiosaurs were recovered from Clark County in southern Kansas. This area represents Early Cretaceous deposits of near to offshore mudstones, sandstones, dark-gray shales,

and shell conglomerates (Scott, 1970; Franks, 1980). The mineral composition of the formation is highly quartz based (Beamon, 1999; Williams and Lohman, 1949).

Faunal lists of the vertebrate fauna of the Kiowa Shale were published (e.g. Beamon, 1999) based on fragmentary materials but few individual specimens were described in the last 100 years. The fauna of this formation includes invertebrates, fishes including sharks, turtles, crocodilians, and plesiosaurs. Short-necked polycotylid plesiosaurs are assigned to the polyphyletic "Pliosauroidea" and represent a significant amount of the plesiosaur fossil material recovered from the Kiowa Shale (Beamon, 1999; Everhart, 2005).

The specimen KUVP 16375 is an Early Cretaceous plesiosaur specimen from the Kiowa Shale composed of cervical vertebrae that differ from the typical morphology of plesiosaur vertebrae. A number of the vertebrae possess excavations of the ventral centra that are not present in other known plesiosaurs. The specimen was collected by O. W. Bonner and M. E. Williams during the summer of 1969 in Clark County, Kansas (Fig. 1). The coordinates and exact location of the collection site are designated as Location #15 by the Natural History Museum at the University of Kansas. This plesiosaur specimen is measured (Table 1), described, compared (Table 2 and Table 3), and its phylogenetic position is interpreted. The skeletal material of the Kiowa Shale is limited in amount, and not much of this material has been described. This description and interpretation is therefore significant because of the few descriptions of Kiowa Shale plesiosaur skeletal material.

LITERATURE REVIEW

The first plesiosaur fossils described were interpreted as fish vertebrae in Richard

Verstegen's (1634) book *A Restitution of Decayed Intelligence*. The treatise was not a

scientific work but used the fossils as support for the idea that Great Britain was once a

continuous part of the European continent. It was not until the 18th century that the

plesiosaurs were first described as unique aquatic reptiles by William Stukeley in 1717.

He described a plesiosaur given to him by R. W. Darwin as including vertebral, sacral,

and limb elements. Stukeley noted that the foot possessed "four of the five Toes [sic]" but

did not describe the limbs as resembling flippers in any way (Stukeley, 1717, p. 964). He

did not name the remains, but he recognized them as aquatic and compared them to

crocodiles and porpoises. The specimen described by Stukeley was eventually attributed

to *Plesiosaurus dolichodeirus* Conybeare 1824 and is housed in the Natural History

Museum in London (Evans, 2010).

Reverend W. D. Conybeare and H. T. de la Beche were the first to recognize and

differentiate plesiosaurs from ichthyosaurs in 1821. Conybeare (1821) described a new

genus, *Plesiosaurus*, meaning "approximate to the Saurians [sic]" (Conybeare, 1824, p.

389) from a specimen collected by himself and de la Beche that he differentiated from the

Ichthyosauria based on characteristics of the head, vertebrae, and ribs. Conybeare noted

that the body of *Plesiosaurus* was markedly more like terrestrial reptiles than that of *Ichthyosaurus* and compared the dental bones of *Plesiosaurus* to those of crocodilians.

Conybeare (1824) described Stukeley's specimens under the name *Plesiosaurus dolichodeirus* and also described the most complete skeleton discovered to date. That skeleton was discovered at Lyme Regis in Dorset by Mary Anning. Anning sold the skeleton to the Duke of Buckingham, and it was then given to William Buckland who passed it on to Conybeare to describe. The nearly complete skeleton allowed Conybeare to draw new conclusions about the morphology and life of *Plesiosaurus dolichodeirus*. Conybeare described the paddles of the limbs and attributed their use as "destined for natation [swimming]" in a manner similar to sea turtles (Conybeare, 1824, p. 388).

Conybeare (1824) also noted that *Plesiosaurus* was a marine reptile, based on the associated fossil assemblages in its area of recovery, and hypothesized that its neck inhibited its swimming ability. The neck was described as extremely flexible and mobile and capable of arching "like the swan" (Conybeare, 1824, p. 389). Conybeare also stated that the terrestrial movement of *Plesiosaurus* was exceedingly awkward. Terrestrial locomotion in plesiosaurs has been questioned and considered unlikely due to the rigid mechanics and low weight bearing properties of the limbs and girdles (e.g., Everhart, 2005; O'Keefe and Carrano, 2005).

During the latter half of the 19th century plesiosaur research continued in Europe and began in North America as the American West was explored. Formations in Kansas and the Dakotas produced numerous specimens of different taxa. The most well-known

of these specimens was *Elasmosaurus platyurus* Cope 1868. E. D. Cope famously

misinterpreted the directionality of the skeleton of *Elasmosaurus* and placed the skull on

the end of the tail instead of the neck (Leidy, 1870). He recognized his error, but failed to

correct it before his mentor, Joseph Leidy, publicly corrected him. Cope suffered some

humiliation but acknowledged his mistake and corrected it by producing a second version

of his original description (Cope, 1870).

Following Cope, S. W. Williston began collecting and describing American

plesiosaur specimens, first at the University of Kansas and later at the University of

Chicago. The majority of the skeletal material Williston studied came from the Late

Cretaceous Niobrara Formation. Williston documented the bulk of these remains in a

multiple part series on North American plesiosaurs (Williston, 1903, 1906, 1908) and in

an additional book that discussed marine reptiles of all kinds including plesiosaurs

(Williston, 1914).

Recent research has focused on functional morphology, phylogeny, and ontogeny

(e.g., Riess and Frey, 1992; Carpenter et al., 2010; Shimada et al., 2010; O'Keefe and

Chiappe, 2011). These recent discoveries and studies illuminated habits of diet that

include the swallowing of gastroliths (e.g., Everhart, 2005; McHenry et al., 2005),

evidence of live birth (e.g., Cheng et al., 2004; O'Keefe and Chiappe, 2011), and

modeling of locomotion in plesiosaurs (e.g., Carpenter et al., 2010; Massare, 1988).

Evolution of the Plesiosauria.— The earliest relatives of plesiosaurs were diapsid sauropterygians such as the Triassic genera *Nothosaurus* and *Pistosaurus*; plesiosaur bodies are very similar to these early semiaquatic relatives but are fully aquatic marine reptiles (Taylor and Cruickshank, 1993; Storrs and Taylor, 1996; Storrs, 1997; Rieppel, 1998). Plesiosaurs are therefore secondarily aquatic reptiles breathing air and possessing four distinct paddle-shaped limbs derived from those of their terrestrial ancestors for aquatic locomotion (Knutsen, 2012).

The Plesiosauria are divided into multiple families in two superfamilies: Plesiosauroidea and Pliosauroidea. These superfamilies contain families that are both short and long-necked. The Plesiosauroidea, a historically long-necked superfamily, contains both long-necked (e.g., Elasmosauridae, Plesiosauridae) and short-necked (e.g., Polycotylidae) plesiosaur families. The Pliosauroidea also contains long-necked (e.g., Rhomaleosauridae) and short-necked (e.g., Pliosauridae) families.

All plesiosaurs possessing long necks also possess distinctly high numbers of cervical vertebrae in comparison to most described taxa with upwards of 20 vertebrae in many cases (Carroll, 1988). Plesiosaurs with shorter necks can also possess high numbers of cervical vertebrae, though these vertebral columns are shorter than those of long-necked plesiosaurs. The cervical series are variable in the actual number of vertebrae present, ranging from 12 in the short-necked pliosaurid *Brachauchenius lucasi* to 71 in the long-necked elasmosaurid *Elasmosaurus platyurus* (Ketchum and Benson, 2010).

Polycotylid plesiosaurs are short-necked members of the Plesiosauria with approximately 23 to 26 cervical vertebrae (Williston, 1925).

Plesiosaurs possess highly specialized pectoral and pelvic girdles with associated limbs ending in dorsoventrally flattened paddles and exhibit hyperphalangy; hyperdactyly is not known to occur in the paddles of plesiosaurs (Knutsen, 2012). The paddles also exhibit reduction of length in the femur/humerus and tibia-fibula/radius-ulna complexes (Andrews, 1910). Their bodies are robust with gastralia covering the abdomen and thoracic cavities. The plesiosaur trunk is bounded and reinforced by the pectoral girdle, gastralia, and pelvic girdle.

Plesiosaurs are hypothesized to have birthed live young from the Middle Triassic onward as evidenced by the sauropterygian *Keichousaurus hui* (Cheng, et al. 2004), an ancestor of the Plesiosauria. The first report of live birth in the Plesiosauria is from a Cretaceous polycotylid, *Polycotylus latippinus* (O'Keefe and Chiappe, 2011). Live birth in these animals obviates the need for the Plesiosauria to pull their bodies onto land to lay eggs as was hypothesized when the fossils of *Plesiosaurus* were initially discovered (Conybeare, 1824).

Plesiosaur Locomotion Models.—Three hypothesized models of swimming locomotion in plesiosaurs have been proposed (Fig 3.). Robinson (1975, 1977) proposed a simplified up and down motion of the limbs akin to extant marine turtles and penguins. This method of locomotion is often described with a portion of the paddle stroke in subaqueous flight,

a figure-eight pattern using the two sets of paddles independently as in penguins, and the

two stroke patterns are frequently confused (Massare, 1988). Plesiosaurs were

hypothesized to use both sets of paddles in asymmetrical motion, which is less efficient

than the symmetrical movements of penguins and turtles (Taylor, 1986; Massare, 1988).

Rowing, or horizontal elliptical paddle movement (Fig. 3), was proposed by

Romer (1956) and reiterated by Riess and Frey (1992). Some authors (e.g., Robinson,

1975; Carpenter, et al., 2010) argue against this rowing movement as a mode of

plesiosaur locomotion. The most likely model of propulsion, stated by consensus (e.g.,

Massare, 1988; Everhart, 2005; Carpenter, et al., 2010), is identified as "comparable to

sealions [sic]" (Massare, 1988, p. 190). Ventral reinforcement of the limb girdles allowed

for a powerful down stroke but a relatively weaker recovery stroke, resulting in a

combination of the two previously described models: a flying power stroke and a rowing

recovery stroke (Godfrey, 1984; Massare, 1988). This model of locomotion provided

increased force to overcome drag that is generated by the elongated neck and increased

body size.

Stabilization of the body in motion also is still debated. Small vertical tail fins

were thought to provide some level of rudder-like control in plesiosaurs, suggested by

Owen (1865). Evidence of a caudal fin structure was interpreted from a carbon film

impression in a slab as evidenced by Dames (1895); the film impression was also

interpreted as indicating that the limb paddles possessed a trailing edge of soft tissue that

aided in control of movement. Wilhelm (2010) reported evidence of tail fin structures as

well by interpreting caudal vertebral organization. Tail rudders also were supported as practical functional appendages in plesiosaurs by Robinson (1975). Head and neck rudder control in plesiosaurs is considered to be detrimental to the ability of plesiosaurs to maintain a straight path of mobility; deviations of the neck would cause drag to alter the course of the animal drastically (Alexander, 1989).

Concise History of the Western Interior Seaway.— The Western Interior Seaway was larger geographically and longer lived temporally than the Kiowa Shale (Early Cretaceous, 105 million years ago) of Kansas (Everhart, 2005). The organismal diversity (Beamon, 1999) of the Kiowa Shale represents a near-shore environment of the Western Interior Seaway during its early expansion into the North American continent (Fig. 2). Franks (1980) stated that the Kiowa Shale represents deep water marine environments and brackish saltwater areas (e.g., marshes) and lagoons whereas Scott (1970) stated that the water depth when the Kiowa Shale was deposited was approximately 15 meters. Scott (1970) also stated that comparisons of southern and central Kansas deposits exhibit a southward slope of the seabed from the near-shore low salinity central Kansas deposits to the more offshore higher salinity southern Kansas deposits.

The Western Interior Seaway began to invade Kansas from the western end of the state during the Albian age and progressed north and east through the Campanian age, and Kansas therefore represents the Eastern shore of the Western Interior Seaway (Everhart, 2005). The Permian soils prevalent in Eastern Kansas were partially eroded

and by finer sands, possibly beach sediments, and then mud layers unconformably deposited atop the Permian soils (Scott, 1970; Beamon, 1999). These layered deposits make up the Cheyenne Sandstones with sandy and muddy shale types of the Kiowa Shale above (Beamon, 1999). This transition from shoreline to deeper ocean is evident in fossils that are recovered throughout the Cheyenne Sandstone and the Kiowa Shale.

The Western Interior Seaway was separated into a number of subprovinces by various studies (Kauffman, 1984; Nicholls and Russell, 1990; Cumbaa, et al., 2010). The most recent subdivision of the provinces includes Northern Interior, Central Interior, Gulf and Atlantic, and Southern Interior Subprovinces, as well as an overlapping Western Interior Endemic Center (Kauffman, 1984). Kansas rests in the Southern Interior Subprovince of the Western Interior Seaway as described by Kauffman (1984). Faunal distribution studies conducted used these subprovinces as references for invertebrate and vertebrate fossil ranges and population studies (Nicholls and Russell, 1990; Cumbaa, et al., 2010). Previous studies noted that fossil distribution did not differ significantly between Canadian and American regions of the Western Interior Seaway meaning subprovince distinctions were not necessary to delineate seaway zones (Jeletzky, 1970).

METHODS

Individual elements of the cervical column were measured to the nearest 0.1 mm with Mitutoyo Digimatic Calipers. Vertebral centrum length was measured across lateral

surfaces from the anterior-most to posterior-most margins of the articular faces (Fig. 4).

Centrum length in obliquely crushed vertebrae was measured from the medial margin of

the articular facets at their ventral-most border. Vertebrae with weathered centra, i.e. in

the disarticulated vertebrae, were measured for anteroposterior length of vertebral centra.

