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REVIEW OF PLESIOSAURIANS (REPTILIA: SAUROPTERYGIA) FROM THE UPPER CRETACEOUS HORSESHOE CANYON FORMATION IN ALBERTA, CANADA

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ABSTRACT

The taxonomic status of three previously reported plesiosaurian specimens from the non-marine Horseshoe Canyon Formation (Campanian-Maastrichtian, Upper Cretaceous) is reassessed. The holotype of *Leurospondylus ultimus* and a previously undescribed partial skeleton from Red Deer River Valley represent indeterminate elasmosaurids, whereas the "plesiosaurian" vertebra from Edmonton is actually an ornithopod caudal. The two plesiosaurian specimens came from different horizons for which different environments are inferred. The larger individual may be closely related to *Elasmosaurus*. This study supports the hypothesized decline of polycotylid plesiosaurs in the North American during the Late Campanian and suggests small adults and juveniles of elasmosaurids existed in both marine and non-marine environments whereas large adults were limited to the latter.

INTRODUCTION

The holotype of *Leurospondylus ultimus* Brown, 1913b was the first plesiosaurian fossil from the non-marine Edmonton Group in Alberta, Canada. Brown (1913b) interpreted *L. ultimus* as an elasmosaurid, and the majority of later researchers accepted this view. Although Welles (1952:95) noted that it is impossible to diagnose this taxon, he and some later researchers retained it (Welles, 1952, 1962; Persson, 1963; Brown, 1981). L. Russell (1931) and Russell and Chamney (1967) reported additional plesiosaurian materials from the Edmonton Group, and pointed out their significance in the interpretation of paleoecology of plesiosaurs. A partial skeleton mentioned briefly by Russell and Chamney (1967) was never described, despite the rarity of plesiosaurian remains from the group.

Plesiosaurs from the Edmonton Group have not been forgotten (e.g., Cruickshank, 1997; Eberth, 1997; Sato et al., 2005), but their taxonomy and stratigraphy has not been reassessed since the work of Welles (1952).

In this contribution we review the taxonomy and stratigraphy of these plesiosaurian specimens, including the description of the specimen in Russell and Chamney (1967). We also discuss the paleoecological inferences of these remains.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, NY, USA; CMN, Canadian Museum of Nature, Ottawa, ON, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, AB, Canada; UALVP, University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, AB, Canada.

MATERIAL AND METHODS

At least three specimens have been reported as plesiosaurian remains from the Edmonton Group in previous studies: AMNH 5261 (Brown, 1913b), UALVP 435 (Russell, 1931), and CMN 9454 (Russell and Chamney, 1967). UALVP 435 is actually an ornithopod caudal centrum (see Appendix 1) and is not discussed further. We examined TMP specimens catalogued as plesiosaurians from the Edmonton Group and determined that they are either hadrosaurid vertebrae (TMP 80.45.1, 80.45.2) or too fragmentary for a positive identification (TMP 84.87.4). Our search in TMP and CMN collections, as well as AMNH and UALVP collection catalogues, did not reveal any additional plesiosaurian fossils from the

Edmonton Group. This study therefore focuses on AMNH 5261 and CMN 9454.

We undertook field surveys in 2004 and 2005 in the areas where the specimens were discovered (Figure 1) based on the collection records. During the surveys, we used GPS to measure the elevation of the localities to help assess the stratigraphy. It is assumed that the collectors referred to the right (west) or left (east) side of the river, because the collectors of that time usually traveled down stream (south) by boat (old field notes in AMNH and CMN). We also examined exposures from both sides of the river to confirm there are no significant differences in stratigraphy. It is most likely that the distances (in miles) and stratigraphic levels (in feet) given by the collectors in the 1910s were not measured precisely enough to pin-point particular localities and beds. Accordingly we regard the original locality and stratigraphic data as roughly approximate, with error factors of 100s of meters in geographic distance and up to ten meters in stratigraphy.

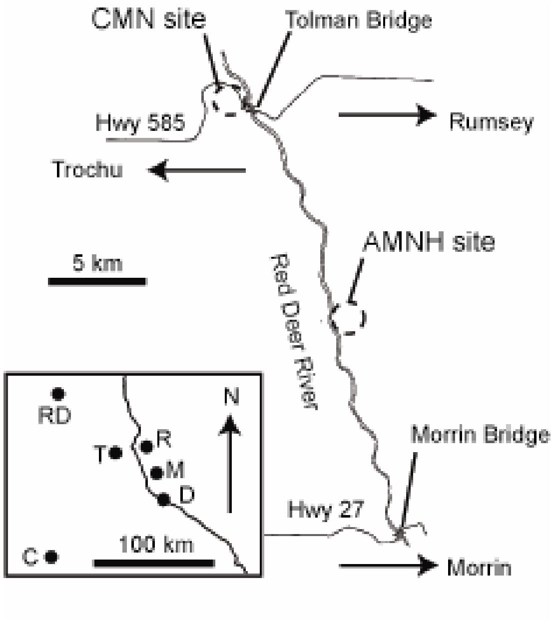

FIGURE 1. Fossil localities. Abbreviations: C, Calgary; D, Drumheller; Hwy, Highway; M, Morrin; R, Rumsey; RD, Red Deer; T, Trochu.

GEOLOGICAL BACKGROUND

The stratigraphy of the Edmonton Group has been revised several times since the collection of the plesiosaurian specimens. The brief summary provided below is mostly based on the most recent studies on the outcrops in this area by Lerbekmo and Braman (2002), Eberth (2004), and Hamblin (2004). The Edmonton Group consists of terrestrial to coastal deposits of the latest Campanian to early Paleocene, and the group is known for vertebrate fossils, coal seams, and the K/T boundary (e.g., Allan and Sanderson, 1945; Russell and Chamney, 1967; Gibson, 1977; Sweet and Braman, 1992; Eberth, 1997).

The lowermost formation of this group is the Horseshoe Canyon Formation (HC in Figure 2A) which crops out extensively along the Red Deer River in southern Alberta (Hamblin, 2004; references therein). The sedimentary succession records the final regression of the Western Interior Seaway, during which time the shoreline shifted east- and southward through this area (Eberth, 2004; Hamblin, 2004). Minor transgressions are recorded in the overall regressing succession (Hamblin, 2004). The Drumheller Marine Tongue (DMT; Allan and Sanderson, 1945) is an important "marine" interval in the middle of the formation and is often characterized by one or more beds containing marine to brackish water invertebrates (Hamblin, 2004). Thin coal seams (numbered 0 to 12; Gibson, 1977) have been used as stratigraphic markers. Coal seam 10 is particularly useful as a local maker bed and occurs within DMT. Several different systems of sub-formational lithostratigraphic subdivisions (members, zones, units, tongues) have been proposed (reviewed in Straight and Eberth, 2002; Hamblin, 2004; Eberth, 2004). Here we primarily use the divisions in Eberth (2004) as summarized in Figure 2B.

Lerbekmo and Braman (2002) and Lerbekmo (cited in Eberth, 2004) place the Campanian-Maastrichtian boundary in southern Alberta a few meters below coal seam 10 at the 31r-32n boundary, approximately at the base of *Baculites baculus* Zone in the Bearpaw Formation in southern Alberta. This level is slightly higher and younger (by about 0.5Ma) than those in some other North American studies in which the boundary is placed at the top of *B. jenseni* (see Lerbekmo and Braman [2002] for summary and justification). Eberth (2004) and Eberth and Deino (2005) reported the radiometric age of 70.3Ma and 70.44 ±0.17Ma just below and above coal seam 10, respectively.

