A NEW ELASMOSAURID PLESIOSAUR (REPTILIA: SAUROPTERYGIA) FROM THE LOWER CRETACEOUS CLEARWATER FORMATION, NORTHEASTERN ALBERTA, CANADA

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ABSTRACT

A new taxon of elasmosaurid plesiosaur from northern Alberta, *Wapuskanectes betsynichollsae* gen. et sp. nov., is described. The specimen was recovered from the Lower Cretaceous Wabiskaw Member of the Clearwater Formation, and is recognized as the oldest elasmosaurid described from the Cretaceous of North America. The holotype specimen, TMP 98.49.02, includes a very well preserved pectoral girdle, and provides many taxonomically informative characters for comparison to other Cretaceous long-necked taxa, including the Aptian taxon *Callawayasaurus colombiensis* (Welles, 1962). Bearing possible ontogenetic variation in mind, *Wapuskanectes* is distinguished from other adult plesiosaurs by the presence of a complete pectoral bar, the absence of a broad medial contact between the ventral rami of the scapulae, a very pronounced ventral process of the coracoids, a fully enclosed cordiform intercoracoid vacuity, and a distinct postaxial epipodial facet on the humerus.

INTRODUCTION

Our understanding of plesiosaur diversity and distribution is notably poor for the Early Cretaceous (144.5–99.6 Ma) (Ogg, et al., 2004). Currently, only four genera of Early Cretaceous long-necked, small-skulled elasmosaurids (*sensu* Brown, 1993) are recognized: *Brancasaurus brancai* Wegner, 1914, *Callawayasaurus* (formerly *Alzadasaurus*; Carpenter, 1999) *colombiensis* (Welles, 1962); *Styxosaurus glendowerensis* (Persson, 1960); and *Eromangasaurus carinognathus* Kear, 2005. Until now, no North American elasmosaur material has been recognized from the Early Cretaceous.

Since 1992, open pit mining of the Athabascan Oil Sands deposit by Syncrude Canada, Ltd. has serendipitously resulted in the discovery of several new plesiosaur specimens in northeastern Alberta, Canada (Druckenmiller and Russell, 2003) (Figure 1). The fossils were discovered in the Lower Cretaceous Wabiskaw Member of the Clearwater Formation (lower Albian), which overlies the bitumen-rich continental sediments of the McMurray Formation, and is removed as overburden in the mining of the oil sands

(Figure 2). Three of the new specimens (TMP 96.97.01, TMP 98.49.02, and TMP 99.68.01) from the Syncrude mine are referable to the Elasmosauridae. One of these, TMP 98.49.02, consists of a partial, uncrushed, postcranial skeleton, including the nearly complete pectoral girdle. Comparisons with other Cretaceous elasmosaurs demonstrate that these remains represent a new taxon of plesiosaur, which is named and described below. The new taxon is significant at a global level in that it adds new information about the morphological diversity and geographical distribution of Elasmosauridae in the Early Cretaceous. Furthermore, TMP 98.49.02 is the oldest North American elasmosaur. As such, it significantly extends the stratigraphic range of this group in North America, which was home to the greatest diversity of Late Cretaceous elasmosaurs anywhere in the world.

PROVENANCE

All three of the elasmosaurid specimens were discovered on the west side of the Syncrude Base Mine, within a 2–3 meter thick, heterolithic, very fine- to medium-grained glauconitic sandstone unit of the
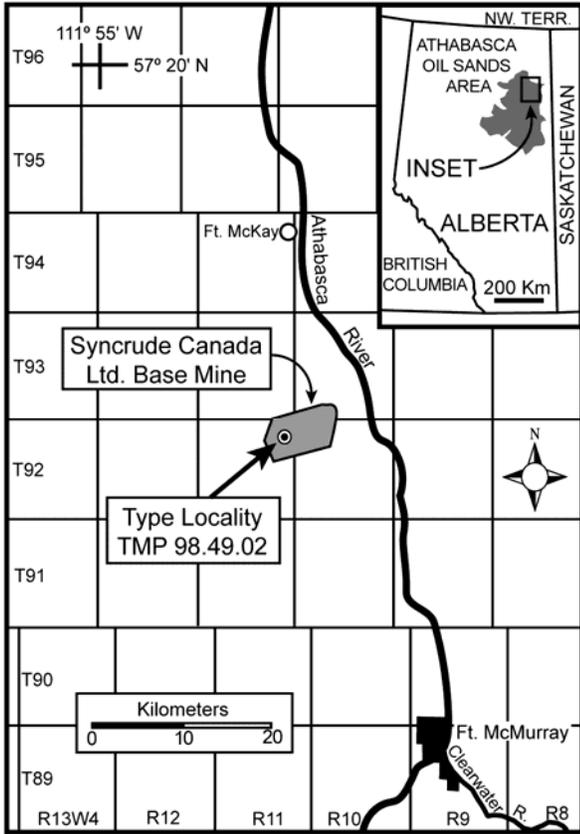
FIGURE 1. Map showing the location of the Syncrude Canada Ltd. Base Mine and the type locality of *Wapuskanectes betsynichollsae*, gen. et sp. nov. in northeastern Alberta, Canada.