Areas of the plaster jacket were trimmed and matrix around structures of interest was

removed to better expose the vertebrae. The removal of this material did not affect the

specimen in any way. The plaster jacket was not entirely removed so as to preserve the

articulation of the vertebral column as found. Articular faces of disarticulated vertebrae

were measured across the widest dorsoventral surface; the outer borders of the articular

faces were used as measuring landmarks (Fig. 4). Vertebral heights measured on

individual elements with crushed centra were measured from the ventral-most margin of

the centrum to the dorsal-most margin of the centrum. These measurements, as they were

affected by the amount of centrum that was preserved, varied among individual vertebrae.

Vertebrae were photographed using natural light, directed light sources, and

camera flash at multiple angles including lateral, anterior, posterior, and dorsal views.

The cameras were a 16.2 megapixel digital SLR camera was used with a semi-dedicated

macro lens and a 10 megapixel camera with high depth of field macro capabilities.

Structures also were illustrated with line drawings of the vertebrae.

Using the characters of Ketchum and Benson (2010) and O'Keefe (2004), the

vertebrae were measured (Table 1) and anatomical features were coded. O'Keefe's

(2004) characters are used instead of those in his later publications (e.g., O'Keefe 2008,

2010) because the 2004 list is more comprehensive. Character sets from O'Keefe (2004) and Ketchum and Benson (2010) were compared to ensure compatibility (Appendices 1 and 2). The characters were coded and entered into character matrices (Tables 2 and 3).

The characters were coded and analyzed by using measurements, proportional characters of the vertebral centrum, orientation of anatomical characteristics of the vertebrae, absence or presences of structures, and overall shape of the vertebrae. Matrices of each character set were compiled by using similar genera; members of the Polycotylidae are used as the ingroup comparison taxa. Outgroups for both matrix comparisons were the same, represented by the hypothetically primitive species *Plesiosaurus dolichodeirus* and *Tricleidus seeleyi*. These taxa are plesiosaurid and cryptoclidid plesiosauroids, respectively. The matrices were compiled and analyzed individually.

Acid testing using hydrochloric acid was used to test mineral crystals preserved with the fossils. The minerals were scratch tested as well. The surface of the crystalline structures was viewed under a dissecting microscope to verify the results of acid testing and scratch testing of the mineral crystals.

DESCRIPTION

Overview of the specimen.—The specimen, KUVP 16375, consists of 17 cervical vertebrae. Ten vertebrae are preserved in articulation. Articulated elements are preserved

in a plaster jacket measuring 28 cm by 58 cm in right lateral view. Seven apparently

disarticulated vertebrae were collected but are not associated with the plaster jacket. The

7 smallest, anterior-most, are disarticulated vertebrae. The 10 larger, posterior-most,

vertebrae were collected in articulation and are preserved in the original plaster field

jacket. The vertebrae are ordered based on their size (Fig. 5), the smallest being the most

anterior vertebra. The orientation of each element was determined by the presence of the

prezygapophyses and postzygapophyses or the bases from which they extend in the case

of broken or absent processes.

Vertebrae of the specimen were organized in this numerical sequence because the

anterior-most cervical vertebrae are anatomically smaller than those following in a

vertebral series. Numbers assigned to the vertebrae are artificial and do not necessarily

reflect anatomical position. The atlas/axis complex is absent from this specimen. Fusion

of the vertebrae and landmarks indicative of this complex are not present. The museum

catalog card of the specimen states that 15 articulated vertebrae are preserved in this

series. However, the plaster jacket contains only 10 articulated vertebrae. The rock matrix

was removed from the right side of the specimen and preparation exposed a right lateral

view of these elements.

Disarticulated vertebrae, numbers 1-7 can be viewed from all angles. The

disarticulated vertebrae are not as robust, with thick barrel-shaped (cylindrical) centra, as

are other vertebrae in the specimen. The most robust vertebrae are found in the posterior

end of the articulated section. The centrum thickness increases in width posteriorly in the

specimen. Disarticulated vertebrae differ from this trend because they appear weathered and crushed. Intervertebral discs, spinal cord, and other soft tissue structures associated with the vertebra were not preserved in this specimen.

Four of the disarticulated vertebrae preserve complete centra; however, the neural spines are entirely absent. Three of these disarticulated vertebrae only consist of incomplete centra material whereas the ten articulated vertebrae in the series are mostly complete. All neural spines in the specimen are absent or broken above the prezygapophyses and postzygapophyses. Many rib facets are absent due to damaged preservation of the centra. A number of the ventral foramina subcentralia of the vertebrae are absent. Vertebrae lacking these foramina possess concave or excavated ventral centra. The centra ends are amphicoelus (concave) in shape. Neural arches are filled with sediment and in one case (vertebra 2) entirely filled with quartz crystals (Fig. 6).

Quartz crystals are present throughout the specimen. The crystals are most often concentrated in the neural canals and on concave surfaces of the articular facets. Crystal deposits are secondary and are not indicative of life conditions of the specimen. Quartz is laid down on the specimen by the settling of silicates in groundwater around the preserved specimen after fossilization occurred (Beamon, 1999). The Kiowa Shale's overlying conglomerate and sandstone layers consist of many fine-grained quartz deposits that leeched silicates and formed quartz crystals on the surfaces of the specimen over time.

A number of the vertebrae of the specimen, four total, appear to be crushed obliquely. Six of the last seven vertebrae of the articulated series (numbers 11-16) do not show signs of crushing, but vertebrae 8-10, and the disarticulated vertebrae are crushed obliquely and anteriorly. Vertebra 17 is also crushed obliquely but in a posterior direction. The crushing force on the vertebrae caused the articular facets to lie at an angle to the centrum. It also caused some of the centra to become crushed laterally producing narrower widths and dorsoventrally shorter heights. The centra of those vertebrae also are much shorter lengthwise between the articular facets in comparison with the articulated column of vertebrae anterior to vertebra 10. Disarticulated vertebrae in the specimen possess the shortest and thinnest centra, when considering length, width, and height, and exhibit the most damage consistent with being crushed.

Taphonomic explanations for the presentation of the specimen include depredation, tidal energy in near-shore environments, and bone damage through other processes prior to and during fossilization. The near-shore environment and the shallow depth of the southern Kansas Kiowa Shale led Scott (1970) to describe the actions and movements of the water in this region as "very turbid." Such conditions might have, in conjunction with evidenced predation or scavenging, aided in the disarticulation of the specimen being described here if Scott's assessment of the water conditions and activity are correct. Compression of the bones might also be accounted for in movements of water and abiotic factors that are unknown. Directionality of crushing on the specimen is

varied. The varied crushing directions indicate possible manipulation of the vertebrae prior to fossilization.

Evidence of predation or scavenging is present in the form of a broken shark tooth embedded in a vertebral centrum. The 7th articulated vertebra, vertebra 14, contains a fragment of broken shark tooth cusp. This tooth was interpreted as belonging to the species *Leptostyrax macrorhiza* (M. Everhart, pers. comm.). The tooth is oriented with the vertebra such that its broken cusp is longest anterior to posterior and is narrow laterally. No other fragments of foreign material are embedded in the vertebrae on visible surfaces.

Disarticulated Vertebrae.—Vertebrae 1 through 7 are fragmentary and damaged. Neural spines are absent in most disarticulated vertebrae except vertebrae 2 - 4 which possess neural arches. The centra of the disarticulated vertebrae are preserved so that most lack all evidence of anterior and posterior articular facets, rib facets, and foramina subcentralia on the ventral surface; strangely, perhaps the best preservation of the foramina subcentralia are located on the centrum of vertebra 5, which was nearly destroyed by weathering and imperfect preservation (Fig. 7). The neural arches also are significantly smaller and laterally crushed in vertebrae that have the arches preserved. Prezygapophyses and postzygapophyses are absent, not adequately preserved, in all disarticulated vertebrae with except vertebra 4, which possesses well-preserved prezygapophyses (Fig. 8).

Vertebra 1 (Fig. 9) is poorly preserved and consists of only the vertebral centrum between the articular facets and the dorsal surface of the centrum. A single articular facet is present. Anatomical orientation of the vertebra is not diagnosable based on this single articular facet. The corresponding articular facet is broken. The remnant of the centrum is crushed between the preserved articular face and the distorted, fragmented centrum facet. This crushed centrum is barrel-shaped and two cavities are formed on either side of the dorsal surface of the centrum. The neural spine is completely absent from this vertebra.

Vertebra 2 (Fig. 10) is damaged by oblique crushing and its centrum is dorsoventrally crushed. Fragments of shale are evident in the excavation as individual pieces of rock projecting ventrally from the centrum. The ventral surface of the centrum is excavated. This dorsoventral excavation of the vertebra reaches the dorsal surface of the centrum, as it does in vertebra 4 (Fig. 11). All evidence of rib articulations and foramina subcentralia is absent in this element due to this crushing and excavation of the centrum. The oblique crushing of the vertebra is the most extreme in the disarticulated vertebrae. The neural arch of the vertebra is obliquely crushed. This resulted in complete loss of the preserved neural spine. However, the broken base indicates it was fossilized and then subsequently lost.

Vertebra 3 (Fig. 12) consists of the medial surface of a centrum and a partial neural arch. The centrum is V-shaped with the point of the V at the ventral base of the centrum. This entire structure is extremely crushed. The anterior and posterior ends of the centrum are smooth and slightly concave. The middle of the centrum is barrel-shaped and

one of the articular facets extends ventrally. The neural arch of this vertebra is largely absent. The left pedicel of the neural spine is partially preserved dorsal to the centrum (Fig. 12).

Vertebra 4 (Fig. 8) exhibits a highly crushed medial surface of the centrum and thin articular facets. The neural arch and the prezygapophysis are preserved in this element. The ventral surface is deeply excavated (Fig. 11). The excavation of this surface potentially destroyed the foramina subcentralia that are present in other vertebrae. The lateral surface might or might not be preserved adequately and cannot be determined to have been destroyed by the formation of this excavation. The lateral wall of the centrum measures half the dorsoventral height of the articular facets at 2.30 cm; the articular facets measure 4.62 cm dorsoventrally.

Medially the centrum is imperfectly preserved such that excavation nearly reaches the dorsal roof of the centrum. The articular surfaces were well-preserved. Existing neural spine processes consist of a well-preserved prezygapophysis; these were newly revealed during recent preparation. These prezygapophyses are entirely present with their articular surface completely intact.

Vertebra 5 is broken into two fragmented pieces of vertebra, which are labeled as portions of number 5 rather than individually (Fig. 7). These broken fragments represent the centrum and a preserved element of the neural spine, specifically the area constituting the base of the prezygapophyses and postzygapophyses.

The weathering of the centrum eliminated all evidence of rib articulations, posterior and anterior centrum articulations, foramina subcentralia, and neural spine articulation with the centrum. The medial centrum fragment appears porous. The neural arch is entirely absent from this fragmented vertebra. The fragment identified as originating from the neural spinous process possesses a shape that appears to represent the medial base of the prezygapophyses and postzygapophyses of the neural spine. This fragment is more weathered than the fragmented centrum.

Vertebra 6 (Fig. 13) is composed of only centrum material and is highly crushed. All articulations except one remnant of a centrum articular facet are absent. The opposite, posterior, end of the centrum is fragmented. The articular facet is smooth, concave, and preserves a small section of the articular margin of the facet intact. The crushed medial centrum can be discerned from the anterior facet and exposed posterior end but is minimal in lateral profile. Crushing of the centrum is extensive anteroposteriorly in this element (Fig. 13) whereas the dorsoventral height of the centrum is consistent with the dorsoventral vertebral height of the other disarticulated vertebrae (Table 1). Neural spine material is absent dorsal to the neural arch, which is present and partially defined.

Vertebra 7 (Fig. 14) is composed of only the centrum and is lacking all articulations. Remnants of the centrum resemble articular facets but cannot be articular facets as the centrum is too short lengthwise. The lateral walls of the centrum appear highly porous due to weathering and a concave excavation is present on the anterior end. This excavation is not pock-marked with holes from weathering as the remainder of the

centrum is. Dorsal to the excavation the surface of the centrum is clearly visible and is also not porous. The saddle shape of the dorsal surface is slightly concave in a manner less noticeable than in other vertebrae that possess full or partial neural arches.

Articulated Vertebrae.—The articulated elements of the specimen differ from the disarticulated elements in that they were not subjected to weathering. Crushing of the vertebrae occurred on both proximal and distal members of the articulated vertebrae. The five posterior-most articulated vertebrae (Fig. 5) consist of nearly complete centra including cervical rib facets and evidence of foramina subcentralia. The anterior vertebrae of the articulated series are not as completely preserved. The centra of these vertebrae are robust, filling the space between articular facets completely with thick barrel-shaped centra.

Due to the increased centrum robustness the vertebrae, which are in right lateral view, are nearly cylindrical in shape. Anterior vertebrae of the specimen are dorsoventrally crushed rather than cylindrical. The posterior-most vertebrae might be "pectoral" cervical vertebrae bordering the thoracic vertebrae. Pectoral vertebrae are distinguished as being the first vertebra with a neural arch that articulates with the transverse process (O'Keefe, 2002). Thoracic or dorsal vertebrae are defined as beginning with the first vertebra that bears a sternal rib (Williston, 1925). The cervical ribs of the vertebrae of plesiosaurs are short lengthwise. The foramina subcentralia are present on the ventral surface of these vertebrae. Posterior-most centra gradually increase in surface

area so that they are barrel-shaped; they are more rounded in anteroposterior view with concave ends (Smith, 2007).

Vertebra 8 consists of the centrum and partial dorsal spinous processes obliquely crushed anteriorly. The margins of the articular facets of the centrum are more robust than the medial area of the centrum. The articular facets of the centrum are damaged by crushing and the dorsal surface of the posterior facet is damaged as well. The angle of the posterior facet is nearly 45° in respect to the median line of the centrum whereas the anterior facet is not angled significantly by crushing. The appearance of the vertebra suggests that the anterior aspect of the vertebra might have been braced and not crushed by the pressure distorting the medial centrum and posterior articular face. The ventral centrum is severely weathered and evidence of articulation facets for ribs as well as foramina subcentralia is absent.