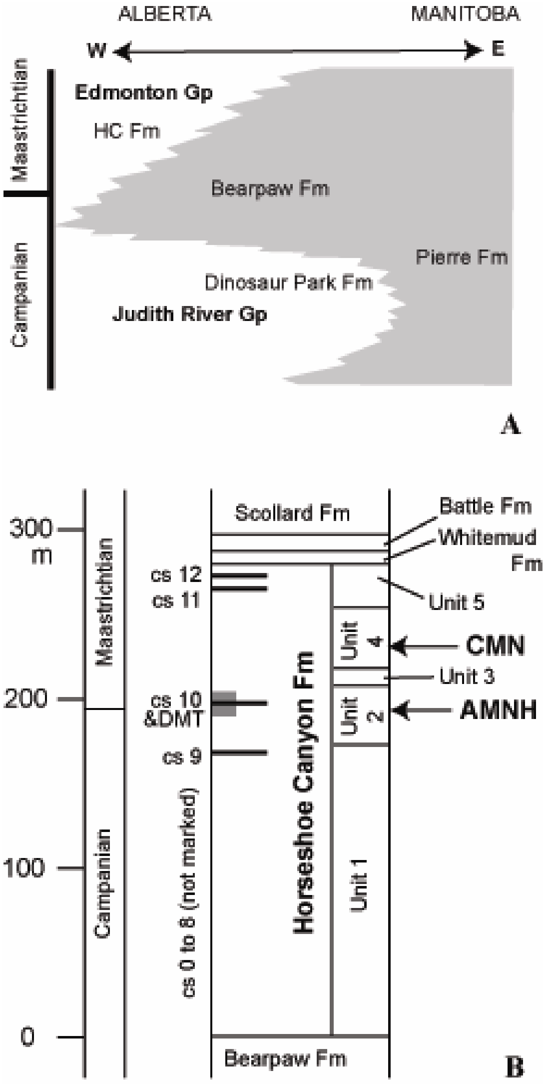

FIGURE 2. Local stratigraphy. Modified after Eberth (2004: Figure 3). Abbreviation: cs, coal seam; DMT, Drumheller Marine Tongue.

LOCALITY AND STRATIGRAPHIC LEVEL OF OCCURRENCES

AMNH 5261 and CMN 9454 were collected from the Horseshoe Canyon Formation of the Edmonton Group, about 40 km northwest of Drumheller, Alberta, Canada (Figure 1). The Tolman Ferry Crossing was replaced with a bridge which was built a few hundred meters south of the original ferry crossing in 1964 (D. Eberth, D. Evans, D. Tanke, pers. comm.., 2005 and 2006).

Using field notes and description of the original collectors, it is possible to approximate locations and stratigraphic levels of the plesiosaur and other vertebrate sites because of the very low dip (virtually horizontal) and lateral continuity of the strata. Although the depositional environment(s) for the specimens remain unknown, it is possible to gain a generalized idea about the paleoenvironment using the subdivisions in Eberth (2004).

The first specimen (AMNH 5261) was collected at "Tolman Ferry 8 mi[les] below [,] AB [=Alberta] [,] left bank 120 feet abover (sic) the river Red Deer River" by a party led by B. Brown in 1912 (collection record in AMNH, square brackets by us). The fossil-bearing horizon was considered approximately at the level of "a bed of *Ostrea glabra* several feet thick and widely distributed" and "about 400 feet above the Pierre", although "no invertebrates were actually associated with" the plesiosaur specimen, which was found "disarticulated and massed together in a steep hillside" (quotations from Brown, 1913b:605). This location is approximately the midpoint between the Morrin and Tolman bridges of today (Figure 1). Coal seams 8 to 12 are exposed in the outcrop in this area. Eberth (2004:fig. 12) and Hamblin (2004: appendix A, "Power Line/Twp Rd 32-32 section") published stratigraphic sections at nearby sites. The level of "120 feet from the river" is approximately at the horizon of coal seam 10. DMT or its correlative stratum include coal seam, but we did not find shell bed(s) at this horizon, consistent with Brown's statement that the plesiosaur skeleton was not associated with invertebrates. The precise stratigraphic level, e.g. whether the fossil-yielding horizon is above or below the coal seam, could not be determined. The strata around coal seam 10 are not particularly fossiliferous in comparison with other parts the formation, but there is at least one layer that yields bones (Eberth, 2004). We did not notice any inconsistencies in Brown's (1913b) information, and concluded that the AMNH specimen must have come from a horizon around the level of coal seam 10, within the unit 2 of Eberth (2004).

Layers of brackish-water bivalve shells, burrows, channel deposits, paleosols, vertical roots, and relatively few coal seams (in comparison with other parts of the formation) are known from unit 2 in the Red Deer Valley (Eberth, 2004; Hamblin, 2004). The degree of marine influence must have varied within the unit, and studies do not always agree on the relative strength of marine/terrestrial influences (e.g., Hamblin, 2004:70). It is, however, clear that this unit as a whole was deposited in an estuarine setting with local freshwater, brackish, and marine influences that resulted from the DMT transgression.

The second specimen (CMN 9454) was discovered by "P. A. Bungart on August 11, 1915, at Tolman ferry, right bank, about 150' above river, in Sec 14?. Twp 33, R. 22 W", and the skeleton was in "a layer of sandstone that frees well" (collection record at CMN). It is unknown whether this specimen was found articulated or not. Local stratigraphic sections on the western side of the river are given by Eberth (2004:fig. 13) and Hamblin (2004: appendix A, "Tolman Bridge Section"). Coal seam 10 is locally present above the river level but is generally obscure in this area. The level "150' above river" is approximately 24 m below the coal seam 11, and above the stacked sandstone zone of unit 3 of Eberth (2004), suggesting that the CMN plesiosaur came from a horizon 30 to 40 m above that of the AMNH specimen. This level belongs to the lower part of unit 4 of Eberth (2004), which consists of paleosols, channel sandstone, and abundant dinosaurian bones (Eberth, 2004; Hamblin, 2004). In contrast to unit 2, no obvious evidence of a marine transgression have been recorded from unit 4. Eberth (2004) interpreted this sequence as representing a coastal to alluvial plain succession. This interval corresponds to the uppermost portion of the Tolman Tongue of Hamblin (2004) for which a floodplain setting was suggested. He also hypothesizes the occurrence of correlative marine strata far to the southeast, at the base of the Carbon Tongue, the unit that immediately overlies the Tolman Tongue.

SYSTEMATIC PALEONTOLOGY

Order SAUROPTERYGIA Owen, 1860
Suborder PLESIOSAURIA de Blainville, 1835
Family ELASMOSAURIDAE Cope, 1869
Elasmosauridae gen. et sp. indet.

Leurospondylus ultimus Brown, 1913b:606, figs. 1-7 (original description)
Elasmosaurid, undet: Russell and Chamney, 1967:13

Specimens—AMNH 5261, holotype of *Leurospondylus ultimus* Brown, 1913b; partial skeleton of very young individual consisting of 35 vertebrae, 30 ribs, 3 gastralia, scapulae (= ischia in Brown, 1913b; corrected by Welles, 1952), coracoids, pubes, ilia, humeri, femora, paddle elements. CMN 9454, partial skeleton of a young individual consisting of four teeth, about 35 vertebrae (partly restored), 45 ribs, one gastralium, coracoids, ilia, right (?) pubis and ischium, humeri, right femur, paddle elements, gastroliths.

Locality and Horizon—Eastern bank (AMNH 5261) of Red Deer River at about the midpoint between the Tolman and Morrin bridges, and western bank (CMN 9454) of Red Deer River at the Tolman bridge, northwest of Drumheller, Alberta, Canada. Middle (AMNH 5261) to upper (CMN 9454) portion of the Horseshoe Canyon Formation of the Edmonton Group. Maastrichtian, possibly including the uppermost Campanian.