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Wabiskaw Member of the Clearwater Formation (Figure 2). The Wabiskaw Member is the basal unit of the dominantly marine Clearwater Formation, which overlies the continental to marginal marine deposits of the McMurray Formation (Figure 2), and is in turn overlain by nearshore marine deposits of the Grand Rapids Formation (Mellon and Wall, 1956; Smith, 1994). The Wabiskaw Member was deposited under marginal marine and fully marine conditions as the Boreal Sea made its first major southward transgression into the Western Interior Basin (Jeletzky, 1971; Wightman et al., 1995). Deposition of the unit in which TMP 98.49.02 was found occurred under fully marine conditions, as demonstrated by its laterally extensive deposits, trace fossil assemblages, and sedimentology (Flach, 1984; Keith et al., 1988; Wightman et al., 1995). Furthermore, facies analysis of cores from the region around the type locality of the new plesiosaur suggests that deposition of the fossil-bearing unit occurred in the lower shoreface-offshore transition zone (Druckenmiller and Zonneveld, 2002).

In terms of age, the base of the Wabiskaw Member marks the division between the Upper and Lower Mannville (Figure 2), and is generally considered to correspond to the Aptian–Albian boundary (Flach, 1984; Hayes et al., 1994). Thus, the Wabiskaw Member is generally considered to be lowermost Albian in age. Unfortunately, numerical dating of the unit has been hampered by the lack of radiometrically dateable volcanic ash/bentonite in the underlying McMurray Formation or in the overlying shale of the Clearwater Formation. Radiometric dates for glauconite pellets from the Wabiskaw Member have proven unreliable (Williams et al., 1962).

Biostratigraphically, the minimum age of the Wabiskaw Member is well constrained by ammonites within the overlying Clearwater Formation. This fauna includes *Beudanticeras affine* and *Arcthoplites* (*Lemuroceras*) spp., which represent the lower Albian substage (Jeletzky, 1968; Stelck and Kramers, 1980; Kauffman et al., 1993). Placement of a maximum age on the unit is somewhat problematic because ammonites from the Wabiskaw Member have not been described, nor have they been reported from the underlying McMurray Formation. However, palynological analyses, based primarily on angiosperm palynomorphs, place the top of the underlying McMurray Formation near the Aptian–Albian boundary (Burden, 1984). This is in close agreement with foraminiferal microfaunas recorded from the upper McMurray Formation and lower Clearwater Formation, which also places this contact within the lower Albian substage (Mellon and Wall, 1956; Caldwell et al., 1993).
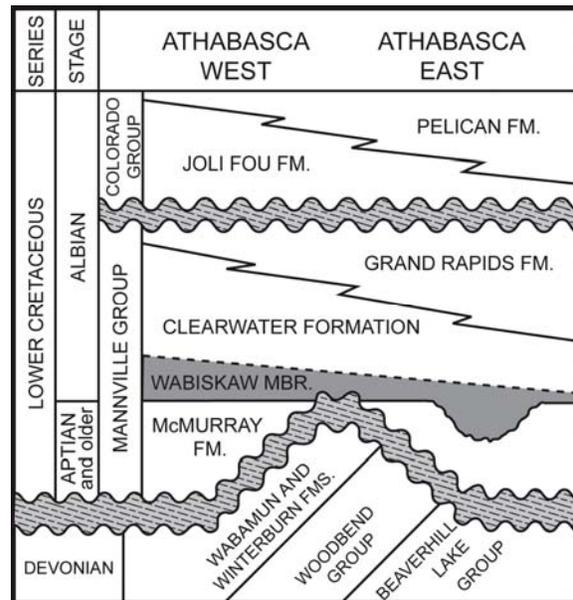

FIGURE 2. Regional stratigraphic relationships of the Mannville Group in northeastern Alberta. The type specimen of *Wapuskanectes betsynichollsae* was recovered from a 2-3 meter thick unit of the Wabiskaw Member (shaded) of the Clearwater Formation.