The postzygapophysis is broken below its articular surface. Due to the direction of crushing, vertebra 8's postzygapophysis does not articulate in its present state with vertebra 9. The neural spine is absent from this destroyed area of the posterior process and above the prezygapophysis. The anterior process and articulating face are nearly completely preserved. Matrix material preserved in the plaster jacket is evident above the neural spine process. This material represents the broken edge of the neural spine. The pedicels of the neural arch are crushed significantly and it is not apparent whether the shale matrix forms a concave filling of the arch or if the matrix filled the arch completely prior to distortion by crushing.

Vertebra 9 exhibits anterior oblique crushing of the centrum and neural arch. Angles of the articular facets are more obliquely angled than those of vertebra 10 and less than those of vertebra 8. Edges of the articular facets are thick. The angle of both articular facets with respect to a medial line drawn through the centrum is approximately 45°. The centrum was crushed significantly in relation to the amount of crushing evident in other articulated vertebra. Facets also are damaged and the excavation of the centrum is exaggerated as a result. The centrum is not cracked. There is no evidence of rib facets or foramina subcentralia.

The neural arch of this vertebra is crushed. The anterior margin of the neural arch is entirely closed whereas the posterior margin is open. The articulation of the postzygapophysis with vertebra 10 is not apparent in present preservation due to disintegration of this process on vertebra 9. The neural spine is fragmented and absent above this crushed expansion of the zygapophyseal processes.

Vertebra 10 consists of a minimally crushed centrum and dorsal spinous processes that do not show signs of crushing. The centrum of vertebra 10 is of medium robustness in comparison to vertebrae 8 and 9 and slight anterior oblique crushing is preserved. Articular facets are particularly thick in this centrum and the margin of the anterior articular facet is thicker than the margin of the posterior articular facet. The articular facets display a shallow angle of anterior deflection, possibly a result of oblique crushing. A short crack extends from the ventral surface of the centrum to the medial surface of the

centrum. Rib facets are not present on this vertebra and damage to the ventral centrum also eliminated evidence of foramina subcentralia.

There are no evident cracks in the preserved portion of neural spine of this vertebra. The sediment in the posterior portion of the neural arch is nearly flush with the edges of the pedicels whereas the sediment in the anterior portion is concave and less flush with the edges of the pedicels. The prezygapophysis of vertebra 10 would articulate with vertebra 9 successfully if the postzygapophysis of vertebra 9 was intact. Postzygapophysis articulation with the following vertebra, vertebra 11, is complete but the neural spine is absent above the zygapophyses. Broken fragments of the neural spine appear to have been preserved but were subsequently lost after collection. No crushing is evident on the zygapophyseal processes.

Vertebra 11 lacks articular surfaces on the posterior side of the centrum and possesses a neural canal that is filled with sediment. The neural spine is absent above the zygapophyseal processes. The posterior articular facet of the centrum is not articulated with vertebra 12. The margin of this portion of the articular facet is damaged. This damage causes separation from the anterior facet of vertebra 12 but still preserves the orientation of articulation between the elements. The centrum does not appear amphicoelus due to the damage present on the articular facet. However, this irregularity is atypical in comparison to the remainder of the series and can be attributed to the damage of the facet. It is not, therefore, considered to be a diagnostic character of the

series and is an anomaly in the series. Rib facets and evidence of the foramina subcentralia are present on the centrum.

The neural spine is fragmentary in vertebra 11. The postzygapophysis is broken posteriorly and therefore cannot articulate with the cracked and broken prezygapophysis of vertebra 12. The prezygapophysis is fragmentary and articulation with the previous vertebra is evident. However, the fragmentation of the articular surface appears to conceal the amount of articulation preserved between the zygapophyses of these two vertebrae. The neural spine is been broken off above these zygapophyses and the neural canal is filled entirely with sediment.

Vertebra 12 consists of a centrum crushed length-wise with articular facets anteriorly crushed across both the width and dorsoventral height and a cracked neural arch missing the neural spine above the zygapophyses. This centrum is obliquely crushed, causing anterior angling of the articular facet. Preserved evidence of cervical rib facets is apparent on the lateral wall of the centrum. The ventral surface is slightly concave and the foramina subcentralia are not clearly evident as a result. Margins of the articular facets are robust despite the crushing of the centrum. This dorsoventrally crushed centrum does not produce a significantly altered lateral vertebral silhouette.

Cracking of the neural arch extends from the dorsal aspect of the posterior articular facet of the centrum to the base of the pedicels and then posteriorly along the area of fusion between neural spine and centrum to the dorsal aspect of the saddle-shaped top of the zygapophyses where the neural spine is broken. The prezygapophysis is broken

posterior to the articulation with the postzygapophysis of vertebra 11 in the series. The postzygapophysis of vertebra 12 is intact and completely articulates with the prezygapophysis of vertebra 13.

Vertebra 13 possesses the most visible articular facet for the cervical ribs on the lateral wall of the most robust centrum in the specimen but also has a cracked neural spine and a sediment filled neural canal. The vertebrae posterior to this element are nearly as robust. This rib facet is for a single-headed rib. The facet is preserved in a posterior position on the centrum. Articular facets of the centrum articulate with the surrounding vertebrae. A fragment of shale sits between the vertebrae 12 and 13. This piece of shale is located between the two vertebrae in a similar fashion to the cartilaginous intervertebral discs that were present in life; however, this material is not preserved soft tissue within the column.

The neural canal is filled completely with sedimentary material but the margins are concave. The neural spine is absent dorsally to the postzygapophysis and the prezygapophysis. The prezygapophysis does not articulate completely with the postzygapophysis of the vertebra 12. A crack is present along the area of fusion between the pedicels and the dorsal centrum. The crack is not representative of suturing at this site. This crack extends from the dorsal articular margin of the anterior centrum facet, dorsally to the medial surface of the pedicel, and ends along the posterior margin of the neural arch.

Vertebra 14 consists of a robust centrum with articulated facets and articulated zygapophyses. Cervical rib facets on the vertebra are visible as well. The centrum of vertebra 14 is one of the most complete in the series and possesses a secondary preservation in the form of an embedded tooth fragment. The centrum appears thinner in the middle than at either end and slightly shorter on the anterior end of the centrum as an artifact of preservation.

The neural arch of vertebra 14 is more sediment filled than previous or following neural arches in the series. The prezygapophysis is well-preserved and articulates completely with vertebra 13 whereas the postzygapophysis is partially broken but still articulates with vertebra 15. The spine is cracked medially along the base of the postzygapophysis from the posterior margin of the neural arch to the center of the dorsal surface of the broken neural spine. The neural spine is broken above the zygapophyses and evidence of the preservation and breakage remains on the dorsal aspects of the zygapophyses.

Evidence of the foramina subcentralia is not well-preserved and the presence of the structure is partially hidden by the shark tooth fragment. The shark tooth broke superior to its base; the cusp of the tooth is not present. The base of the tooth and is approximately 0.5 cm wide and protrudes from the ventral centrum less than 1 cm (Fig. 15). The tooth was tentatively referred to *Leptostyrax macrorhiza* Cope 1875 based on the shape of the broken tooth (M. Everhart, pers. com.). Positive identification was not possible without damage to the vertebra. The base is situated so that its narrow aspect lies

anterior to posterior with the centrum. Despite knowing the orientation of the tooth, it is difficult to ascertain the orientation of the body of the shark that left the tooth in relation to the cervical vertebrae. Sharks attack prey from all directions, whether scavenging or preying, which can result in "feeding frenzies" (Springer, 1967; Shimada et al., 2010). Remodeling of the bone is not evident around the tooth. Absence of remodeling indicates the animal was dead prior to or died shortly after the attack. No other teeth or punctures attributed to teeth were discovered.

Vertebra 15 is articulated with vertebrae 14 and 16 at the centrum and the zygapophyses. The oblique angle of crushing in vertebra 17 prevents full articulation with the centrum of vertebra 16 making the articulations between vertebrae 14 - 16 the last full articulations in the series. Transverse processes of the vertebra are absent as are their articular points. A recognizable cervical rib facet on the centrum is present. The centrum is more robust than that of vertebra 16. The cervical rib facet is not distinctly seen. Both articular facets are well-preserved and overall shape of the centrum is well defined.

The neural arch is concave in shape on the anterior surface; the posterior surface of the neural arch is filled completely with sediment. The broken neural spine is evident in a line of fragmentation dorsal to the zygapophyseal structures. Zygapophyseal structures are articulated with the zygapophyses of vertebrae 16 and 14. A crack is present from the posterior to anterior faces of the neural spine superior to the fusion site with the centrum and inferior to the neural arch. A second crack extends from this

anteroposterior crack dorsally to the breakage line of the neural spine above the zygapophyses.

The centrum of vertebra 16 is fully preserved with less oblique crushing than vertebrae 8, 9, or 17 in the articulated section. This centrum is not dorsoventrally crushed. The centrum is slightly laterally crushed, but it is mostly cylindrical and retains an amphicoelus shape. A rib facet is visible on the lateral wall of the vertebral centrum and is preserved despite the lateral crushing of the posterior portion of the centrum.

Neural spine material preserves the zygapophyses but is also crushed laterally so that the zygapophyses appear laterally flattened and narrow. Transverse processes on the neural spine are absent and the spine is broken above the zygapophyses. The neural arch is sediment filled medially. The anterior and posterior margins of the arch's filling are concave in shape. Incomplete preservation of the pedicels left the preserved neural arch anteroposteriorly shortened in comparison to other neural arches that were preserved in the specimen. Some of the laterally crushed material of the neural spine appears to be spread dorsally above the prezygapophyses. Breakage of the neural spine is clearly evident dorsal of the preserved neural spine material.

Vertebra 17 possesses a robust centrum, obliquely angled posteriorly, with an articular facet for the cervical rib visible. The oblique angle of crushing on the centrum is angled posteriorly rather than anteriorly, as in vertebrae 8-10. A notching in the dorsal aspect of the centrum near the point of fusion with the pedicels appears to be preservational. The crushing of the vertebra angles the posteriorly but does not affect the

angle of the articular facets relative to the centrum. However, the posterior articular facet is not as prepared as the anterior facet due to this angle.

The neural arch remains intact but the neural canal is not open along its length. Sediment filled the canal and closed it posteriorly. The neural spine was broken ventral to the zygapophyses on a diagonal line and a notch in the centrum is present at the site of fusion between the dorsal centrum and the pedicels. This notch is preservational and not present in any other elements of the specimen. The pedicels are more anteriorly well-preserved than posteriorly. The prezygapophyses are more completely preserved than the postzygapophyses. The postzygapophyses are broken and have been lost during preparation and transport. Transverse processes are absent from this element.

DISCUSSION

Discussion of Physical Description.—KUVP 16375 possesses many interesting preservations. Excavations of the centra, artifacts of preservation (e.g., crushing, breakage, and weathering), and an embedded tooth are represented on the various elements of the specimen. The articulated and disarticulated elements of the specimen represent an adult plesiosaur, evidenced by both complete fusion of the neural spine with the vertebral body and by comparison to one of the more complete undescribed fossils of the Kiowa Shale. The preservational state of the specimen is varied along the length of

the present vertebral column. The anomalies and unique preservation are unknown in other Kiowa Shale plesiosaurs in the FHSM and KUVP collections (pers. obs.).

The excavations on the ventral surfaces of the centra are seen most prominently in the disarticulated vertebrae (Figs. 10 and 11). The excavations cause the lateral walls of the centra to appear visibly crushed and shortened dorsoventrally in preservation. Centra lost their ventral surfaces, including evidence of foramina subcentralia, and the middle of the centrum is also completely lost. The excavations are dorsoventrally deep while remaining laterally and anteroposteriorly short and crushed. These ventral surfaces are assumed to have existed in living specimens as these vertebral bodies bore some of the weight of the neck and skull and are not indicative of being either the atlas or axis (C1 or C2) vertebrae with unique vertebral body morphologies.

Loss of these areas could be the result of many different biotic or abiotic processes. Possible explanations include loss due to predation, scavenging, and decomposing organisms, weathering after exposure, incomplete fossilization, and the crushing responsible for the obliquely crushed vertebrae in the specimen. The evidence for predation, scavenging, and decomposers in these vertebrae is exemplified by the shark tooth material in the ventral surface of vertebra 14 (Fig. 15). Evidence of crushing can be seen in broken margins of articular facets and centra as well as the angles of the facets compared to the centrum. The particular cause of centrum loss in these vertebrae is not known.

As a whole, the neural processes of the vertebrae are minimally preserved as the articulated elements of the specimen preserve the neural processes better than the disarticulated elements. The absence, damage, or extent of completeness of preservation of these structures is different in each vertebra with some possessing a small projection of material dorsal to the prezygapophyses and postzygapophyses and some possessing no material dorsal to the centrum. The neural arch and centrum of these vertebrae are fused where they contact one another, not through a secondary diapophyseal structure. Fusion of the vertebral centrum and the neural arch is a diagnostic characteristic of adulthood in the specimen (Romer, 1956; O'Keefe, 2004). This specimen, because of this fusion of the neural arch and centrum, is hypothesized to be an adult specimen.

Well-preserved neural spines typically consist of neural arch, pedicels, and zygapophyseal structures. The disarticulated elements of this column possess limited zygapophyseal structures; however, the postzygapophyses of vertebra 4 are very well preserved and their articular facets, after additional preparation, are preserved in excellent condition. The neural canals in the series are mostly filled with sediment but are preserved with adequate precision to note their position in the ventral aspect of the neural spine. Transverse processes are not preserved on neural spines.

Comparisons of centrum length to height appear to remain the same throughout the specimen (Table 1). The centra of KUVP 16375 are shorter in length than they are tall in height making the vertebrae dorsoventrally deep but anteroposteriorly short. Schumacher and Everhart (2005) noted that some specimens with smaller and more

laterally placed foramina subcentralia appear to be lacking these structures altogether. Reduced and lateral foramina are typically noted as a derived pliosaurid character (O'Keefe, 2001; Schumacher and Everhart, 2005) and might be easily lost in fossilization; damage, crushing, and weathering of the vertebral centrum as noted in this specimen might lead to loss of this structure.