Description—Brown (1913b) gave a full description of AMNH 5261, and Welles (1952) noted the misidentified scapulae and provided additional comments. Brown's estimation of the length of missing neck and tail does not seem to have a solid basis. Poor ossification is evident in various features such as the lack of defined facets on limb bones and the complete separation of neural spines from the centra. Although Brown considered this animal to be nearly mature, it is actually a very young, immature individual.

It is difficult to determine the exact count of each segment of the vertebral column (cervicals, dorsals etc) in AMNH 5261 because of the incomplete ossification and gradual transition of morphological features. Most vertebrae in Brown's "B" series (Brown, 1913b: Figure 1) have the lateral longitudinal ridge, a common feature for the cervicals of Late Cretaceous elasmosaurids (Bardet et al., 1999). None of the cervical centra have the typical dumb-bell shape of elasmosaurid cervicals, but a faint ventral notch near the anterior end of the preserved cervical series suggests that the missing anterior portion of the neck and/or more mature individuals may have had the typical elasmosaurian morphology. Two coracoids form an asymmetrical intercoracoidal vacuity, and the "keel" on the ventral side of the median symphysis (see detailed explanation in the description of CMN 9454) is prominent, despite immaturity. The median element of the gastralia is a gently curved rod, with a rounded tubercle on the anterior surface of the median line. All propodial bones are irregularly pierced by several nutritional foraminae of different size.

CMN 9454 was once on exhibit, and modifications (e.g., coating of the bone surface, drill holes in centra, restoration of missing parts) obscure the original morphology of some parts. The specimen includes four teeth, of which two are fairly complete (Figure 3). Exact positions of these teeth are unknown, but based on their curvature and size we assume both are anterior teeth of either the left lower or right upper jaws. The crowns bear no carina, but they are striated with ridges that vary in length and spacing (Figure 4). Most ridges start at the base of the crown, but several short ridges occur in the middle of the crown. None of the ridges reach to the very tip of the tooth. The enamel is damaged near the base of the crown. The preserved portions of the labial side lacks the ridges.

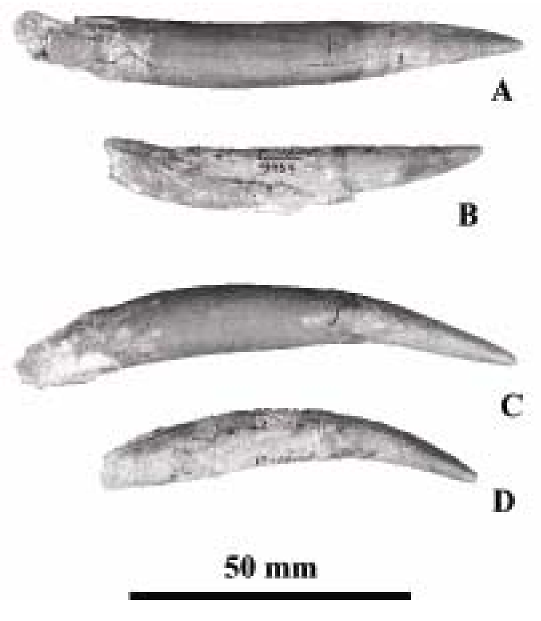

FIGURE 3. Teeth of CMN 9454. Lingual (**A, B**) and distal (?) (**C, D**) views of the teeth A (**A, C**) and B (**B, D**).

The vertebral column was restored by previous workers, and includes a mixture of original bones and models. The anteromost original vertebra is painted as “1D”, and the following vertebrae bear sequential numbers (“D” follows the number until “19D”). The original fossil bones include 6 posterior cervicals (“1D” to “6D”), three posteromost cervicals (= pectorals; “8D” to “10D”), 15 dorsals (“11D” to “23”, “26”), three sacrals (“28, “29”, “30”), and six caudals (“32”, “34” to “36”, “145”). The posteromost caudal “145” is not incorporated into the column, and did not suffer from the drilling that penetrate all other centra. There are 29 dorsal and 16 caudal ribs that are partially restored, and a few sacral ribs are attached to the vertebrae. The neural arch is fused to the centrum in some vertebrae, but the suture remains open in others, and in the posteromost caudal only the facets for the arch remains.

The posterior cervicals (Figure 5A-D) lack the ventral notch and lateral longitudinal ridges. The anterior surface of the neural spine has a complicated pattern at and above the prezygapophyses, as in some elasmosaurs from the underlying Bearpaw Formation (Sato, 2003a). The articular face of the dorsal centrum is almost circular in shape (Figure 5E), whereas it is wider than tall in other parts of the column. Constriction of the centrum is very weak to absent throughout the preserved series. The rib facet in the first sacral (vertebra “28”, Figure 6A-B) is small, but those in other two are large oval depressions. The two anteromost caudals do not have chevron facets, but the rest have them on the posterior edge. The caudal centrum is longer on the ventral side than the dorsal side. The “145” caudal (Figure 6C-H) is probably the second from the end of the tail, and the centrum is in a shape of a truncated cone, with the larger circle being anterior articular facet. Its broken rib and chevron facets indicate their presence in all preserved caudals probably except for the one at the very end of the tail.

Anterior dorsal ribs have a prominent lamina along the anterior edge near the head (Figure 7A-B). This lamina and the curvature of the shaft become less significant in more posterior ribs (Figure 7C-D). The caudal ribs are straight bars with a round head and flattened shaft. The only preserved gastralium (Figure 7E-F) is missing both free ends and measures 296 mm wide at the broken ends and 20 mm thick at the thickest portion. Damage and crushing of the surface obscures the furrow(s) to fit neighboring gastralia, but the strong curvature, asymmetry, and the lack of anterior projection at the midline suggest it is a lateral segment (cf. Wegner, 1914).