Institutional Abbreviations—AMNH,American Museum of Natural History, New York City, New York, USA; CM, Canterbury Museum, Christchurch, New Zealand; SDSM, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860
Order PLESIOSAURIA De Blainville, 1835
Family ELASMOSAURIDAE Cope, 1869
Wapuskanectes new genus

Type and Only Species— *W. betsynichollsae* sp. nov.

Horizon—Wabiskaw Member of the Clearwater Formation, lowermost Albian, Lower Cretaceous.

Etymology—*Wapuska* – Wabiskaw is a corruption of this word, derived from the Cree language meaning "a body of water with whitecaps on it" (Aubrey, 1996) and –*nectes* (Greek) "swimmer" (gender; masculine).

Diagnosis—As for type and only species, *W. betsynichollsae* sp. nov.

Wapuskanectes betsynichollsae new species
(Figures 3–9)

Holotype—TMP 98.49.02

Locality and Horizon—West side of the Syncrude Base Mine, near Ft. McMurray, Alberta, Canada (Lat. 57° 00′ 57′′ N, Long. 111° 40′ 28′′ W); Wabiskaw Member of the Clearwater Formation.

Etymology—Matronym in memory of Elizabeth ("Betsy") Nicholls, curator of marine reptiles at the Royal Tyrrell Museum of Palaeontology, for her enduring influence on research in Mesozoic marine vertebrates (gender; feminine).

Diagnosis—Elasmosaurid plesiosaur possessing the following unique combination of character states: interclavicle rectangular with rounded corners and possessing a notch along either the anterior or posterior margin (orientation to be confirmed upon discovery of articulated material); ventral ramus of scapula reaches midline but lacks a broad contact with its opposite; scapula with a prominent posteriorly directed prong extending toward the coracoid; well-developed midline contact between scapula and coracoid (pectoral bar) present in adult; presence of a well-developed anterior process of the coracoid along the midline, contributing
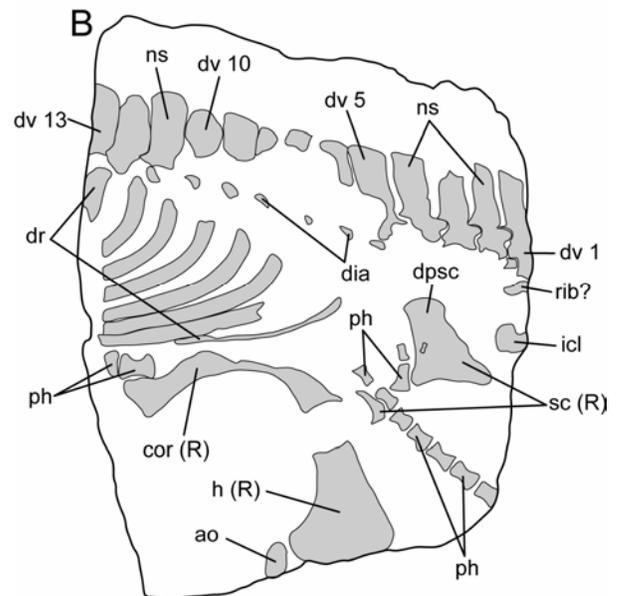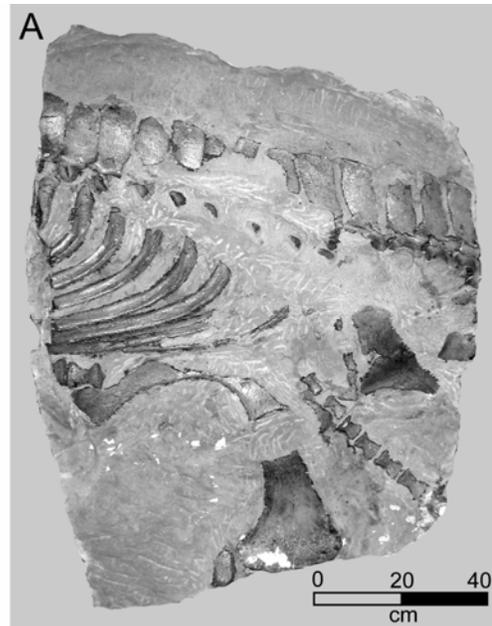