Throughout the column articulation of the elements is preserved inconsistently. Associated soft tissues (e.g., fossilized ligaments, spinal cord elements, and intervertebral cartilages) are not present in this specimen. Articular facets of the centra that are of more robust preservation are typically articulated. The zygapophyseal structures of the vertebrae articulate without much intermediary soft tissue as is seen between the articular facets of the centra. These are observed in their natural articulation in this fossilized skeletal material whereas the articulated centra articulate with more lost soft tissues. The zygapophyseal structures are not obliquely crushed as often as the centra of the cervical column; this preserves articulation in a better state than the crushed centra.

The disarticulated and obliquely crushed centra of anterior cervical elements are not able to articulate as well as posterior vertebrae either at the articular facet of the centra or at zygapophyseal structures of the neural spine. The centra orientation is discernible, as is the order of the vertebrae in the column, due to the size of the individual elements and the orientation of the zygapophyseal structures. Numbering of the elements of the specimen reflects this inferred order but does not equate to the anatomical

numbering of the cervical vertebrae. Disarticulated members lacking complete zygapophyseal structures are placed in the column based on centrum size.

The number of vertebrae associated with this specimen, adding in the atlas and axis vertebrae not present, is fewer than the number of cervical vertebrae in most polycotylids; however, elements might be missing from the specimen. The cervical rib articulations of the polycotylids are single-headed and dorsally located on the centrum. This is representative of the more derived character of rib facets in plesiosaurs.

Identification of the specimen based on physical description of vertebral characters indicates that the cervical series belongs to a close relative of either *Trinacromerum* or *Dolichorhynchops*; this is consistent with the original identification by O. W. Bonner and M. E. Williams while collecting the material as *Trinacromerum* sp. (pers. obs.) because apomorphies separating the species are not apparent in this region of the vertebral column (Carpenter, 1996; O'Keefe, 2010). However, temporally this specimen is much older (Early Cretaceous) than the Late Cretaceous genera *Dolichorhynchops* and *Trinacromerum*. Due to this the species is referred to the Polycotylidae and uncertain genus but is related to *Dolichorhynchops* and *Trinacromerum*.

KUVP 16375 is morphologically similar to other polycotylids. The specimen possesses similar articular facets (zygapophyseal and centrum), centrum shape, and nutritive and nervous foramina as other described polycotylids such as *Dolichorhynchops* and *Trinacromerum* (Tables 2 and 3). Comparison of this specimen to typical polycotylid

vertebrae (Williston, 1908) leads to the determination that these vertebrae represent a member of the Polycotylidae. Throughout the cervical column typical elements of plesiosaur anatomy are exhibited; these do depend on the quality of preservation and outside factors such as weathering as seen in some of the disarticulated vertebrae of the anterior portion of the cervical column. The atlas and axis complex is not preserved as an element of this specimen. This means the anterior-most vertebra associated with the specimen is potentially the third cervical vertebra.

Character Analysis.—Compared matrices (Tables 2 and 3) included the species *Trinacromerum bentonianum* (O'Keefe, 2008; Ketchum and Benson, 2010), *Dolichorhynchops osborni* (O'Keefe, 2008; Ketchum and Benson, 2010), *Dolichorhynchops herschelensis* (Sato, 2005; Ketchum and Benson, 2010), and *Dolichorhynchops bonneri* (O'Keefe, 2008); these species were chosen due to their close morphology with one another and the specimen described here. An outgroup consisting of *Plesiosaurus* and *Tricleidus* (O'Keefe, 2004; Ketchum and Benson, 2010) was used in this character analysis. *Plesiosaurus* was chosen because it represents long-necked plesiosauroids significantly different from polycotylids. *Tricleidus* is considered by O'Keefe (2001) to occupy a position near the Polycotylidae and is a "sensible source for comparison" with polycotylids (O'Keefe, 2010 p. 326).

The specimen is incomplete and fragmentary and therefore the number of characters fewer than are ideal for a complete identification of the material to species.

Twelve characters from O'Keefe (2004) and 17 characters from Ketchum and Benson (2010) describing the cervical vertebrae in described species are used here. These characters include morphological states of the vertebral centra, neural processes, zygapophyses, and other anatomical structures of vertebrae. Characters were coded as present or absent with exceptions requiring more derived characters. One character was coded for proportional aspects of vertebrae; centrum height and width were compared to determine the proportional relationship coded in this character.

The specimen lacks neural spines, thus comparison of the characters for neural spines are not possible; these characters are coded as unknown where appropriate. Characters requiring a column of vertebrae are coded. Assumptions for length of the entire cervical series are not made at this time. Unknown characters within the cervical vertebral series such as those for the atlas and axis are not addressed due to their absence from the specimen. Characters concerning cervical rib facets are coded for the specimen; however, characters concerning the cervical ribs cannot be coded in this analysis. Ventral foramina are addressed in the data matrix based on the centra in the specimen that retain adequate ventral centrum materials that can be analyzed for these anatomical structures.

The centra are not binocular-shaped as described by O'Keefe (2004, 2008) and O'Keefe and Street (2009) as looking down the centrum from anterior to posterior and seeing that the centrum appears to be medially, dorsally and ventrally, pinched. This character is referred to in Appendix 1 but it is not used by Ketchum and Benson (2010);

Appendix 2 does not, therefore, mention the character but does contain a character that references the centrum shape in a different manner.

Length-width ratios differ along the column due to crushing of vertebral centra; however, the assumption is made that uncrushed centra appropriately represent the living anatomical situation of this specimen and are used for coding ratio related characters. The length of the vertebral centrum was shorter than it was tall in all cases. Ontogenetic variation is noted as occurring within this character (Welles, 1952). Ossification and fusion of the neural spine and centrum suggest that this plesiosaur reached adulthood.

These characters include the length of the neck, cervical spine processes, and all characters pertaining to articulation of the neural spines. The proportions of the vertebrae, ventral and dorsal notches in the centra (the "binocular-shape" mentioned character Appendix 1), width of zygapophyses, and cervical rib articulations are consistent with other short necked polycotylids; *Dolichorhynchops bonneri, Dolichorhynchops osborni,* and *Trinacromerum bentonianum*. The necks of these taxa were coded as reduced in comparison to the primitive state; however, the described specimen could not be accurately coded for this character. The lack of a ventral keel on KUVP 16375 is notable whereas the polycotylid specimens analyzed by O'Keefe (2004) did not possess discernible areas to either uphold or refute the trait. Change in zygapophyseal angle along the cervical column was noted within the O'Keefe (2004) polycotylid samples. KUVP 16375 did not exhibit changes in the angles of articulations of the zygapophyses; this might be an artifact of the oblique crushing of the vertebrae.

The outgroup taxa, *P. dolichodeirus* and *T. seeleyi*, possess increased length and primitive necks respectively. The vertebral centra are of equal length and height. This represents the primitive state of the centra and is contrary to the character state of the described specimen. Changes in zygapophyseal articulation angle also are different between the outgroup and specimen states. The zygapophyseal angle is coded as unknown in *P. dolichodeirus* but is coded as changing in *T. seeleyi*. Most other known characters are similar in all of the described taxa; however, cervical rib articulation, crushing and flanges of the neural spines are not similar between ingroup and outgroup taxa.

A single unique character, disregarding the character coding for neck length, differentiates KUVP 16375 and polycotylids from the outgroup taxa. Neck length is no longer thought to be indicative of family or order level of organization in the Plesiosauria (O'Keefe, 2002; Druckenmiller and Russell, 2008) and therefore this character is not directly indicative of the lineage of this specimen.

The analysis of the characters in the matrix generated using the characters of Ketchum and Benson (2010) contains the same ingroup and outgroup taxa as the previous analysis with the exception that *Dolichorhynchops bonneri* is replaced with the species *Dolichorhynchops herschelensis* Sato 2005. The characters used in this analysis are more numerous and more specific in their scope but are still limited in overall number. Rather than indicating length of neck as "short" or "long", the neck length character is described quantitatively. This allows for more precise comparison of that character.

These unknown characters include height, morphology, and shape of the neural spines in dorsal and cross-section views (Table 3). Three characters, including the character coding for neck length, differentiate KUVP 16375 and polycotylids from the outgroup taxa. The vertebra being shorter in length than they are tall is a derived condition of the cervical column. Rounded ventral surfaces of the vertebrae, potentially an artifact of preservation, are consistent in at least one known polycotylid genus.

The neck length character is quantitative rather than qualitative and is specifically noted as including pectoral vertebrae; pectoral vertebrae are those vertebrae displaying transitional morphology between cervical and dorsal vertebrae. The number of vertebrae, 17, in KUVP 16375 is identical in number to *Dolichorhynchops herschelensis*; however, the atlas and axis are missing and the neck of KUVP 16375 therefore consists of at least 19 vertebrae. *Dolichorhynchops osborni* and *T. bentonianum* are coded as possessing 22 and 23 vertebrae respectively. *Plesiosaurus dolichodeirus* is coded as possessing 46 vertebrae. *T. seeleyi* is coded as unknown for this character.

The presence of ventral foramina and proportions of the centra where length is less than height are similar to other polycotylids. The ventral surfaces of the centra, while lacking a keeled surface where the centra are completely preserved, do exhibit some keeling where the centra are crushed, weathered, or a combination of the two. As such, they are coded as being flat or slightly convex while other polycotylids in this study exhibit sharply keeled ventral centra. This singularly different character does not necessarily preclude the specimen from being interpreted as a polycotylid as it might be

an artifact of preservation or weathering. The concavity of the articular facet is gently

convex in KUVP 16375 and *T. bentonianum* but is unknown in *D. osborni* and strongly

convex in *D. herschelensis*.

Rib facets on the centrum, contact of the neural arches and the centrum, and the

absence of zygosphene and zygantrum articulations on the centrum are shared characters

of KUVP 16375 and the polycotylid species of the ingroup. The width of zygapophyses

in these species is also similar; all are subequal to the width of the centrum. Neural

spinous processes are not coded for KUVP 16375 in this character analysis. The anterior

process of the cervical rib is present in *D. herschelensis* and *T. bentonianum* but cervical

ribs are missing, and uncoded, in both KUVP 16375 and *D. osborni*.

Presence of ventral foramina, combined width of zygapophyses, absence of a

longitudinal ridge on the centrum, convex articular surface, neural arch and centrum

contact not involving diapophyses, and absence of zygosphene and zygantrum

articulations are shared characters of KUVP 16375, *P. dolichodeirus*, and *T. seeleyi*.

These characters also were shared between the described specimens and the ingroup as

well and represent symplesiomorphies or characters shared among all plesiosaurs

represented here. These are not characters tying the specimen to the outgroup in

identification of the specimen. Medial contact of the zygapophyses is present in *T.

seeleyi*, a trait not exhibited in any other of the specimens compared in this character set.

Proportions of the vertebrae of the outgroup and the described specimen are all

different; KUVP 16375 is shorter anteroposteriorly than tall dorsoventrally, *P.*

dolichodeirus is equally long as tall, and *T. seeleyi* is longer than tall. The morphology of

the ventral surface of the centrum is not described, according to coding, in *P.*

dolichodeirus (Ketchum and Benson 2010) but it is sharply keeled in *T. seeleyi* as in *D.*

herschelensis. The gently convex concavity of the articular facet is similar in *P.*

dolichodeirus and KUVP 16375 while *T. seeleyi* is strongly convex. Articular rib facets

are similarly derived in *T. seeleyi* and KUVP 16375, as is seen between KUVP 16375

and members of the Polycotylidae that are compared in this analysis; *P. dolichodeirus*

exhibits a more primitive condition of dual co-joined rib facets. The majority of the

characters in the set are complimentary with other polycotylids, including those that are

plesiomorphic. Unique characters in the analysis including neck length, ventral surface

shape, and proportions of the centra are consistent with identification of a polycotylid.

The analysis of KUVP 16375 using the characters of O'Keefe (2004) and

Ketchum and Benson (2010) allows for identification to family for the specimen. The

Polycotylidae, represented by three species in each analysis, and the specimen shared

numerous characters in both character sets despite the lack of neural spine characters for

the specimen. The specimen is a member of the Polycotylidae based on available

characters. The compared character analyses communicate that a single character favors

KUVP 16375 as a species of *Trinacromerum* rather than *Dolichorhynchops*.

Trinacromerum and *Dolichorhynchops* are quite similar genera, were

synonymized at one point by Williston (1908), but are noted to possess a few

autapomorphies separating them (O'Keefe, 2010; Carpenter, 1996). Those

autapomorphies that are hypothesized, and could potentially identify the specimen to species, are features of the skulls of *Trinacromerum* and *Dolichorhynchops*. None of the vertebral characters are considered autapomorphies. Therefore, despite the ability to separate these genera when material is adequately available to be analyzed, KUVP 16375 can only be said to be a polycotylid closely associated with either *Trinacromerum* or *Dolichorhynchops* and favoring an identification of *Trinacromerum* sp.

Probable placement of the vertebrae in *Trinacromerum* is hypothesized (Fig. 16). This is based on the fact that there are three unique shared characters between KUVP 16375 and *Trinacromerum* and one unique shared character between KUVP 16375 and *Dolichorhynchops* in Ketchum and Benson's (2010) characters and no unique characters separating the specimen and two genera from one another in O'Keefe's (2004) characters. The original identification of the specimen as *Trinacromerum* sp. is consistent with these character analyses. More precise determination to species would require more skeletal material however.

CONCLUSIONS

Plesiosaur remains of the Western Interior Seaway in the Kiowa Shale are often fragmentary and composed of minimal materials. Taphonomic explanations for this include predation and scavenging, tidal energy in near-shore environments, and bone damage through other processes prior to and during fossilization. KUVP 16375

exemplifies the physical damage of bone through predation and scavenging, evidenced by the tooth fragment, as well as other processes, particularly potential weathering, crushing, and incomplete preservation of crushed and excavated centra. The identification of KUVP 16375 is based on a character analysis and described anatomical characteristics. The family level designation Polycotylidae can be confidently referred to with the available character set and described material.

Excavations in the vertebral centra of elements of the specimen are unique in comparison to other described plesiosaur vertebrae. The excavations are of indeterminate origins and the source of the excavations cannot be determined at this time but bone removal due to predation, scavenging, and decomposing organisms, weathering after exposure, incomplete preservation, and the crushing responsible for the obliquely crushed vertebrae in the specimen are possible explanations of the origins of these centrum excavations. More extensive, invasive, and, potentially, destructive tests could be used to confirm the origins of the excavations but were not conducted on these vertebrae at this time; potentially damaging tests were not conducted on any elements of this specimen during this study.