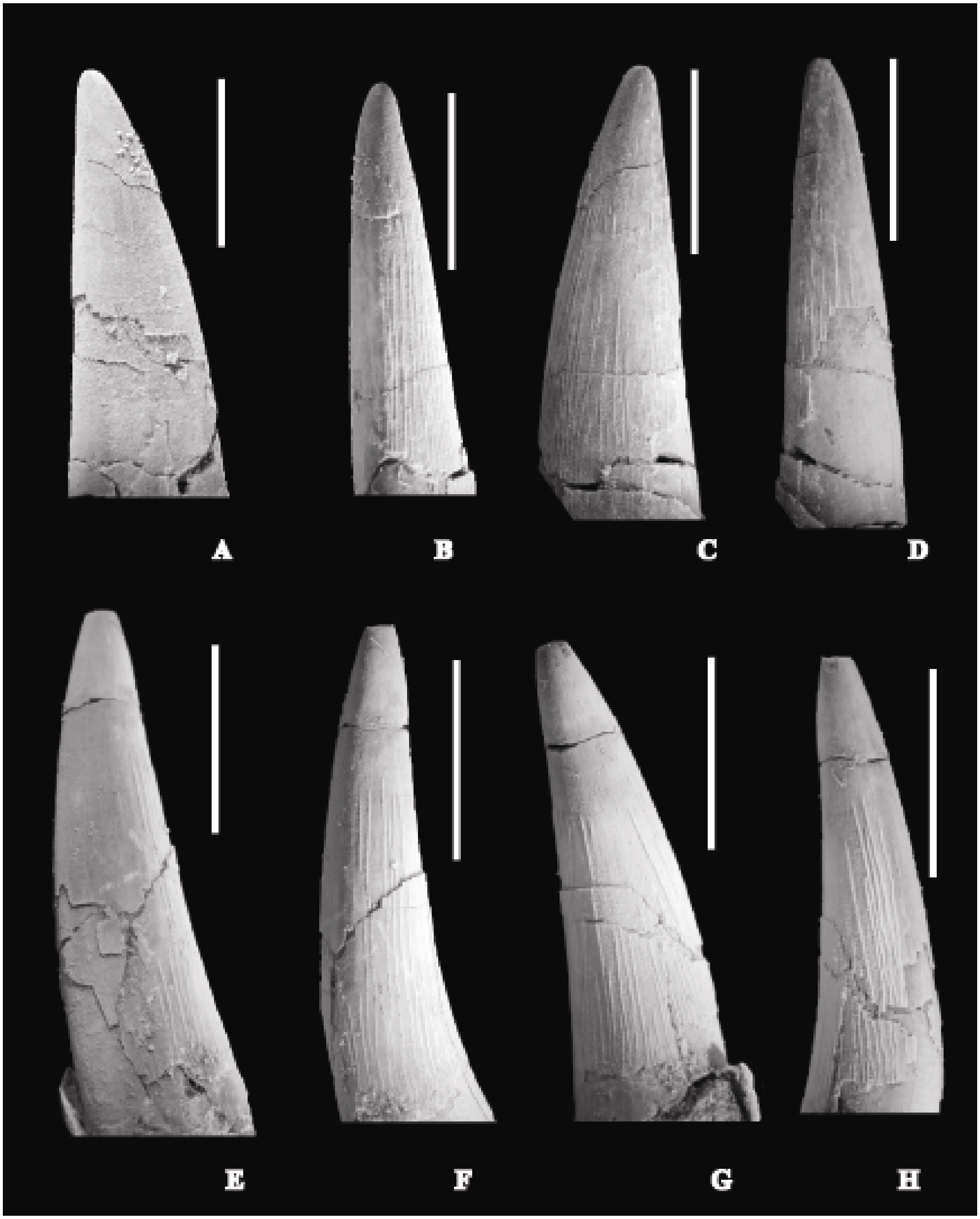

FIGURE 4. Close up of tooth crowns of CMN 9454. Teeth A (**A to D**) and B (**E to H**) in labial (**A, E**), distal (?) (**B, F**), lingual (**C, G**), and mesial (?) (**D, H**) views.

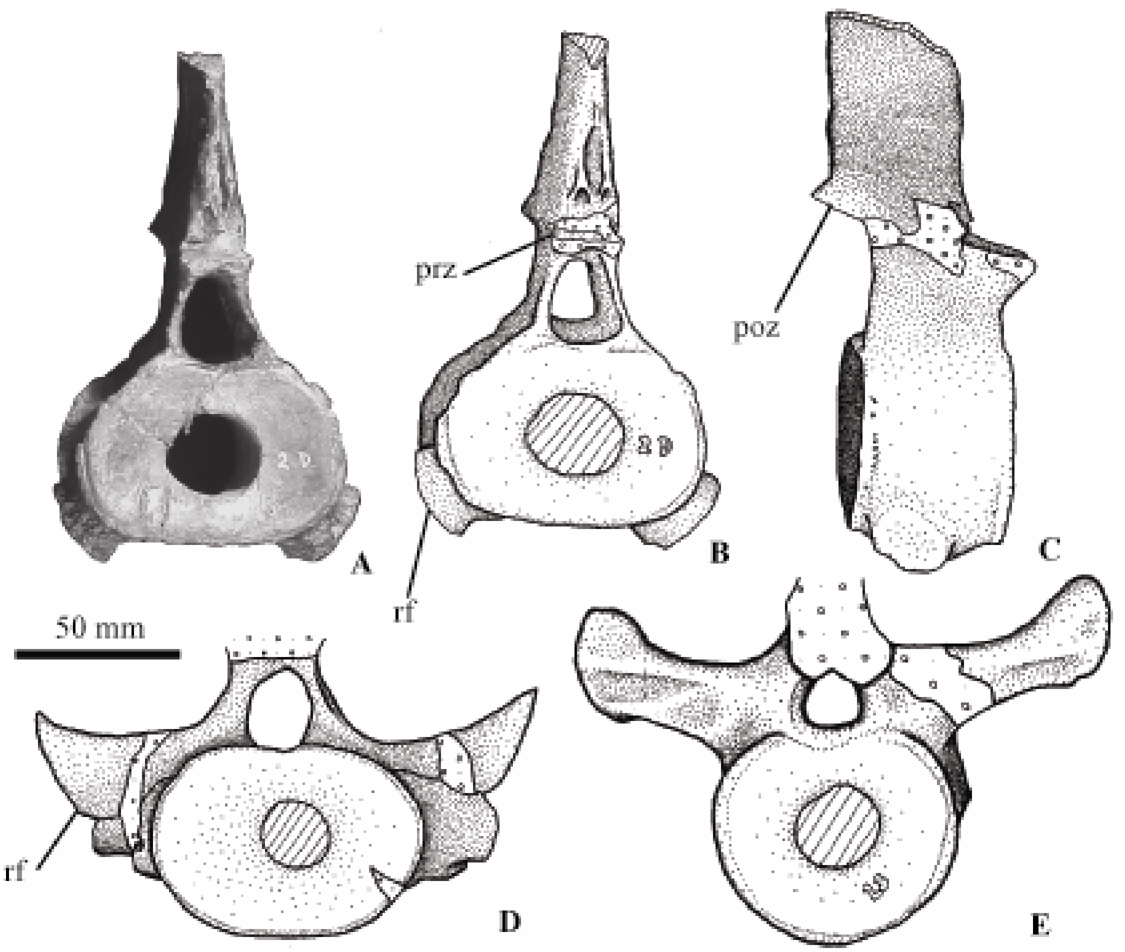

FIGURE 5. Vertebrae of CMN 9454. Anterior (**A, B**) and left side view (**C**) of posterior cervical, posterior view of posteromost cervical (= "pectoral") (**D**), and anterior view of dorsal (**E**). Abbreviations: poz, postzygapophysis; prez, prezygapophysis; rf, rib facet.

The wide cracks in the posteromedial portion of both coracoids are filled with artificial material, but the preserved parts suggest that the restored outline of the bone is fairly reliable (Figure 8). The width of the posterior blade exceeds the width at the glenoid. A well-developed anteromedian process is uncommon among adult elasmosaurids of the Upper Cretaceous (e.g., Welles, 1962: Figure 23; see DISCUSSION). There is a prominent ventral projection ("keel" in Figure 8D-F) close to the midpoint of the median symphysis. Its anterior edge reaches the level of the edge of pectoral fenestra. This projection is much stronger and more anteriorly positioned that in AMNH 5261.

The pubis and ischium (Figure 9) are short and typical for an elasmosaurid, with their median margins much straighter than in AMNH 5261. The posteromedian projection of the pubis is truncated and unfinished, suggesting the presence of a cartilaginous pelvic bar. The ischium also has a similar condition in its anterior projection at the symphysis.