FIGURE 3. Photograph, **A**, and interpretation, **B**, of the dorsal surface of TMP 98.49.02, holotype specimen of *Wapuskanectes betsynichollsae*. Anterior is to the right in both figures. **Abbreviations**: **ao**, accessory ossicle; **cor**, coracoid; **dia**, diapophysis; **dpsc**, dorsal process of scapula; **dr**, dorsal rib; **dv**, dorsal vertebra; **h**, humerus; **icl**, interclavicle; **ns**, neural spine; **ph**, phalanx; **R**, right; **sc**, scapula.

extensively to the pectoral bar; coracoid of adult with a very prominent, ventrally extending midline process; cordiform intercoracoid vacuity fully enclosed posteriorly by coracoids; humerus with a pronounced postaxial accessory facet.
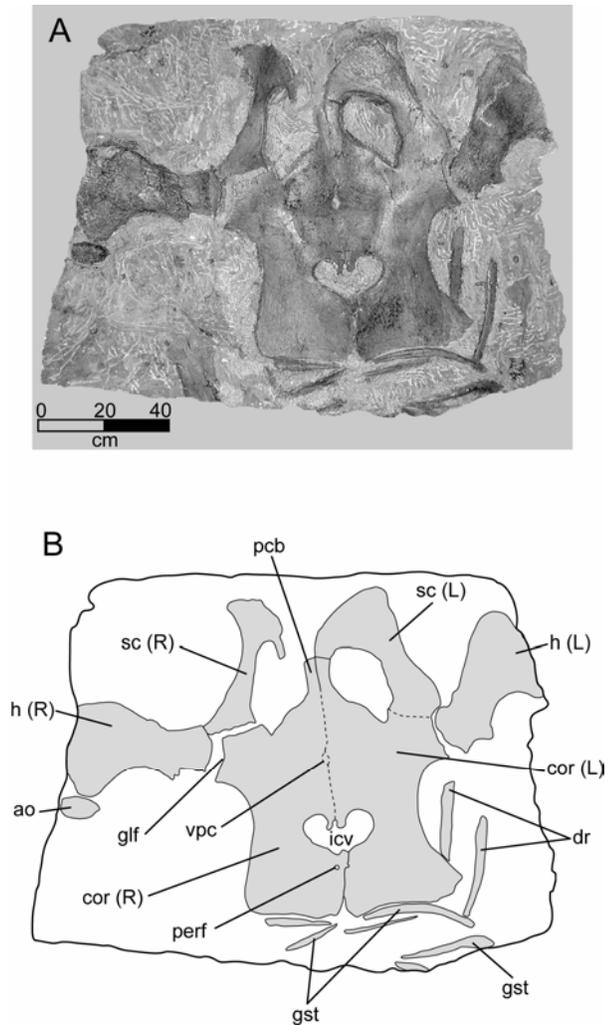
FIGURE 4. Photograph, **A**, and interpretation, **B**, of the ventral surface of TMP 98.49.02, holotype specimen of *Wapuskanectes betsynichollsae*. Dashed lines indicate fused sutures. Anterior is to the top in both figures. **Abbreviations**: **ao**, accessory ossicle; **cor**, coracoid; **dr**, dorsal rib; **glf**, glenoid fossa; **gst**, gastralia; **h**, humerus; **icv**, intercoracoid vacuity; **L**, left; **pcb**, pectoral bar; **perf**, perforation; **R**, right; **sc**, scapula; **vpc**, ventral process of the coracoid.

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Description—TMP 98.49.02 comprises the incomplete but largely articulated remains of an adult elasmosaurid plesiosaur, entirely contained within a single large block of rock measuring 1.1 meters in length and 1.35 meters in width (Figures 3–5). Given the well-preserved nature of the specimen, and the fact that the elements are also mostly articulated, it is likely that these remains constitute only a small part of what was once a considerably more complete fossil.

Prior to preparation, bones visible along both the anterior and posterior broken surfaces of the block were observed to be uncrushed. For this reason,

preparation was carried out from both the dorsal and ventral surfaces. The dorsal surface (Figure 3) exposes portions of 13 articulated vertebrae, eight partial dorsal ribs, the dorsal process of the right scapula, the lateral margin of the right coracoid, the partial interclavicle, the dorsal surface of the right humerus and an associated accessory ossicle, and three partially articulated phalangeal series. The prepared ventral surface of the block (Figure 4) reveals a very well preserved pectoral girdle exposed in ventral view, including both articulated coracoids and scapulae, the nearly complete right and left humeri, a single right accessory ossicle, two partially exposed left dorsal ribs, and portions of six gastralia. No clavicular remains are evident.