The characters used to taxonomically analyze the undamaged portions of the vertebrae were derived from O'Keefe (2004) and Ketchum and Benson (2010). The characters of plesiosaurs have been fairly standard since Williston (1903) and Andrews (1910, 1913), though characters have been augmented and added since that time. The

characters available for cervical vertebrae are comprehensive and intricate in detail despite the low number of individual characters.

The Kiowa Shale sample of plesiosaurs is proportionately small compared to remains of fishes and invertebrates recovered from the Kiowa Shale but constitute one of the largest populations of vertebrate orders in the formation (Everhart, 2005). Plesiosaur specimens of the Kiowa Shale are rarely as complete as KUVP 16375 in number. The museum collections at the University of Kansas house the most complete specimens of the formation including partial pectoral and pelvic girdles (KUVP 16374 and KUVP 16225, respectively). This description significantly adds to the knowledge of the plesiosaurs recovered from the Kiowa Shale. More detailed descriptions and character analyses need to be done throughout the Kiowa Shale plesiosaurs to identify specimens and catalog the tetrapod vertebrate fauna further.

APPENDIX 1

Descriptive list of characters used to construct the character matrix in Table 2 comparing

KUVP 16375 and O'Keefe's (2004) taxa.

Character Number	Character	State and Coding
1	Number of cervical vertebrae	primitive (0), increased (1), reduced (2), greater than 50 (3)
2	Proportions of cervical centra	length equal to height (0), length greater than height (1), length less than height (2)
3	Distinct change in zygapophyseal angle along cervical column	no change in angle (0), change (1)
4	Ventral keel on cervical vertebrae	absent (0), present (1)
5	Binocular-shaped anterior cervical centra	absent (0), present (1)
6	Width of cervical zygapophyses	wider than centrum (0), subequal with centrum (1), more narrow than centrum (2)
7	Posterior articulation for succeeding neural spine, cervical vertebrae	absent (0), present (1)
8	Cervical rib articulation greatly elongate	circular or subcircular (0), elongate (1)
9	Anterior process of cervical ribs	present (0), absent (1)
10	Anterior neural flange on cervical neural spines	absent (0), present (1)
11	Neural spines, cervical vertebrae	backward angle (0), no angle (1)
12	Lateral compression of neural spines	not compressed (0), compressed and blade-like (1)

APPENDIX 2

Descriptive list of characters used to construct the character matrix in Table 3 comparing

KUVP 16375 and Ketchum and Benson's (2010) taxa.

Character Number	Character	State and Coding
1	Number of cervical vertebrae, includes "pectoral" vertebrae	quantitative
2	Ventral surface of cervical vertebrae	subcentral foramina absent (0); present (1)
3	Proportions of the anterior cervical centrum	as long as high (0); longer than high (1); shorter than high (2)
4	Lateral surface of anterior cervical centra	longitudinal ridge absent (0); present (1)
5	Articular face of cervical centra in anterior view	uniformly convex (0); notched ventrally (1)
6	Ventral surface of cervical centra	flat or only slightly convex (0); rounded ridge (1); sharp keel dividing deep depressions (2); pair of lateral ridges (3)
7	Concavity of the articular face of the cervical centra	strongly convex (0); gently convex (1); nearly flat (2)
8	Rib facets of the cervical vertebrae	rib facets broadly separated (0); two co-joined rib facets (1); one rib facet (2)
9	Contact of cervical neural arches on anterior vertebrae	contacts centrum only (0); contacts diapophysis (1)
10	Combined width of cervical zygapophyses	broader than the centrum (0); subequal with the centrum (1); distinctly narrower than the centrum (2)
11	Medial contact of the left and right prezygapophyses	absent (0); present (1)

12	Zygosphene and zygantrum articulations	present (0); absent (1)
13	Height of cervical neural spines	taller than their anteroposterior length (0); longer than tall (1)
14	Shape of posterior margin of cervical neural spines	convex (0); grooved (1)
15	Shape of neural spines in dorsal view	square (0); transversely compressed (1); transversely elongate (2)
16	Cross-sectional shape of the cervical ribs	circular to oval (0); greatly depressed (1)
17	Anterior process of cervical ribs in dorsal view	present (0); absent (1)

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TABLE 1. Measurements of vertebral centra in KUVP 16375. Measurements taken as indicated in Fig. 4. With notes on the amount of oblique crushing and damage.

Vertebra #	Length (cm)	Height (cm)	Notes
1	3.82	4.10	Centrum crushed/weathered
2	3.57	3.58	Distorted due to crushing; centrum crushed/weathered
3	3.75	4.40	Centrum crushed/weathered
4	3.27	3.82	Distorted due to crushing; centrum crushed/weathered
5	2.49	4.00	Height measurements reflect series trend; centrum crushed/weathered
6	2.36	4.61	Severely damaged; centrum crushed/weathered
7	2.37	4.12	Severely damaged; centrum crushed/weathered
8	3.37	4.22	1st articulated member; some oblique crushing
9	3.48	4.11	Distorted due to anterior oblique crushing
10	3.67	4.30	
11	3.83	4.45	
12	3.78	4.60	
13	3.80	4.64	
14	3.93	4.62	Tooth fragment (broken cusp) preserved in ventral surface of centrum
15	3.80	4.60	
16	3.88	4.62	
17	3.86	4.62	Distorted due to posterior oblique crushing

TABLE 2. Character matrix of KUVP 16375 and O'Keefe (2004). Species included in the analysis are ordered with ingroup at top followed by outgroup and KUVP16375. Character coding as noted in Appendix 1.

	1	2	3	4	5	6	7	8	9	10	11	12
Dolichorhynchops bonneri	2	2	1	?	0	2	1	0	?	1	1	0
Dolichorhynchops osborni	2	2	1	?	0	2	1	0	?	1	1	0
Trinacomerum bentonianum	2	2	1	?	0	2	1	0	?	1	1	0
Plesiosaurus dolichodeirus	1	0	?	0	0	2	1	0	0	0	1	1
Tricleidus seeleyi	0	0	1	0	0	2	1	0	1	1	1	0
KUVP 16375	?	2	0	0	0	2	?	0	?	?	?	?

TABLE 3. Character matrix of KUVP 16375 and Ketchum and Benson (2010). Species included in the analysis are ordered with ingroup at top followed by outgroup and KUVP16375. Character coding as noted in Appendix 2.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Dolichorhynchops herschelensis	17	1	2	0	0	2	0	?	0	1	0	1	0	1	1	0	1
Dolichorhynchops osborni	22	1	2	0	0	?	?	?	?	1	?	1	0	1	1	0	?
Trinacomerum bentonianum	23	1	2	0	0	1	1	2	0	1	0	1	0	?	?	0	1
Plesiosaurus dolichodeirus	46	1	0	0	0	?	1	1	0	1	0	1	0	?	1	0	0
Tricleidus seeleyi	?	1	1	0	0	2	0	2	0	1	1	1	0	0	1	1	1
KUVP 16375	17	1	2	0	0	1	1	2	0	1	0	1	?	?	?	?	?
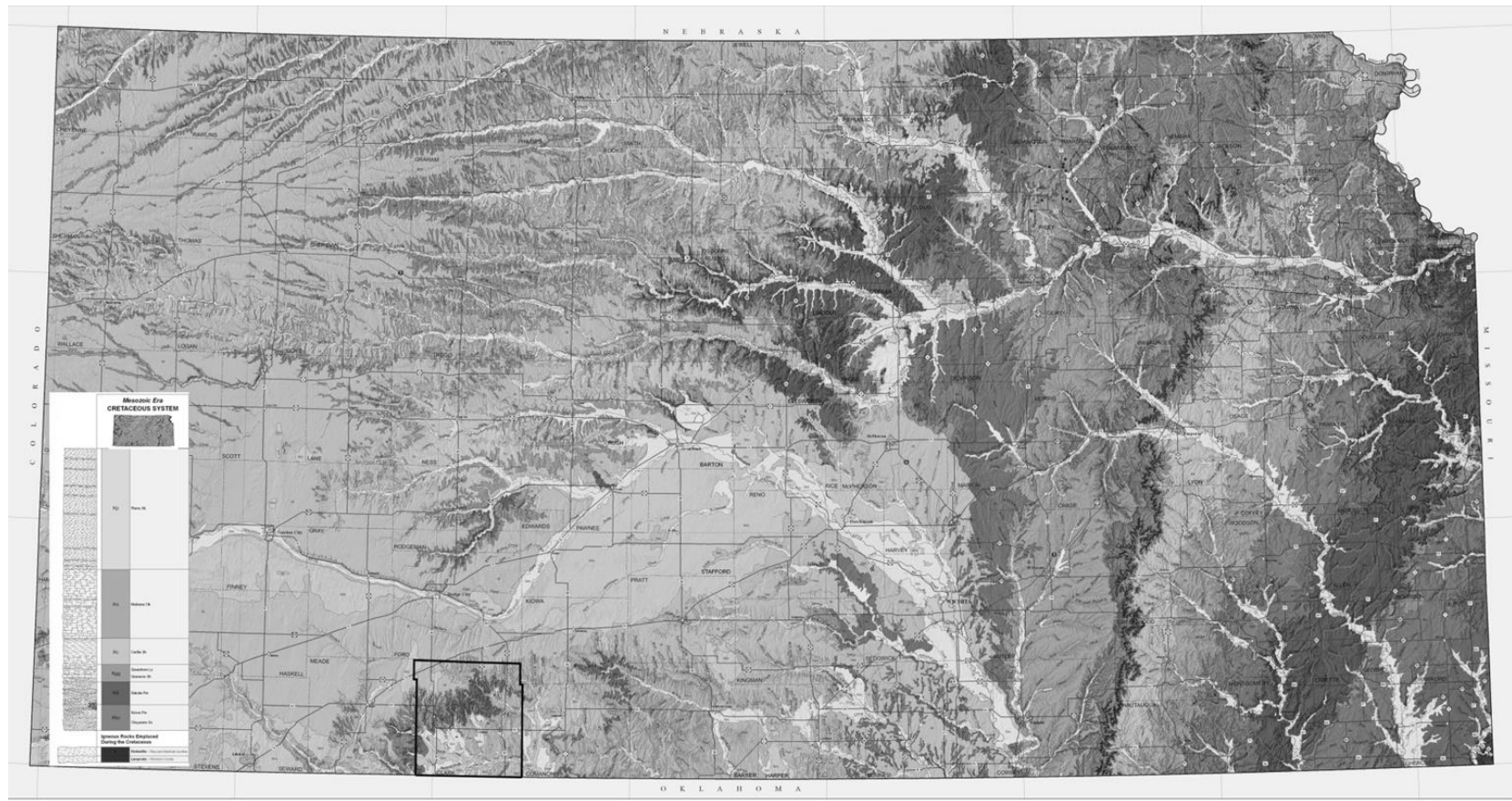
FIGURE 1. Generalized map of Kansas geology. Formations of the Cretaceous are represented by the scale on left. Clark County, general location of the fossil recovery location, is outlined. Adapted from Kansas Geological Survey.
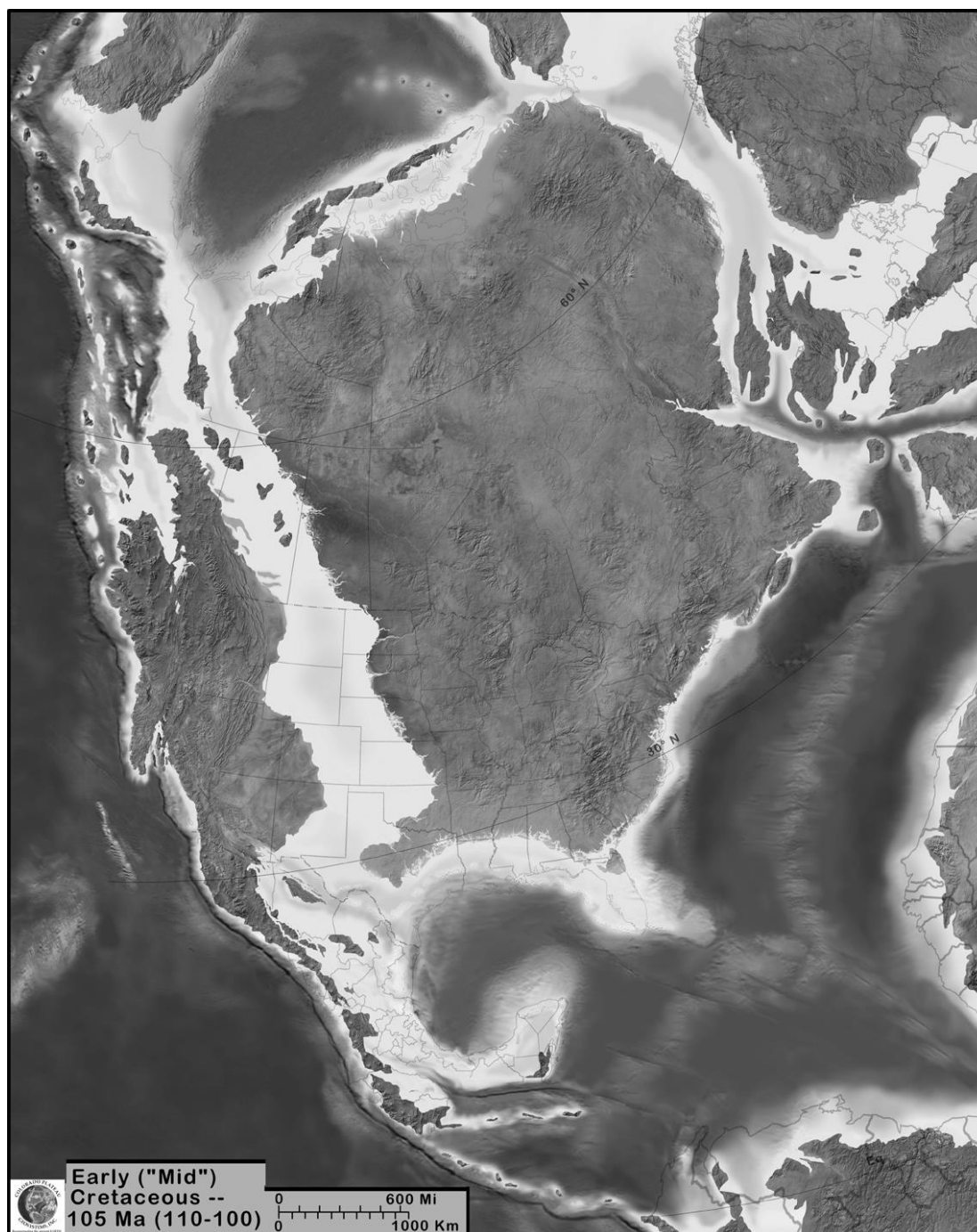
FIGURE 2. Map of the Western Interior Seaway as it appeared during the deposition