The proximal and distal ends of the femur are damaged, but the humerus is clearly much longer and wider than the femur (Figure 10). The humerus has well-defined epipodial facets, but the capitulum and tuberosity is incompletely separated. In dorsal view, the humerus is asymmetrical in its distal half, because its radial facet faces distally whereas the ulnar facet is inclined posteriorly. The outline of the femur suggests a similar condition in the hind limb. The disarticulated epipodials are identified as two radii, two ulnae, and one tibia, primarily based on the size of articular facets. There is a

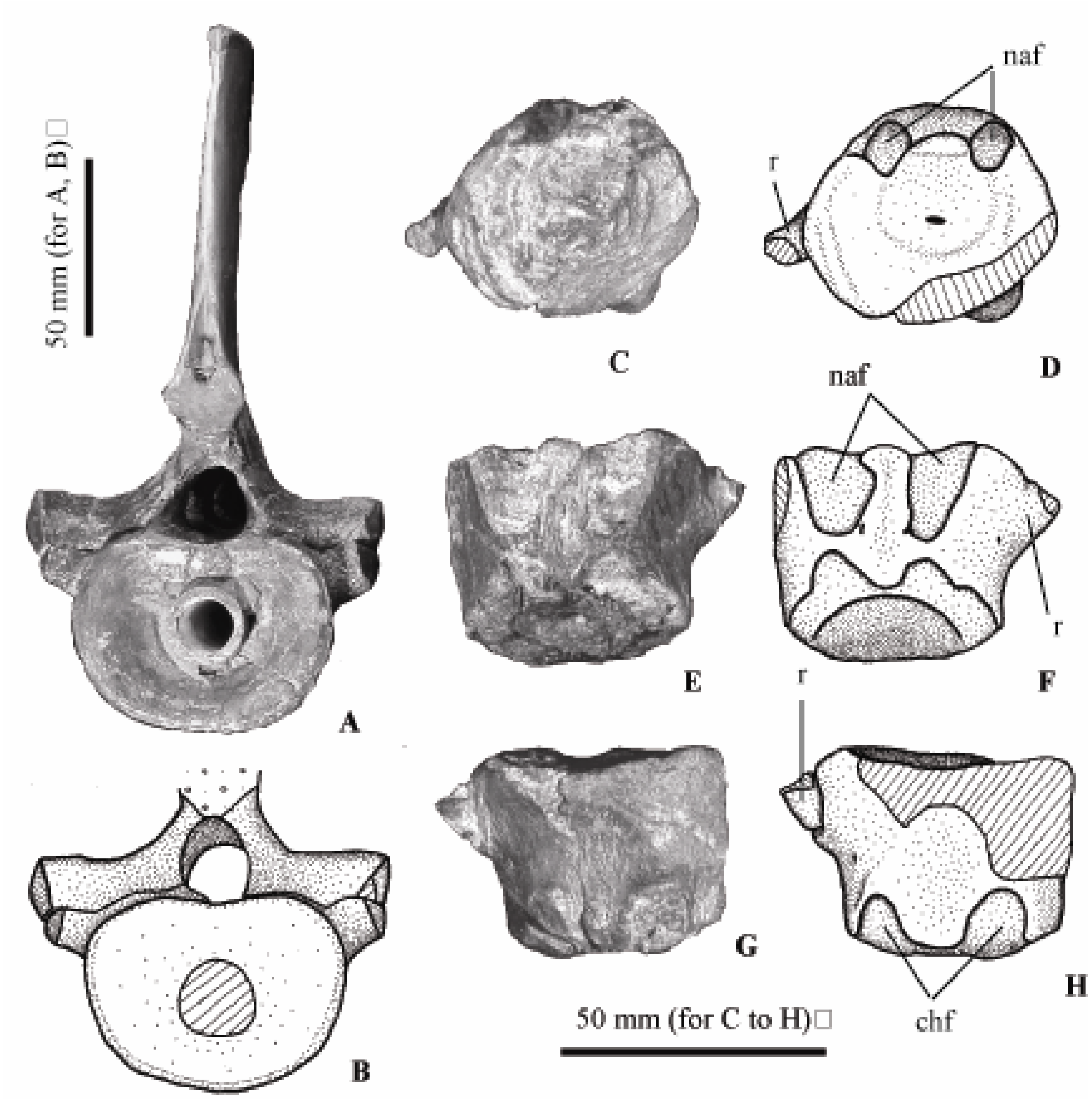

FIGURE 6. Vertebrae of CMN 9454. Posterior view of first (?) sacral (**A, B**), and distal caudal in anterior (**C, D**), dorsal (**E, F**), and ventral (**G, H**) views. Abbreviations: chf, chevron facet; naf, neural arch facet; r, rib.

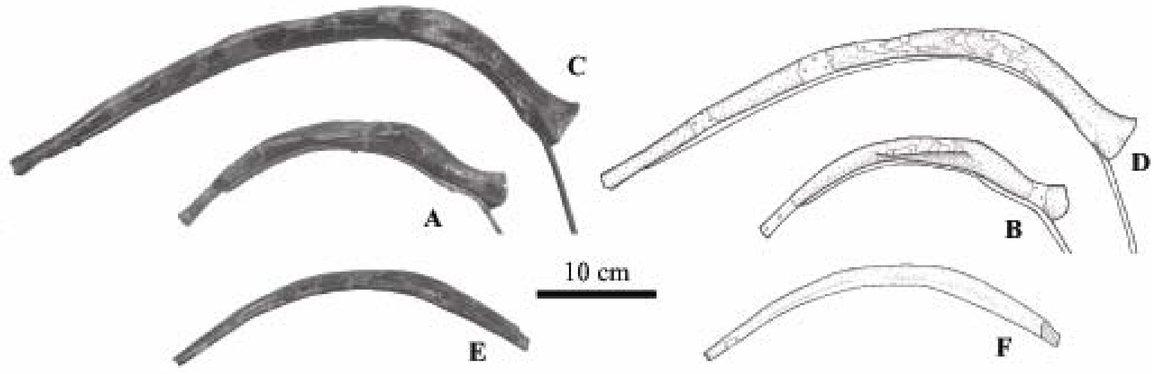

FIGURE 7. Ribs of CMN 9454. Anterior view of posteromost cervical (**A, B**) and anterior dorsal ribs (**C, D**), and ?anterior view of gastralium (**I, J**).

well-defined epipodial foramen between the radius and ulna, but the tibia does not have a corresponding structure. An intermedium (or centrale?: Caldwell, 1997) of a forelimb was identified, but the rest of carpal/tarsal elements were not confidently identified. There are at least 70 phalanges and metacarpals/metatarsals.

More than 60 pebbles were associated with the specimen (Figure 11), and they are regarded as gastroliths because gastroliths are common for elasmosaurids (e.g. Cicimurri and Everhart, 2001). Their exact location(s) within the skeleton at the time of collection is unknown. Most of them are flat and rounded to well-rounded, and they vary in size from a few centimeters to a few millimeters in the long axis.

DISCUSSION

Taxonomic Status—We consider *Leurospondylus* and its only species *L. ultimus* as *nomina dubia* because they are not based on diagnostic material. Accordingly, we identify the AMNH and CMN specimens as indeterminate elasmosaurids. Welles (1952) for AMNH 5261 and Russell and Chamney (1967) for CMN 9454 share our views, although Welles (1962) retained the genus and species. Brown (1913b:606) listed several characters as "generic and specific characters" of *L. ultimus* based on AMNH 5261, but the characters of the vertebrae and obturator foramen are attributed to the nature of very young age, whereas the characters of the ribs and coracoids are widely known among other elasmosaurids (e.g., Welles, 1943). The scapula (Welles, 1952), and its morphological distinction no longer holds. The equal length of the humerus and femur noted by Brown (1913b) "ischium" in Brown (1913b) is a misidentified should not be taken at its face value because of the poor ossification and preservation of the ends of the bones. AMNH 5261 cannot be confidently identified at lower taxonomic ranks because it is so immature. CMN 9454 is 60 to 90 percent larger than the AMNH 5261 (Appendix 2). The fusion of the neural arch to the centrum in some vertebrae, well-defined epipodial facets of the humerus, and the almost square median margins of the pubis and ischium suggest that it is much more mature than AMNH