Ontogenetic Status—Apart from its large size (Table 1; Figure 6), several features of the pectoral girdle suggest that TMP 98.49.02 is a fully mature individual (Brown, 1981). The coracoids display considerable fusion with adjacent elements. Specifically, the left and right coracoids are fused with one another along much of their midline length (Figure 4), particularly between the posterior end of the pectoral bar and the anterior margin of the intercoracoid vacuity. The left coracoid and left scapula are also fused at the glenoid fossa. However, fusion has not occurred along this same contact on the right side, nor has it occurred between the left scapula and coracoid at the anterior end of the pectoral bar. *Wapuskanectes* also exhibits a complete pectoral bar, a feature that is at least partially controlled ontogenetically (Welles, 1952; Carpenter, 1999). A modestly developed posterolateral cornu of the coracoid is also observed; however, it is not as prominently developed as in old individuals of *Cryptoclidus* (Brown, 1981). Other features of the coracoids that may be indicative of ontogenetic state include the development of a prominent, ventrally projecting midline process, and the presence of perforations along the posterior midline of the coracoids (Figure 4) (see DISCUSSION below). Finally, there is no trace of a suture between the neural arch and centrum on any vertebra (Figure 3).

Axial Skeleton—Thirteen articulated vertebrae, preserved in right lateral view, are exposed on the dorsal surface of the block (Figures 3 and 7A). All are interpreted to be dorsal vertebrae, with vertebra number one and possibly number two being equivalent to "pectoral vertebrae", which share the rib facet between the neural arch and centrum. The articular facet of vertebra number one, exposed along the broken anterior margin of the block (Figure 7A), is broader than tall (Table 1), and its posterior margin is in line with the anterior margin of the scapula. The centra of subsequent vertebrae remain hidden in matrix. The prezygapophyses and postzygapophyses are narrow
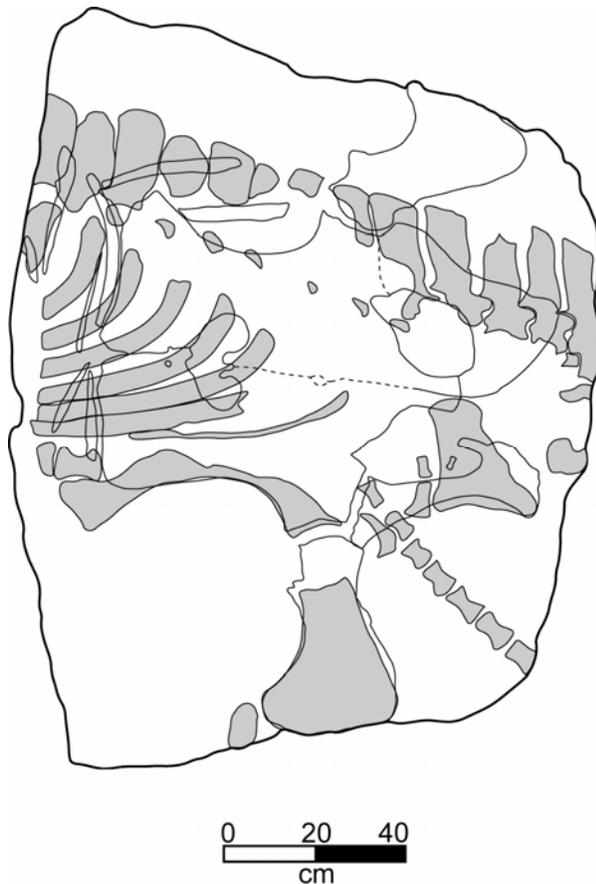
FIGURE 5. Transparent reconstruction of block comprising TMP 98.49.02, holotype specimen of *Wapuskanectes betsynichollsae*. Anterior is to the right, and elements visible on the top (dorsal) surface are shaded, whereas those visible on the lower (ventral) surface are unshaded.

mediolaterally; in dorsal view their combined width is approximately half the width of the centrum. The zygapophyseal facets of the anterior dorsal vertebrae (one through four) are inclined toward the midline at approximately 45 degrees from the horizontal, while those of the posterior three vertebrae lie nearly in the horizontal plane. The diapophyses are massive, and increase in length posteriorly throughout the preserved series. They extend laterally from the vertebrae, and are not conspicuously inclined vertically or posteriorly; however, the rib facet is directed ventrally and posteriorly. The neural spines are tall and rectangular; those of the anterior dorsal vertebrae are gently inclined posteriorly and have 2–4 cm of space between successive vertebrae (Figure 7A). Caudad, the neural spines are oriented nearly vertically, with little to no space between neighboring spines. The dorsal surface of each neural spine bears an irregular, pitted surface and is trapezoidal in outline, being broadest posteriorly and tapering in width anteriorly.