of the Kiowa Shale. Map courtesy of Ron Blakey.
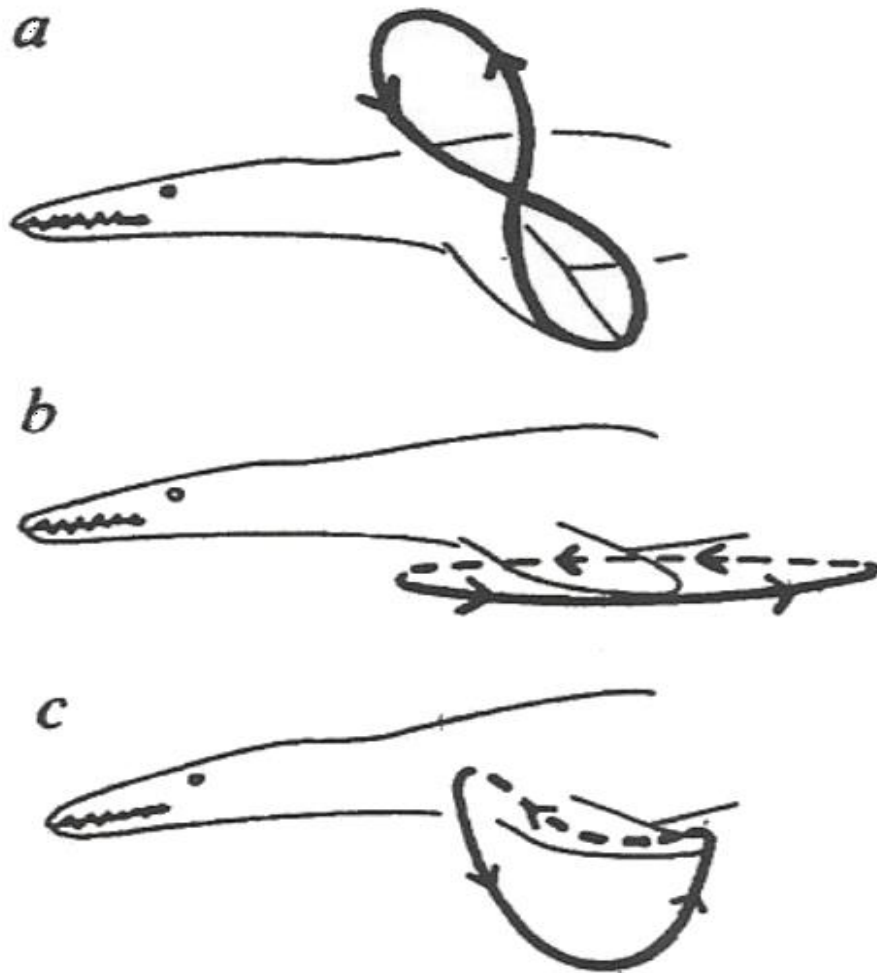
FIGURE 3. Idealized representations of models of proposed plesiosaur swimming styles from Taylor (1986). Models depict figure-eight (A), elliptical (B), and combination elliptical rowing (C) patterns of swimming.
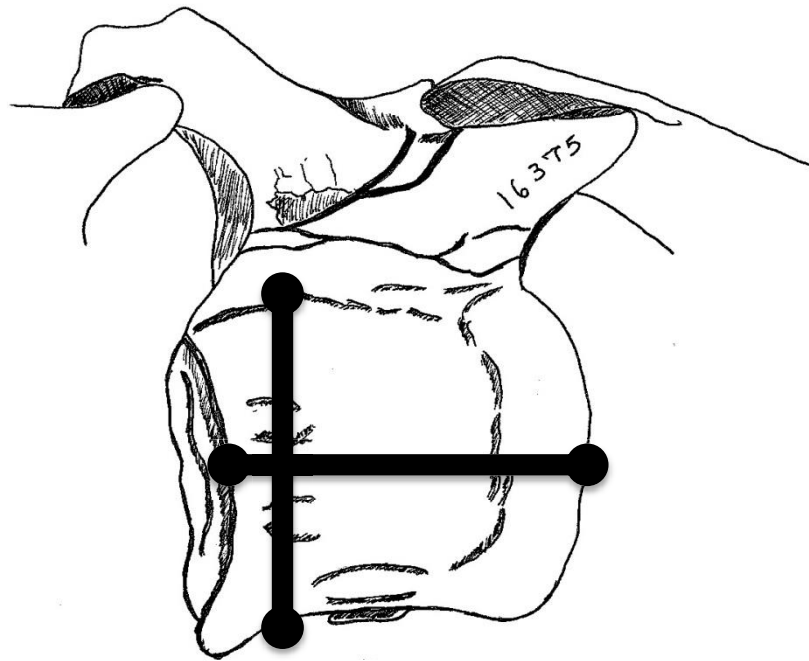
FIGURE 4. Diagram of measurements taken. Length of centrum was measured from the anterior to posterior edge of the centrum as defined by the margins of the articular facets. Height of centrum measurements were taken from the ventral to dorsal margins of the centrum on the posterior edge of the articular facet margin. Vertebrae with compressed centra were measured from the posterior edge of the articular facet margin.

FIGURE 5. Plesiosaur specimen KUVP 16375. Anterior cervical vertebrae are disarticulated from posterior vertebrae and are numbered accordingly. Scale bars equal 1cm in each of their respective series of photographs: 1-4 (A); 5-7 (B). Plaster jacket measures 28 cm by 58 cm 8-17 (C).

FIGURE 6. Quartz crystals in vertebra 2. Individual crystal deposits vary depending on where on the specimen they were seen.
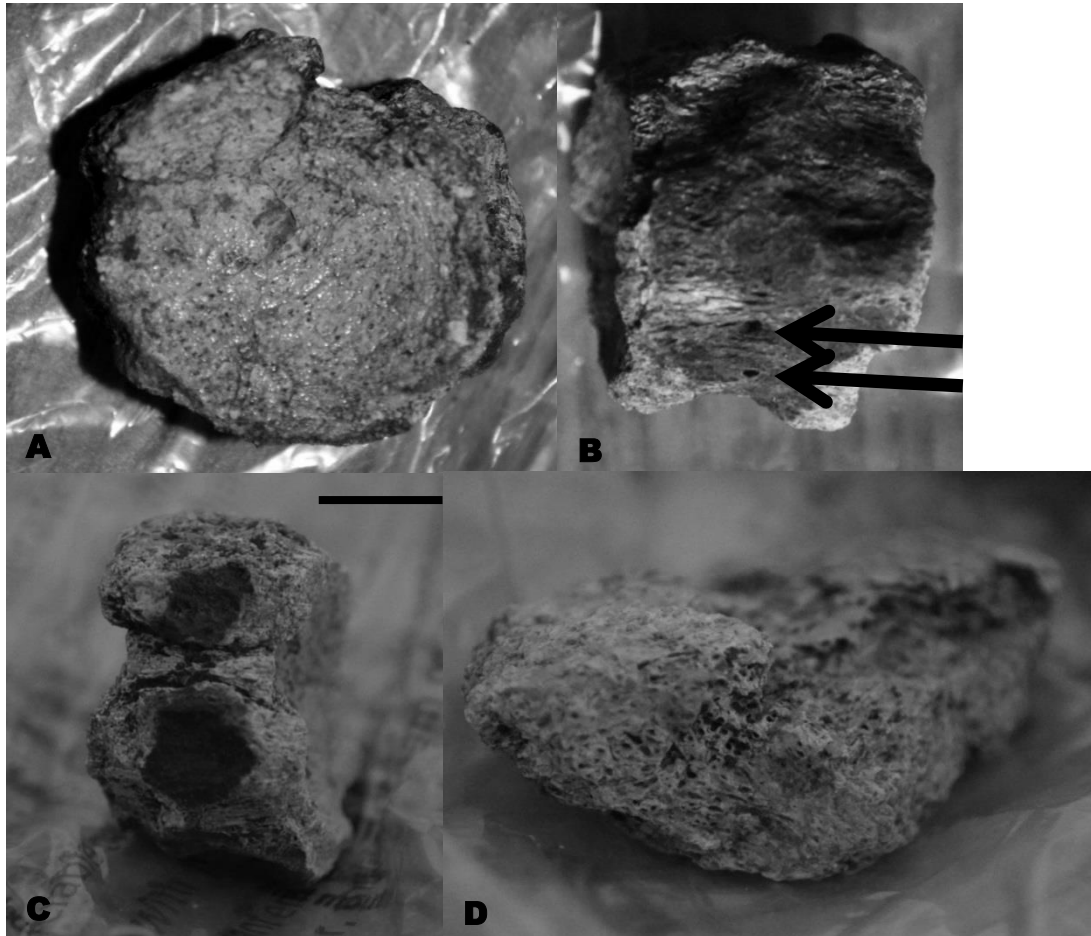
FIGURE 7. Plesiosaur specimen KUVP 16375 Vertebra 5 fragments in anterior (a), left lateral (b), and dorsal views (c). Secondary fragment (d) from the neural spine and base of zygapophyseal structures in left lateral view. Left lateral view of the centrum shows the foramina subcentralia; arrows added to emphasize their location. Scale bar equals 1 cm.
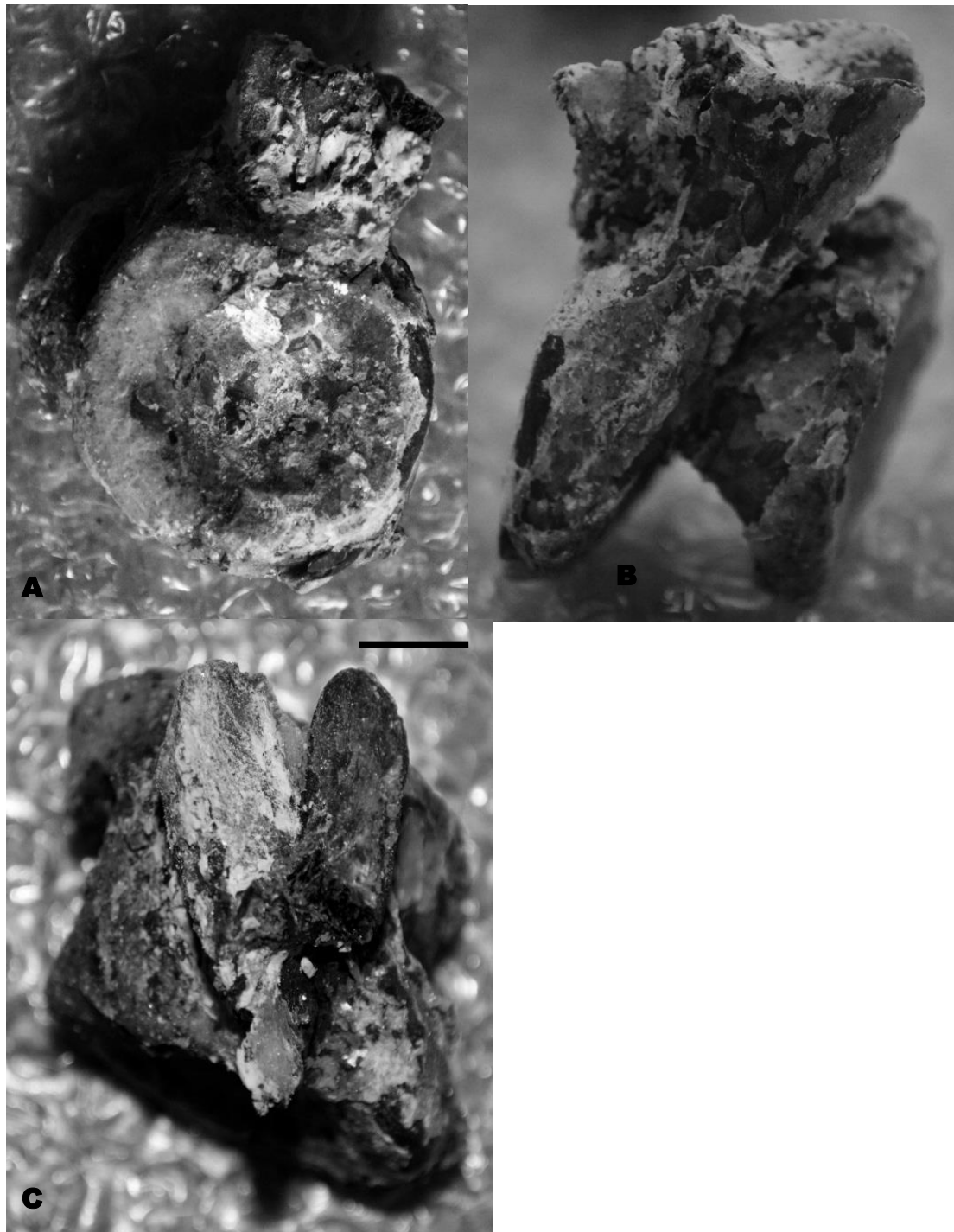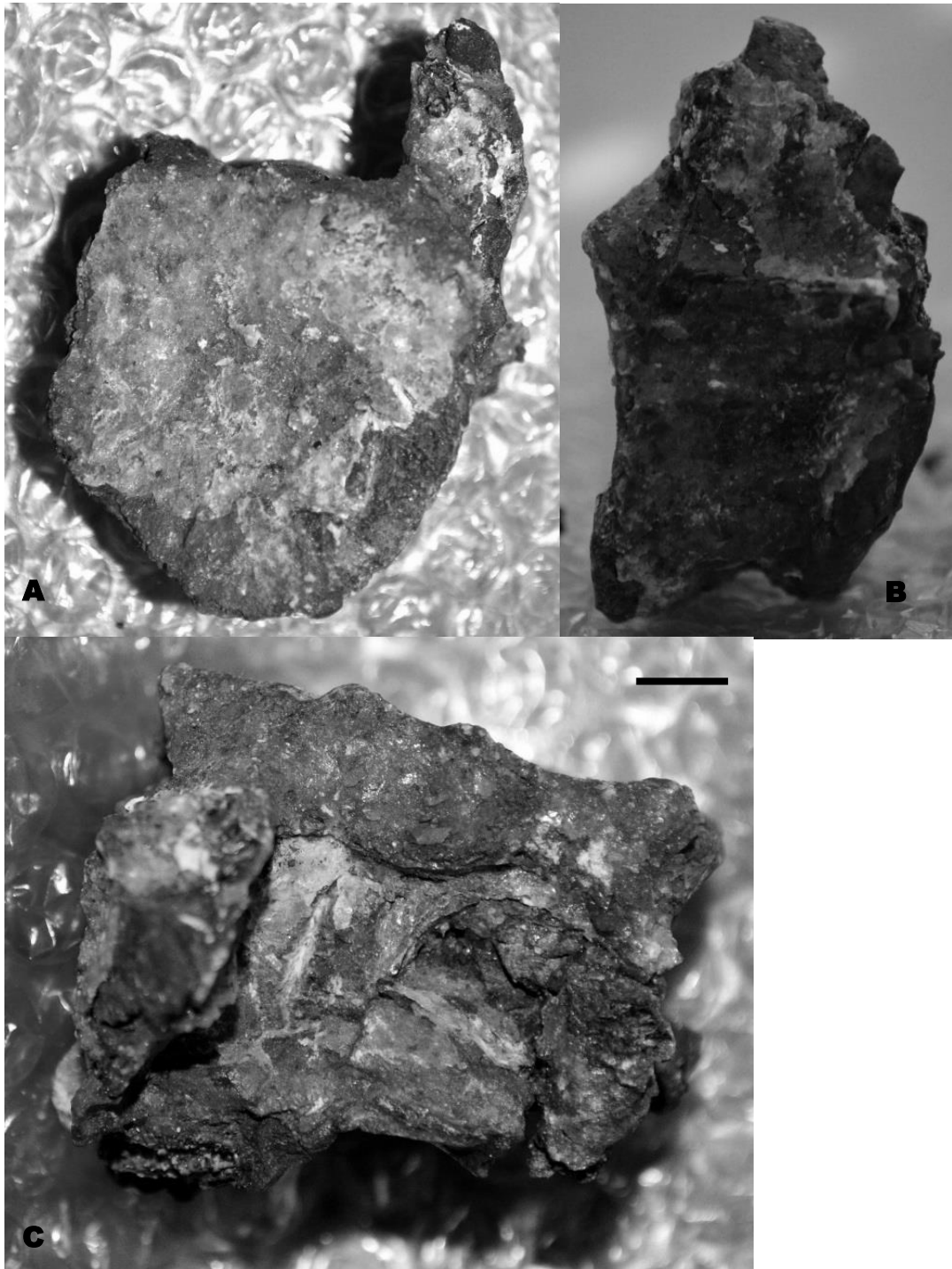
FIGURE 8. Plesiosaur specimen KUVP 16375 Vertebra 4 in anterior (a), left lateral