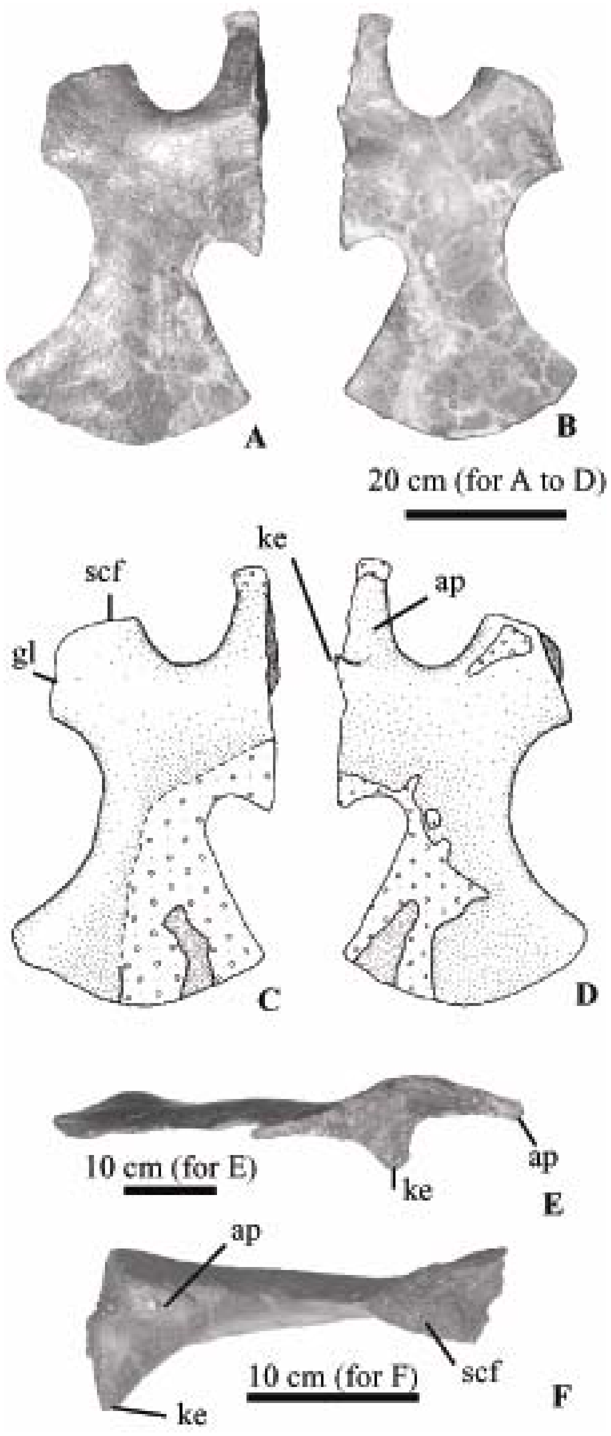

FIGURE 8. Coracoids of CMN 9454. Dorsal (**A, C**), ventral (**B, D**), medial (**E**), and anterior (**F**) of the left coracoid. Abbreviations: ap, anterior process; gl, glenoid; kl, "keel"; scf, scapular facet.

5261. Ossification is incomplete in certain areas, and it is still "juvenile" sensu Brown (1981) because of the incomplete fusion of neurocentral sutures.

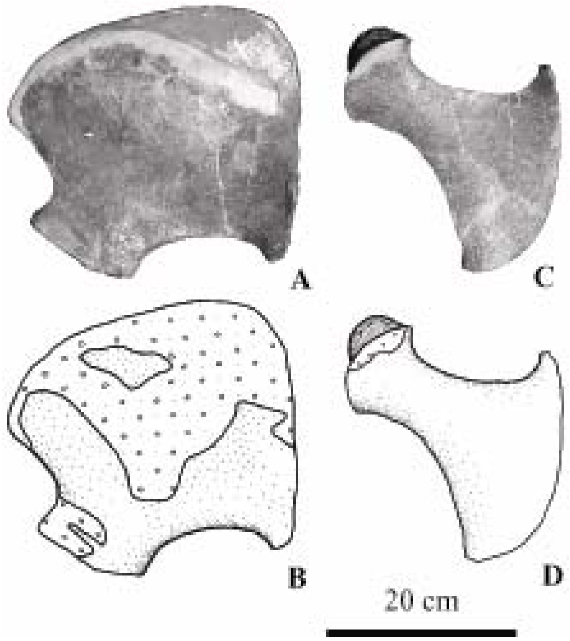

FIGURE 9. Pelvis of CMN 9454. Dorsal view of left (?) pubis (**A, B**) and ventral view of right ischium (**C, D**).

Because of the extreme immaturity of AMNH 5261, it is difficult to demonstrate whether it is conspecific with CMN 9454. Both are elasmosaurids from the same formation in a fairly small area, and it is possible that they represent different ontogenetic stages of a single species. However, they are from different horizons within the formation and have morphological differences; for example, in CMN 9454 the humerus is much larger than the femur and the "keel" of the coracoid is positioned much more anteriorly. These differences may be attributed to the advanced ossification and/or allometric growth in the CMN specimen, but there are elasmosaurid species in which adults lack these features. For example, the femur is longer than in *Hydralmosaurus* and *Terminonatator*. The position of the "keel" of the coracoid is obviously much more posterior in all known elasmosaurids that have this structure [Welles, 1943, 1952, 1962]). For these reasons we do not consider the two specimens conspecific.

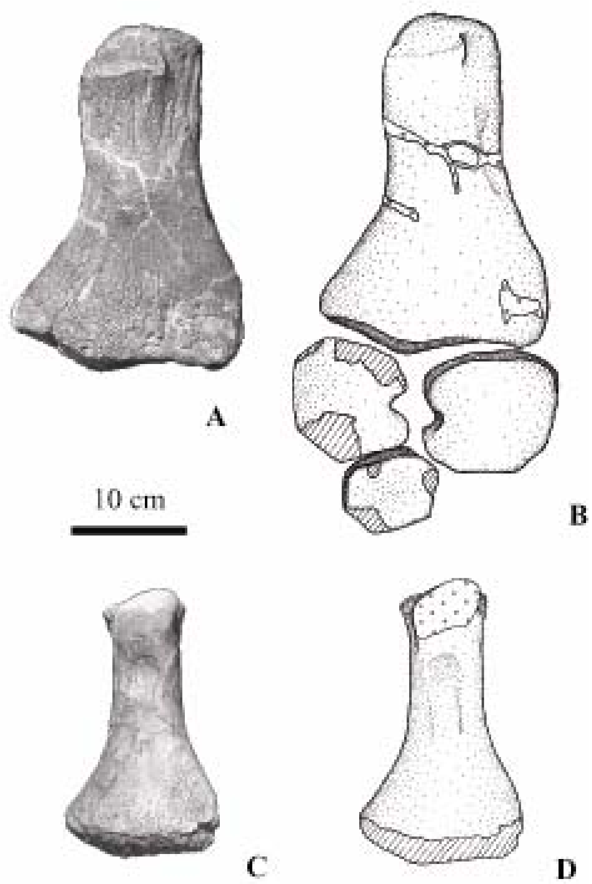

FIGURE 10. Limbs of CMN 9454. Dorsal view of right humerus (**A**), same with radius, ulna, and carpal (**B**), and right femur in dorsal view (**C, D**).

CMN 9454 may be diagnosable. The unusually elongated anteromedian process and the anterior position of the "keel" in the coracoid possibly form a unique combination of features among elasmosaurids. The anteromedian process of the coracoid is common in elasmosaurids but it is either short or strong and broad. A coracoid "keel" is, as mentioned above, positioned much more posteriorly in other known taxa (where is preserved) than in CMN 9454. However, there are no other features that are obviously distinctive. For this reason, and the unknown situation of the aforementioned two features in many other elasmosaurids, we treat, at present, CMN 9454 as an indeterminate elasmosaurid. The extremely developed anteromedian process and greatly developed "keel" of the coracoid may, on the other hand, indicate that CMN 9454 represents, at least, a young adult if compared with the growth pattern of the anteromedian process in *Cryptoclidus* (e.g., Andrews, 1910: text-Figure 89).

The more mature nature of CMN 9454 makes it more suitable than AMNH 5261 for comparison with other elasmosaurids, and this narrows the list of taxa that may be potentially related or even synonymous. The incompleteness of the skeleton in this specimen and a few other comparable taxa such as *Elasmosaurus*, however, does not confirm a synonymy or any interrelationships of the taxon represented by CMN 9454 (see below).