With the possible exception of a small portion of rib that occurs immediately ventral to vertebra one (Figure 7A), the anteriormost dorsal ribs are not exposed. However, portions of eight large dorsal ribs are associated with vertebrae five through 12. These remain largely in articulation with the vertebrae, but have been folded anteriorly so that their posterior surfaces are exposed (Figure 3). Proximally, the ribs are strongly curved ventrally. In cross section the ribs appear T-shaped, with the broadest, dorsal surface forming the top of the T.

Appendicular Skeleton—A small, incomplete element is exposed along the anterior margin of the dorsal surface of the block (Figures 3 and 7B). This bone is interpreted as the interclavicle due to its general morphological similarity to the interclavicles of other elasmosaurid taxa, small size, and apparent bilateral symmetry. Assuming bilateral symmetry, the bone is approximately twice as broad as it is long. The dorsal surface is flat medially, and curves dorsally along its lateral margins. Due to considerable morphological variation within plesiosaurs (Andrews, 1910; Welles, 1943), it is difficult to establish which end of the element is anterior, and which is posterior. One margin, possibly anterior, is relatively straight, while the other has a prominent embayment along the midline. The ventral surface is not exposed; thus, the presence or absence of a ventral keel cannot be established until further preparation is completed.
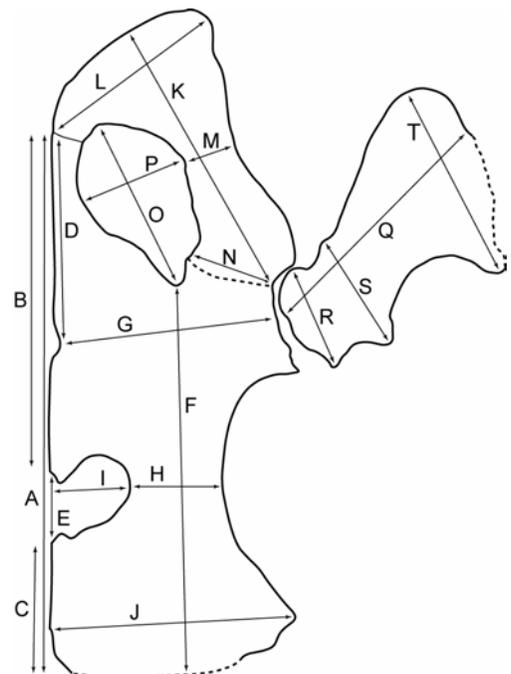

FIGURE 6. Location of measurements of TMP 98.49.02 listed in Table 1. Orientation as seen in Figure 4.

TABLE 1. Selected measurements (in mm) of TMP 98.49.02, holotype specimen of *Wapuskanectes betsynichollsae* (* dimension estimated due to concealment by matrix or incompleteness). See Figure 6 for key.

Coracoid (left)	
A	745*
B	480
C	200*
D	288
E	68
F	540*
G	305
H	143
I	116
J	355*
Scapula (left)	
K	390
L	246
M	69
N	130
O	250
P	150
height of dorsal process (from ventromedial margin)	245
anteroposterior length of dorsal process (midheight)	85
Humerus (left)	
Q	355
R	143*
S	152*
T	260*
Interclavicle	
length (anterior-posterior)	85
width	160*
Vertebra 1	
centrum width (anterior surface)	116
centrum height (anterior surface)	96
Vertebra 2	
maximum length, pre- to post zygapophysis	129
height of neural spine (from dorsal margin of postzygapophysis)	145
anterioposterior length of neural spine (at midpoint)	65
Vertebra 11	
height of neural spine (from dorsal margin of postzygapophysis)	163
anterioposterior length of neural spine (at midpoint)	84

Both scapulae are preserved (Figures 3–5, 7B, and 8A); however, the right one has been displaced such that its lateral margin has been dorsally rotated, causing the ventral ramus to become detached medially from its contact with the left scapula. The anterolateral margin of each scapula is gently concave both laterally and ventrally. The anteromedial margin of the ventral ramus is broadly convex, and its posteromedial margin abuts the anterior end of the pectoral bar along an oblique suture. Although displaced, it is clear that the medial portion of the ventral rami of the scapulae shared only a short, unfused contact along the midline, approximately 5 cm in length. Together, the scapulae and coracoids equally enclose a teardrop-shaped pectoral fenestra (Figure 8A), and contribute nearly equally to the glenoid fossae. The dorsal process of the scapula (Figure 7B) is incompletely exposed, but reveals a moderately convex posterior margin and a slight dorsal expansion.