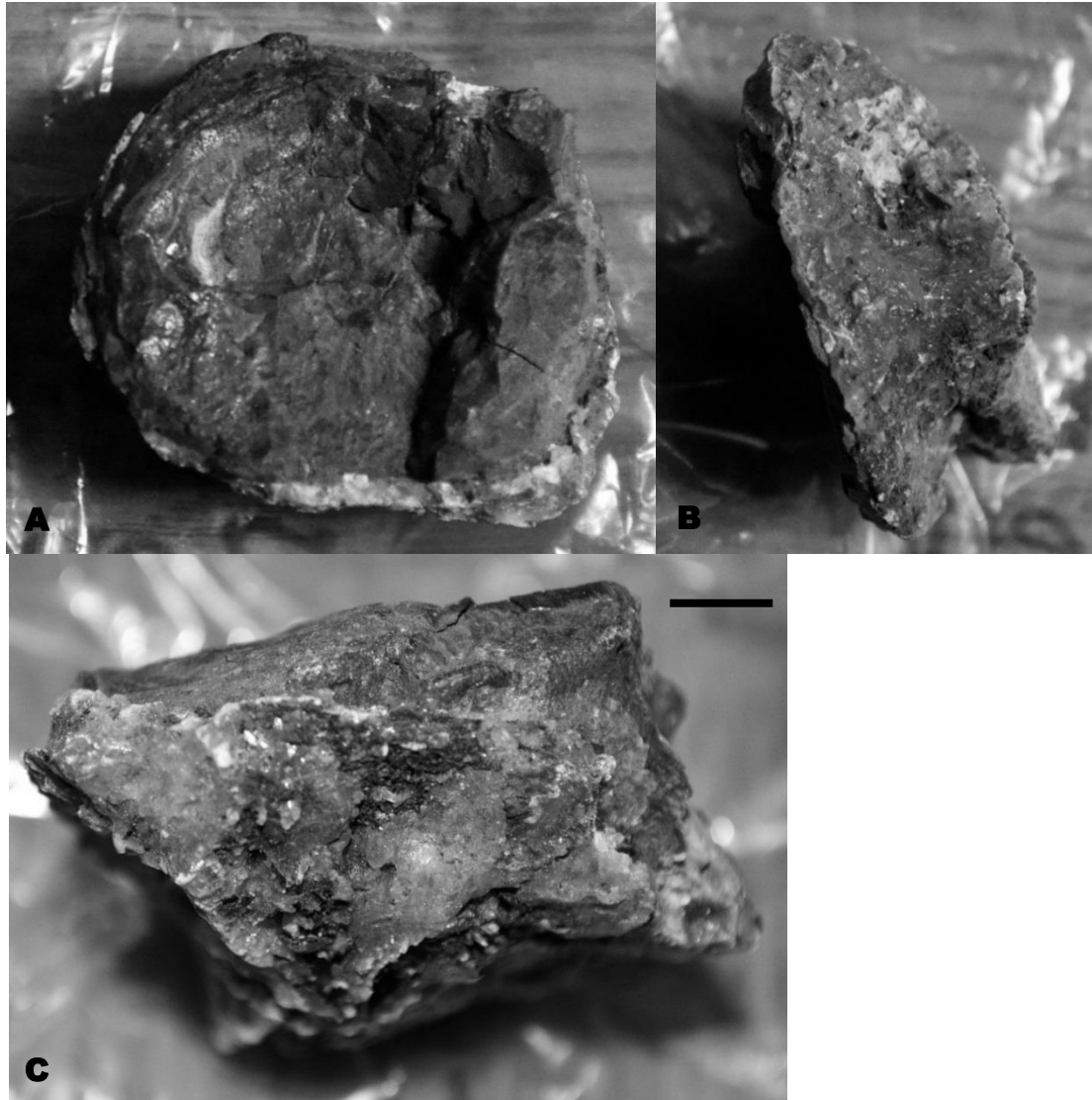(b), and dorsal views (c). Scale bar equals 1 cm.
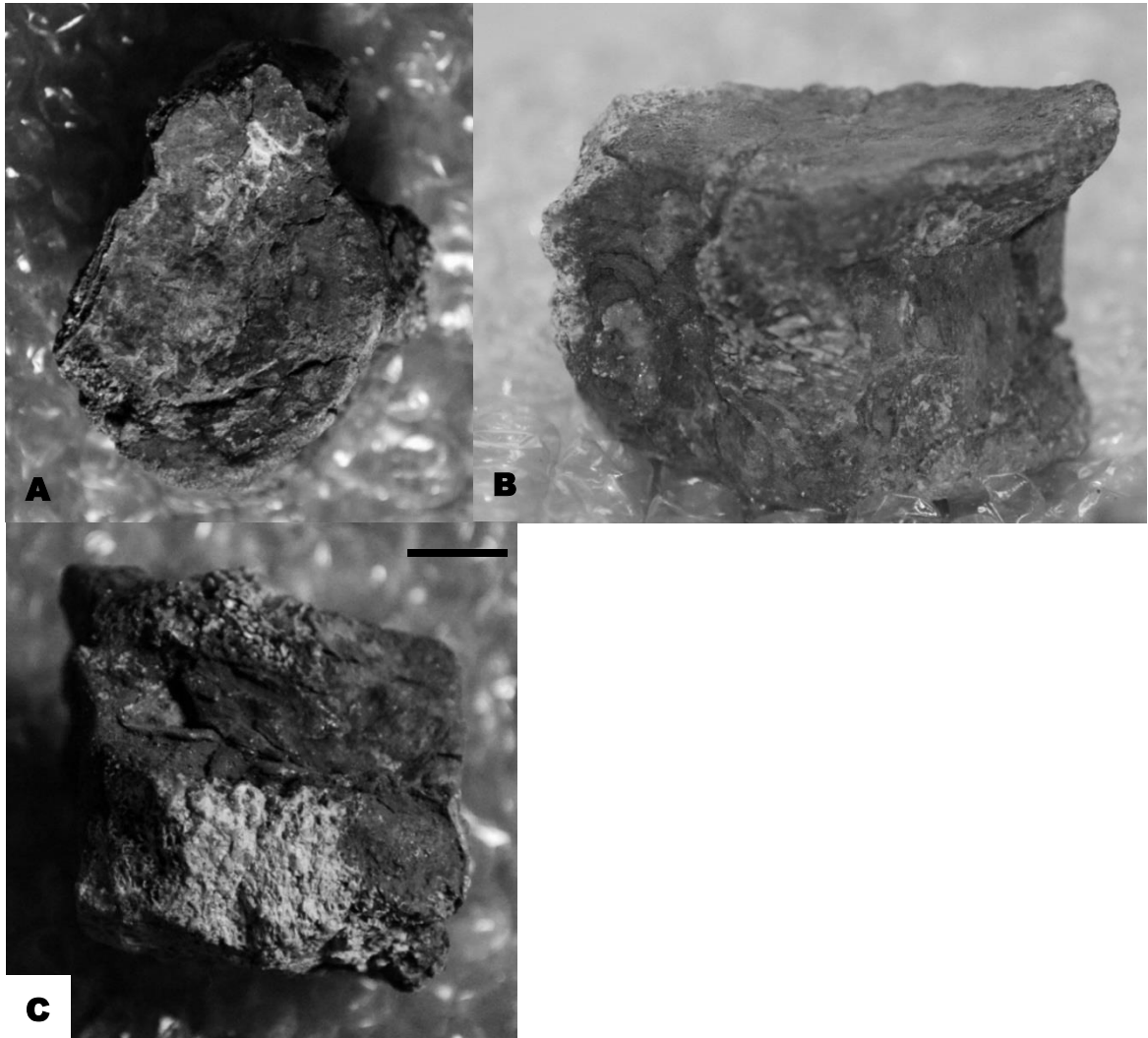
FIGURE 9. Plesiosaur specimen KUVP 16375 Vertebra 1 in anterior (a), left lateral (b), and dorsal views (c). Scale bar equals 1 cm.
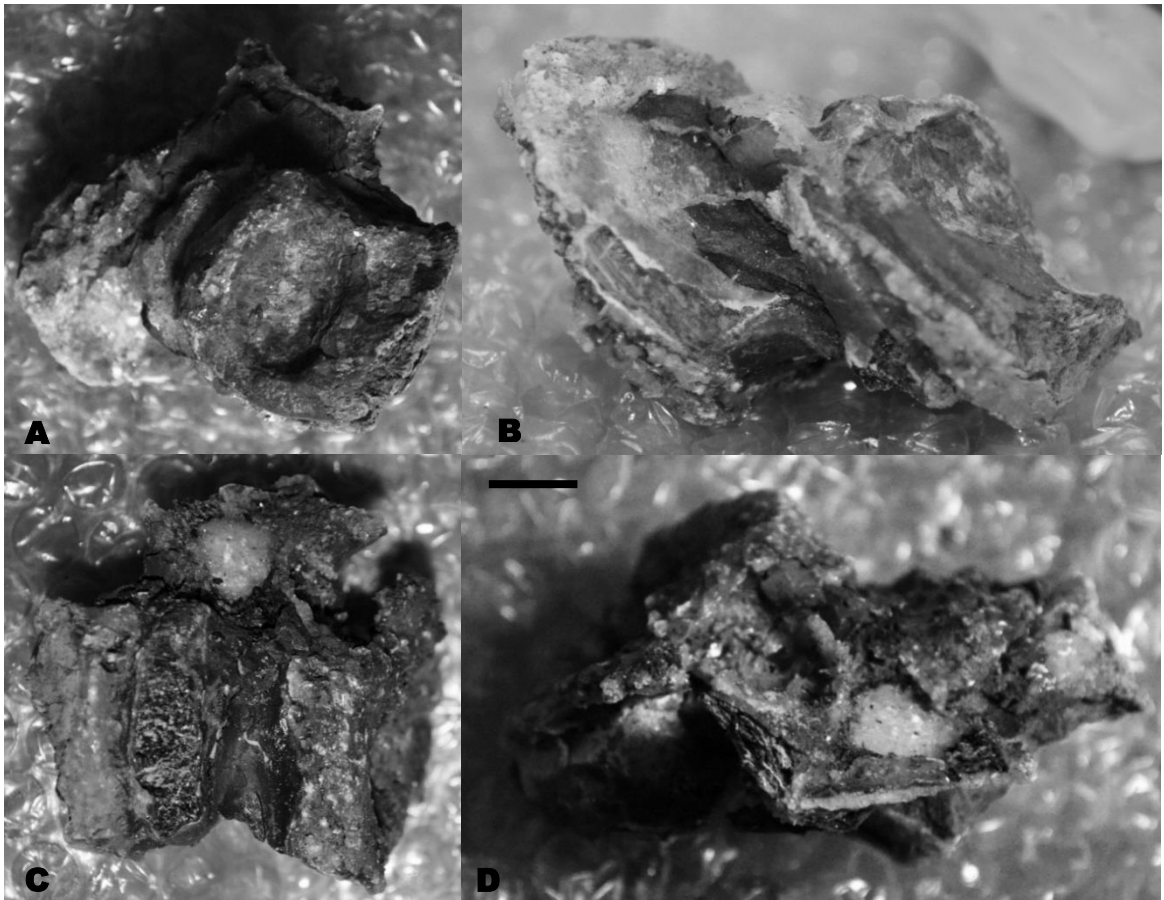
FIGURE 10. Plesiosaur specimen KUVP 16375 Vertebra 2 in anterior (a), ventral (b),