FIGURE 11. Gastroliths of CMN 9454. Scale bar 10 cm.

Comparison with Other Elasmosaurids—Characters such as the lateral longitudinal ridge of cervicals (Gasparini et al., 2003) and intercoracoidal vacuity indicate the elasmosaurid affinity of both AMNH 5261 and CMN 9454. Cervical centra are relatively short compared with adult elasmosaurids, but this is most likely attributed to the ontogenetic variation (e.g., Williston and Moodie, 1917; Brown, 1981). Relatively short cervicals are also known among the "adult" (sensu Brown, 1981) elasmosaurids from the Dinosaur Park Formation (Sato et al, 2005).

The ventral "keel" of the coracoid is another character that supports the close relationship to elasmosaurids; there is a ventral projection at the median symphysis of the coracoids ("knob" in Sato, 2003a) in several genera of Upper Cretaceous elasmosaurids such as *Hydralmosaurus* and *Aphrosaurus* (Welles, 1943, 1952). The "keel" in the Horseshoe Canyon specimens (especially in CMN 9454) is obviously an elaborated version of this structure. An undescribed elasmosaur from the Lower Cretaceous of Alberta (Druckenmiller and Russell, 2006) also possesses a prominent projection. To our knowledge, this structure is absent in known non-elasmosaurids.

The anterior process of the coracoid is well-developed only in *Elasmosaurus* (Cope, 1870) and *Libonectes* (Welles, 1949; Carpenter, 1999) among the Cretaceous elasmosaurids of Western Interior Seaway (condition unknown for *Terminonatator* Sato, 2003b). It is however common in Maastrichtian elasmosaurids outside of the seaway (*Morenosaurus*, *Aphrosaurus*; Welles, 1943), as well as in many earlier elasmosaurids and non-elasmosaurid plesiosaurs (e.g., *Callawayosaurus*, *Microcleidus*, polycotylids, cryptocleidids sensu O'Keefe 2001; Watson, 1909; Welles, 1962; Carpenter, 1996). The phylogenetic relationship among the Cretaceous elasmosaurids is unstable (Sato, 2003a, 2004), but the presence of this process in potential outgroups and early elasmosaurids suggests that CMN 9454 is plesiomorphic among the elasmosaurids.

Assuming an original length of 270 mm for the slightly eroded femur of CMN 9454, the humerus is 17 to 20 per cent longer than the femur in this individual. The humerus is usually (but not always; e.g., *Hydralmosaurus*, *Terminonatator* in Welles, 1952 and Sato, 2003b) longer than the femur in elasmosaurids, but the difference is less than 10 per cent in most cases. In fact, *Callawayosaurus* (Welles, 1962) and *Futabasaurus* (Sato et al., 2006) are the only elasmosaurids for which a difference of over 10 per cent has been confirmed. Unfortunately, this ratio is not available for several taxa including *Elasmosaurus* and *Libonectes* for which the fore- and/or hind limbs are unknown.

The comparison above suggests a close relationship of CMN 9454 with a limited number of taxa such as *Elasmosaurus* (Campanian) and *Libonectes* (Turonian) from the Western Interior Seaway, *Callawayosaurus* (Aptian, Columbia), and *Futabasaurus* (Santonian, Japan). The wide temporal and geographic ranges of these taxa may also suggest the plesiomorphic nature of the CMN plesiosaur compared with other elasmosaurids from the Western Interior Seaway excluding *Elasmosaurus* and *Libonectes*. When the morphological, stratigraphic, and geographic data are all considered, *Elasmosaurus* from the Campanian Pierre Formation in Kansas is the best candidate for a close relationship with CMN 9454. However, it is a problematic taxon represented by a single specimen in which all limb elements were originally missing and the girdle bones were insufficiently described before being lost (Cope, 1870; Welles, 1952; Carpenter, 1999; Sachs, 2005). Potential synonymy or relationship with any other taxa is less likely because of the temporal and geographic distances, but cannot be ruled out.

Paleoecological Inference—Although the exact depositional environments remain unknown for the plesiosaurian specimens from the Horseshoe Canyon Formation, AMNH 5261 obviously came from an estuarine setting, whereas CMN 9454 came from an alluvial setting. Plesiosaurian remains from non-marine sediments have been sporadically reported from the Jurassic and Cretaceous in various parts of the world (summarized in Cruickshank, 1997; Sato et al., 2003), but many are represented by poorly preserved specimens. In fact, both AMNH 5261 and CMN 9454 are among the best-preserved specimens from non-marine environments. Interestingly, most of good specimens from non-marine environments are juvenile (sensu Brown, 1981) (e.g., holotype of *Bishanopliosaurus youngi* Dong 1981; TMP 81.31.1 in Sato et al., 2005).

Sato et al. (2005) noted the abundance of small-sized adult specimens and lack of large adults individuals in the non-marine Dinosaur Park Formation plesiosaurian fauna. Poor preservation did not allow a quantification of the number of individuals, but about one-third of the specimens were juvenile in the studied fauna. Based on a histological study of elasmosaurids from the Upper Cretaceous of New Zealand, Wiffen et al. (1994) suggested that juveniles with relatively dense bones as better suited for life in shallow water than adults with less dense bones. Because juvenile plesiosaurian specimens are common in the marine Bearpaw Formation and other marine strata of Campanian to Maastrichtian age (e.g., Welles, 1943; Sato, 2003a), it cannot be assumed that juvenile plesiosaurians lived only in non-marine environments and adults only in open sea in North America. Rather, the data suggest that juvenile and small adult plesiosaurians lived in (but were not limited to) the fluvial to coastal setting, whereas large adults were more limited to more fully marine setting at least in Western North America during this time. It however remains unknown whether the populations in different environments represent different species, because most of studied materials are indeterminate elasmosaurids.

Nicholls and Meckert (2002) suggested that the polycotylids declined and elasmosaurids became dominant during the late Campanian. Assuming the elasmosaurid affinity of "*Cimoliasaurus*" specimens from the Atlantic coast (Russell, 1988; Kear, 2002), the Elasmosauridae is the most common component of the Late Campanian-Maastrichtian plesiosaurian faunas of North America (Russell, 1988; Sato, 2003a). Although only two specimens do not allow a generalization of the plesiosaurian fauna of the Horseshoe Canyon Formation, the two elasmosaurids do not disagree with this generalized picture.

Andrews (1922) suggested that non-marine environments served as a refuge for primitive plesiosaurs such as *Leptocleidus*. The primitive traits noted in CMN 9454 supports this interpretation, but it is also possible that the Horseshoe Canyon plesiosaurian specimens represent the young individuals of *Elasmosaurus* or other marine taxa for which a close relationship is suggested. Andrew's hypothesis remains viable, but taxonomic distinction between marine and non-marine faunas is yet to be proven.

An enigmatic aspect of the Horseshoe Canyon plesiosaurs is the rarity of their occurrences. The two relatively complete specimens were recovered in the 1910s but no other specimens have been discovered since then, despite the long history of fossil collecting and geological studies in this area. This contrasts with the situation in the Dinosaur Park Formation where a large number of plesiosaurian specimens, although mostly fragmentary, have been collected during a similar period of time (Sato et al, 2005). The rarity of well-preserved specimens from the Dinosaur Park Formation suggests that we are more likely missing fragmentary specimens from the Horseshoe Canyon Formation. There is certainly a strong collection bias against the plesiosaurian remains in fluvial sediments because they tend to be poorly preserved and might be easily misidentified because they are fragmentary and unexpected. Hopefully our current contribution will serve as a reminder for the collectors and researchers who may encounter "marine" reptiles in non-marine sediments.