The coracoids are very well preserved and remain in their original life position (Figures 4 and 8B). The anterior process of the coracoid is large and contacts the posteromedial process of the scapula, forming a complete pectoral bar. The left and right scapulocoracoid sutures are symmetrical, and demonstrate that most of the pectoral bar consists of the anterior process of the coracoid and not the posteromedial process of the scapula.

Viewed edge-on, from either anterior or posterior aspect, the left and right coracoids do not lie in the horizontal plane, but rather articulate in a broad V, with the glenoid fossae lying slightly dorsal to the ventral midline suture. The midline coracoid-coracoid symphysis shows considerable fusion, which begins anteriorly approximately 6 cm posterior to the scapulocoracoid suture (Figure 4). The coracoids are solidly fused along the symphysis in the region lying between the glenoid fossae, and remain so posteriorly, almost to the intercoracoid vacuity, at which point fusion ceases.

Typical of many Cretaceous elasmosaurs, a cordiform intercoracoid vacuity is present in *Wapuskanectes* (Figures 4 and 8B), and is completely enclosed by the left and right coracoids. Posterior to the intercoracoid vacuity and close to the midline, the right coracoid bears a small (approximately 2 cm in diameter) perforation (Figure 4B), almost opposite which there is a second, incomplete perforation on the left coracoid, represented by an embayment along the midline margin. The posterolateral margins of the coracoids are developed into modestly sized cornua, which extend only slightly more laterally than the glenoid fossae.

Wapuskanectes possesses a prominent, ventrally projecting midline process of the coracoid-coracoid symphysis, contributed to equally by the left and right

coracoid. The process is noteworthy in terms of its vertical dimensions, extending ventrally approximately 10-12 cm below the horizontal plane in which the coracoids are preserved. Its apex, measuring 3 cm in length and 2.5 cm in width, occurs in line with the posterior margin of glenoid fossae. The process is also laterally buttressed by a less prominent, transverse ridge. Together, the midline and transverse ridges divide the region surrounding the apex of the process into four quadrants, each representing a broad, shallow depression for the origin of the major adductor muscles of the forelimbs. The two anterior quadrants are slightly deeper than the posterior two, and all four are more rugose than the rest of the ventral coracoid surfaces.

The humeri are massive elements, as is typical of Cretaceous elasmosaurs (Figure 9). Neither humerus is completely exposed at its proximal end; however, most of the right, uncrushed capitulum is visible (Figures 8B and 9B). The articular surface is a flattened dome and is nearly round in outline. Its surface bears an irregular pattern of miniature hummocks perforated by small foramina. A very large rugosity, for insertion of adductor muscles, is present along the ventral surface of the humeral shaft. Beginning at a point approximately one-third of the way along the preaxial margin, the rugosity angles posteromedially across the ventral surface of the humerus, and is very pronounced posteriorly, where a rugose spur projects approximately 3 cm beyond the postaxial margin of the humerus.

A small portion of the distal end of each humerus is missing (Figure 4); however, the complete shape of the distal humeral margin can be reconstructed based on complementary portions of both humeri. Distally, the preaxial margin of the humerus is gently convex. The radial facet is shallowly concave, while the smaller ulnar facet is more strongly concave. The distal-most, postaxial margin of the right humerus bears a distinct facet, for the single preserved accessory ossicle. The postaxial margin, between the accessory ossicle and the spur of the ventral rugosity, is strongly convex.

A total of 12 phalanges are preserved, consisting of seven elements that remain articulated as part of a single digit, and two partially articulated clusters of phalanges (Figure 3B). The phalanges are unremarkable, other than having undergone more postmortem disturbance than the remainder of the skeleton, with the preserved portions considerably displaced from their life position.