left lateral (c), and dorsal views (d). Scale bar equals 1 cm.
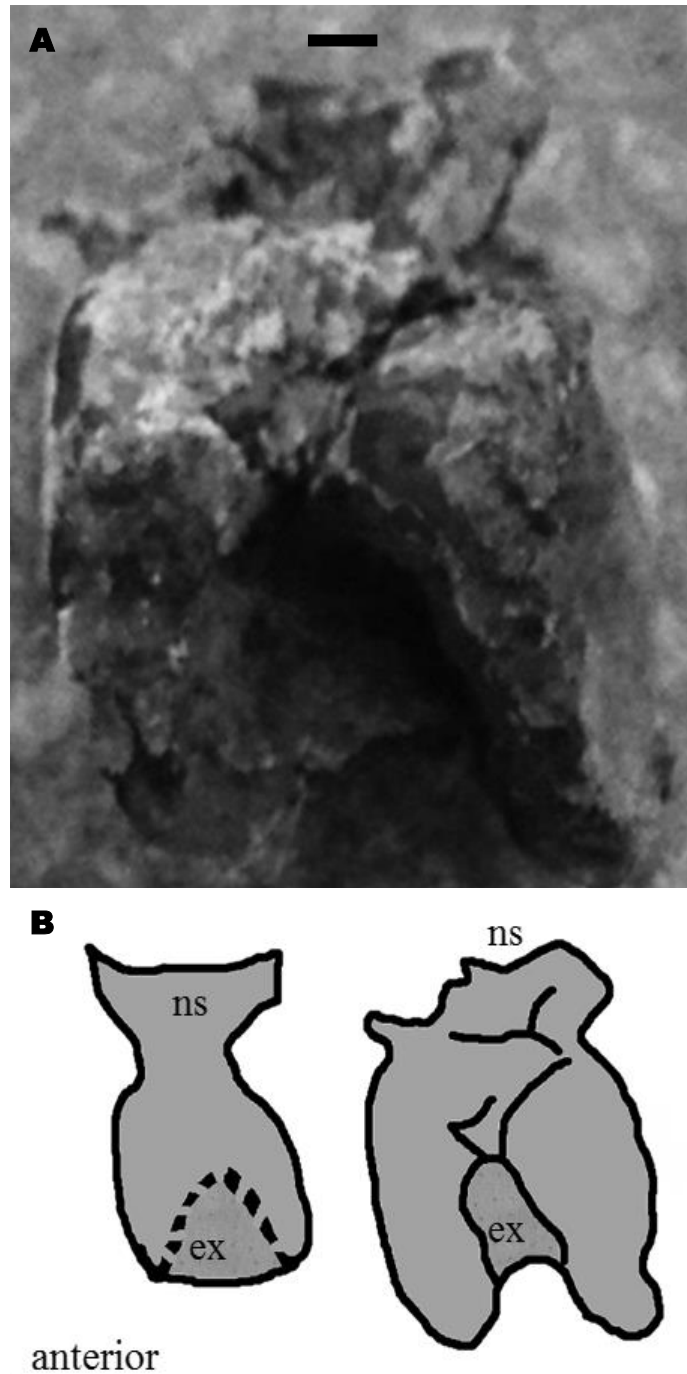
FIGURE 11. Diagram of the dorsoventral excavation of vertebra 4.
Excavation of the ventral surface of the centrum on vertebra 4 is
notably larger than in other vertebrae (A). Line Drawing (B) depicts
extent of the excavation of the centrum. Scale bar equals 1 cm.

FIGURE 12. Plesiosaur specimen KUVP 16375 Vertebra 3 in anterior (a), left

lateral (b), and dorsal (c). Scale bar equals 1cm.

FIGURE 13. Plesiosaur specimen KUVP 16375 Vertebra 6 in anterior (a), left

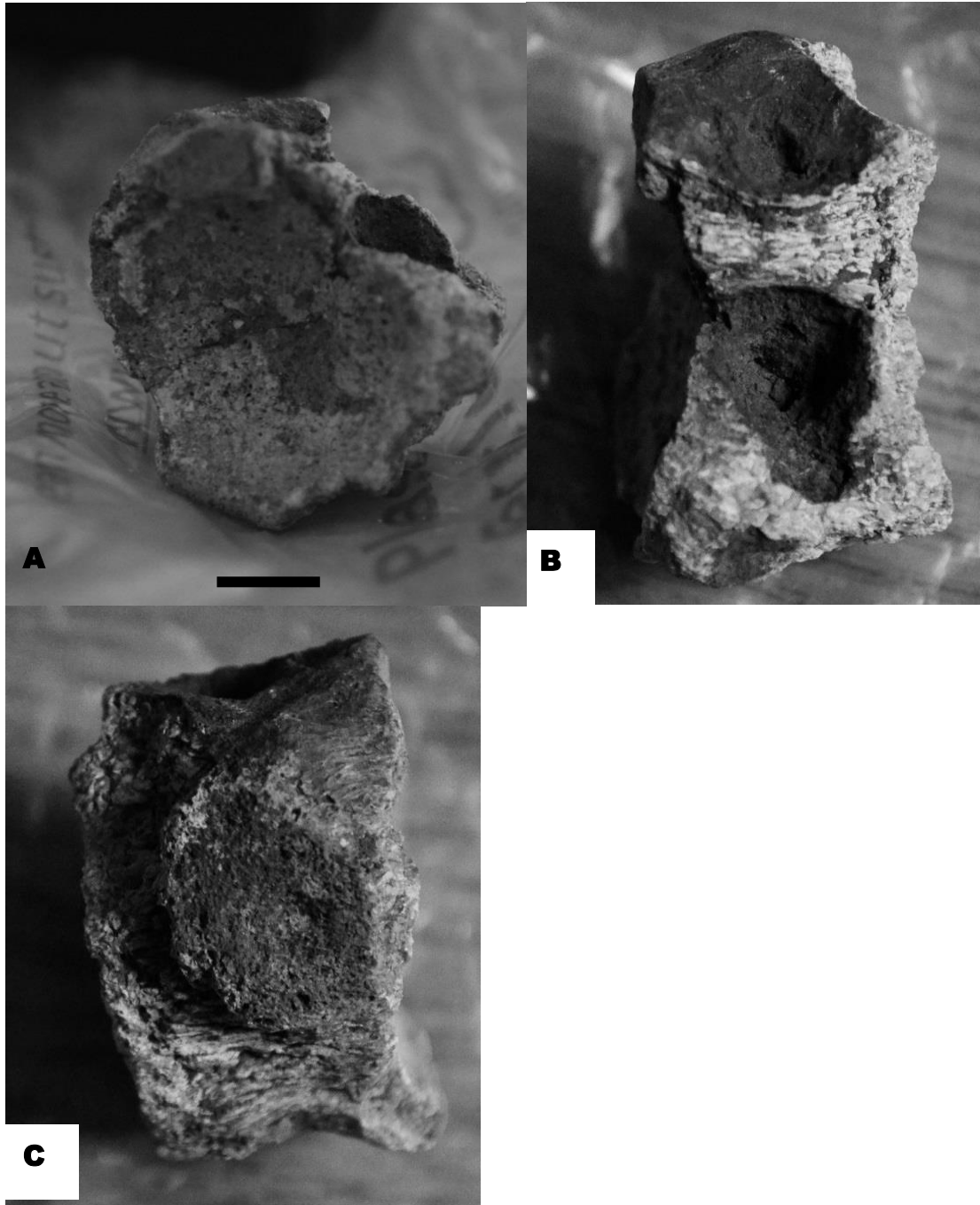lateral (b), and dorsal views (c). Scale bar equals 1cm.

FIGURE 14. Plesiosaur specimen KUVP 16375 Vertebra 7 in anterior (a), left lateral

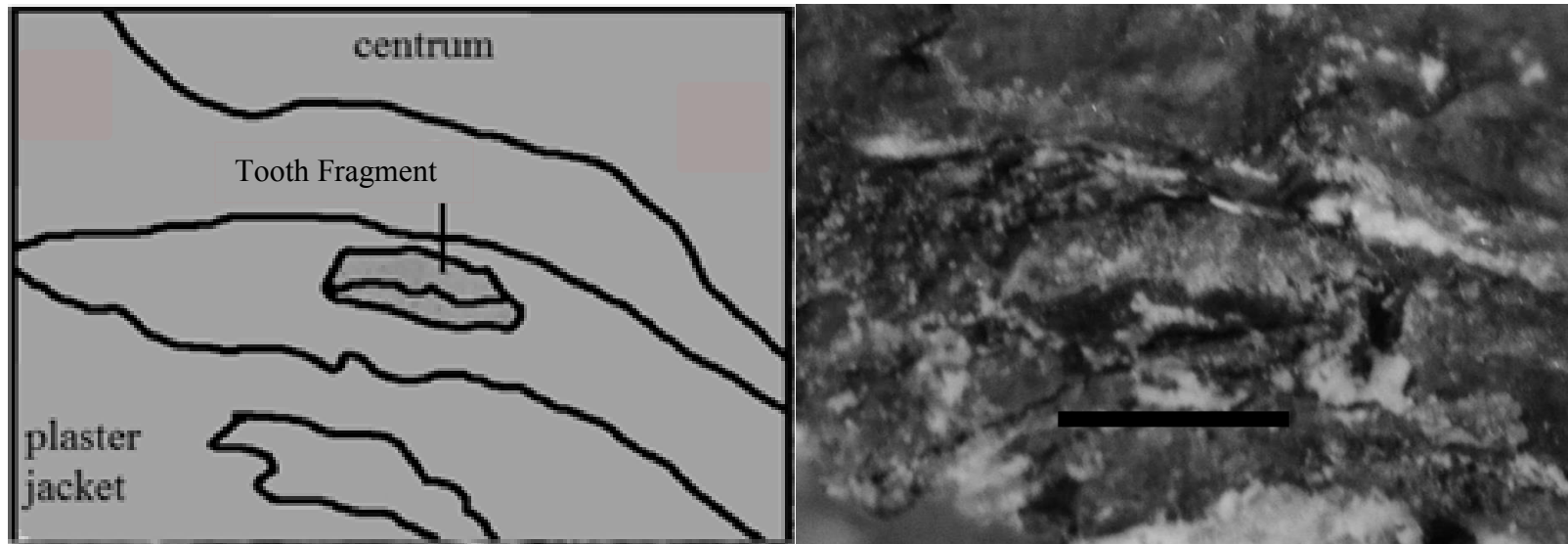(b), and dorsal views (c). Scale bar equals 1cm.

FIGURE 15. Shark Tooth Material Location. Shark tooth belonging to *Leptostyrax macrorhiza* as it appears in the ventral surface

of the centrum of vertebra 14. The broken cusp's length cannot be determined without destruction of the vertebral centrum. Scale
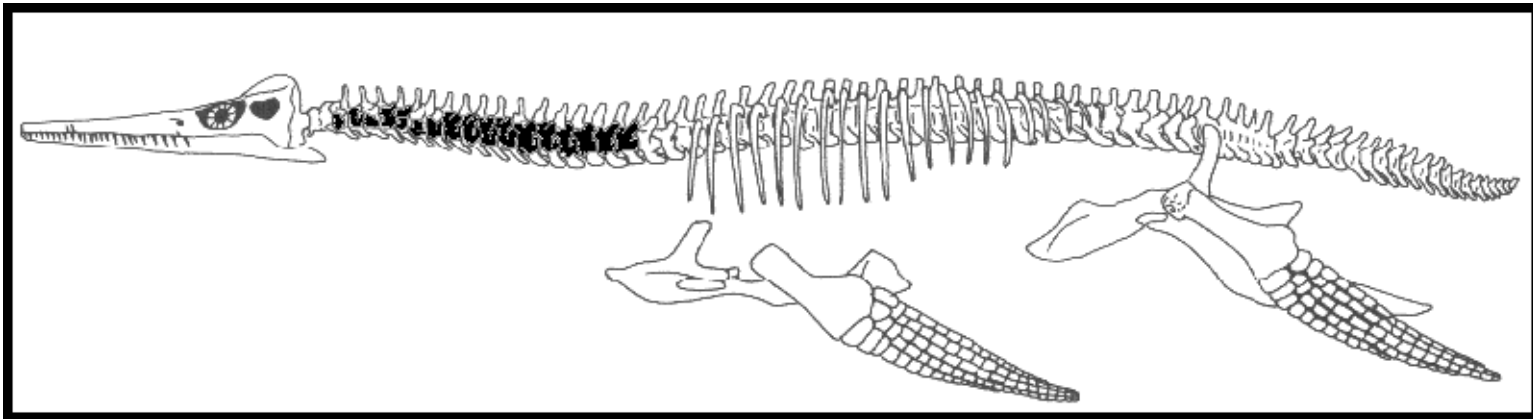
bar equals 1 cm.

FIGURE 16. Hypothesized position of specimen KUVP 16375 is highlighted in black on an articulated skeleton. The

illustration is adapted from Buchanan (1984) based on KUVP 1300, holotype of *Dolichorhynchops osborni* originally

described as *Trinacromerum osborni*.