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APPENDIX 1

SYSTEMATIC PALEONTOLOGY
DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1888
ORNITHOPODA Marsh, 1881
EDMONTOSAURUS Lambe, 1917

Edmontosaurus? sp.

Leurospondylus? in Russell, 1931:135

Referred specimen—UALVP431, isolated caudal centrum.

Locality and horizon—"an outcrop of the Edmonton formation [sic] on North Saskatchewan river, about six miles above the city of Edmonton" (Russell, 1931:135).

Description—see Russell (1931)

Discussion—The chevron facets indicate this is a caudal vertebra, but it lacks the transverse process or rib facet, unlike plesiosaurian caudal that have caudal ribs throughout the series (e.g., CMN 9454). Comparison with other large vertebrates from the Edmonton group indicates that UALVP431 belongs to an ornithopod dinosaur, and mostly like a hadrosaur. The original specimen was not relocated in the UALVP collection (T. Konishi, pers. comm., 2005).

The stratigraphic level of this specimen is roughly estimated based on the locality information in Russell (1931) and the geological data in Kathol and McPherson (1975). The Horseshoe Canyon Formation is unconformably overlain by Quaternary sediments in the vicinity of Edmonton, but it is exposed along the North Saskatchewan River in the southwest of the city. The upper portion of the formation is irregular due to glacial erosion, and the thickness of the formation ranges from 140 to 190 meters in the study area of Kathol and McPherson (1975). Considering the smaller size of the city around 1931 and the meandering course of the river, the fossil locality cannot be very far from the southwestern corner of the study area in Kathol and McPherson (1975). If we assume a conformable Bearpaw-Horseshoe Canyon transition and an estimated original thickness of the formation as 250 to 300m (based on the isopach in Dawson et al., 1994), the specimen probably came from a middle to lower portion of the formation.

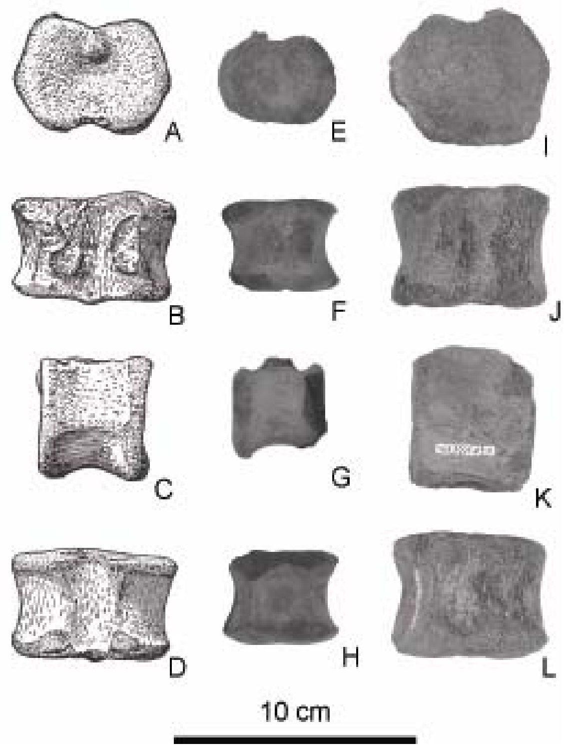

FIGURE A1. Ornithopod caudal vertebrae. UALVP431 (**A-D**, after Russell 1931:figs. 2-5), holotype of *Edmontosaurus regalis* CMN 2288 (**E-H**), and TMP 2005.7.1 (**I -L**), in anterior (?) (**A, E, I**), dorsal (**B, F, J**), lateral (**C, G, K**), and ventral (**D, H, L**) views.

Six species of ornithopods are known from Horseshoe Canyon Formation (Eberth, 1997; Weishampel et al., 2004); *Parksosaurus warrenti* (Parks, 1926); *Thescelosaurus neglectus* Gilmore 1913 (basal ornithopods; Norman et al., 2004), *Edmontosaurus regalis* Lambe, 1917; *E. annectens* (Marsh, 1892); *Saurolophus osborni* Brown, 1912 (above Hadrosauridae: Hadrosaurinae; Horner et al., 2004); and *Hypacrosaurus altispinus* Brown, 1913a (Hadrosauridae: Lambeosaurinae in Horner et al., 2004). Details of the morphological variation throughout the tail was documented only in *Thesceleosaurus* and *Edmontosaurus* among the Horseshoe Canyon ornithopods. The single caudal centrum of UALVP 431 cannot be identified at genus or species level, but of the two genera for which detailed tail morphology is comparable, the UALVP specimen is comparable to *Edmontosaurus* because;

- In *Thesceleosaurus*, caudals without transverse processes are elongated (Gilmore, 1915; Sternberg, 1940)
- The proportion and size of the UALVP centrum is similar to the middle caudal vertebrae of a specimen comparable to *E. annectens* (*Thespesius* cf. *edmonti* [sic] in Parks, 1935)
- Two ?distal caudal vertebrae of the holotype of *E. regalis* (CMN 2289) are smaller but similar in morphology (Figure A1)

Edmontosaurus is the only or at least the most common ornithopod reported from the lowermost portion of the formation up to coal seam 10, and also known from the interval between coal seam 10 to 11 from which other ornithopods have been also reported (Russell and Chamney, 1967). Remains of *Edmontosaurus* and indeterminate hadrosaurids are known from this formation along the North Saskatchewan River in the Edmonton area (in TMP collection; Tanke, 1984). A centrum of similar size and morphology (Figure A1, TMP 2005.7.1) was collected as a float in the AMNH site area, at the bottom of the outcrop in which coal seams 9 to 11 are exposed (see LOCALITY AND STRATIGRAPHIC LEVEL OF OCCURRENCES in main text).

APPENDIX 2

Measurements of CMN 9454 (in mm). Italics indicate estimates. “N/A” means “measurement not available due to poor preservation and/or restoration”.

tooth	Height of crown	Diameters at base of crown
A	31	10 x 8
B	25	*9* x 7

Centrum (number on specimen)	Length	Height	Width
1D	49	57	80
2D	51	59	86
3D	49	60	84
4D	49	59	N/A
5D	49	58	87
6D	*50*	60	88
7D	Restoration		
8D	51	61	85
9D	54	62	86
10D	56	64	85
11D	56	N/A	N/A
12D	60	*69*	79
13D	*57*	68	*80*
14D	*63*	*72*	*80*
15D	65	*72*	*73*
16D	67	*75*	N/A
17D	N/A	73	N/A
18D	N/A	N/A	N/A
19D	*64*	*72*	
20	60	70	74
21	57	72	*74*
22	59	*72*	*74*
23	58	67	71
24	Restoration		
25	Restoration		
26	53	63	75
27	Restoration		
28	50	58	73
29	Restoration		
30	40	*55*	*68*
31	Restoration		
32	41	55	68
33	Restoration		
34	39	*54*	72
35	Restoration		
36	39	53	*72*
37	Restoration		
145	*39*	*40*	*52*

Girdle bone [dimension]	
Left coracoid [maximum length]	*520*
Left coracoid [length, posterior to glenoid]	330
Left coracoid [maximum width (at glenoid)]	269
Left coracoid [maximum thickness at medial symphysis]	103
Left (?) pubis [maximum width (at acetabulum)]	279
Left (?) pubis [maximum thickness at medial symphysis]	52
Right (?) ischium [maximum length]	238
Right (?) ischium [maximum width]	218
Right (?) ischium [maximum thickness at medial symphysis]	39

Limb bone	Length	Width
Right humerus	317	207
Left humerus	323	201+
Right (?) radius	119	124
Left (?) radius	117	125
Right (?) ulna	113	107
Left (?) ulna	114	107+
Right femur	265+	154+
Right (?) tibia (?)	84	100