Portions of six gastralia occur immediately posterior to, and even slightly overlap, the posterior margin of the coracoids (Figure 4). The lateral termination of one gastralium is flattened, but uncrushed, and anteroposteriorly expanded.
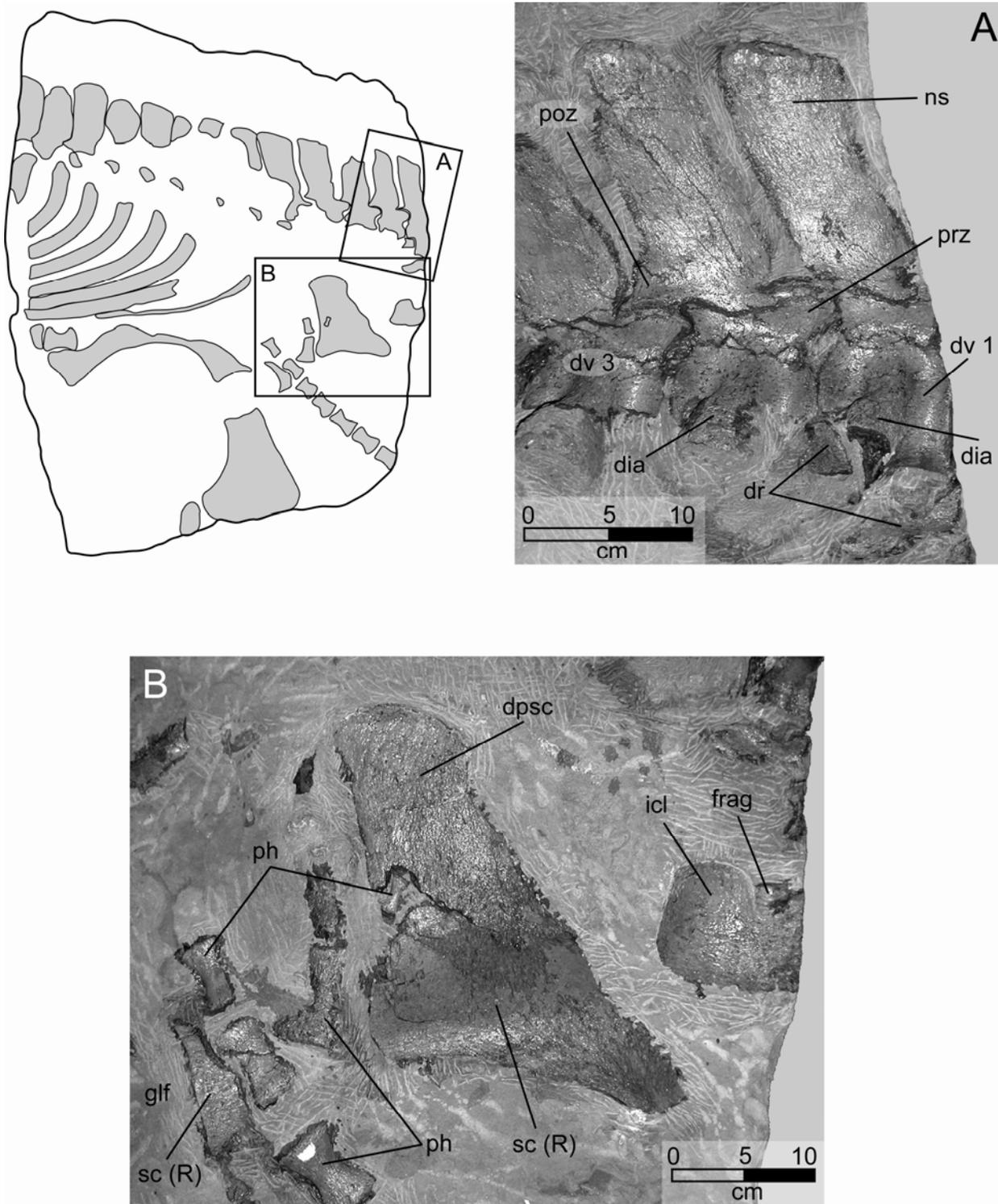
FIGURE 7. Detail of two areas on the dorsal surface of TMP 98.49.02, illustrating **A**, portions of three anterior dorsal vertebrae; **B**, lateral view of the interclavicle, right scapula, and associated phalanges. Anterior is to the right in all figures. **Abbreviations**: **dia**, diapophysis; **dpsc**, dorsal process of scapula; **dr**, dorsal rib; **dv**, dorsal vertebra; **frag**, fragment; **glf**, glenoid fossa; **icl**, interclavicle; **ns**, neural spine; **ph**, phalanx; **poz**, postzygapophysis; **prz**, prezygapophysis; **R**, right; **sc**, scapula.
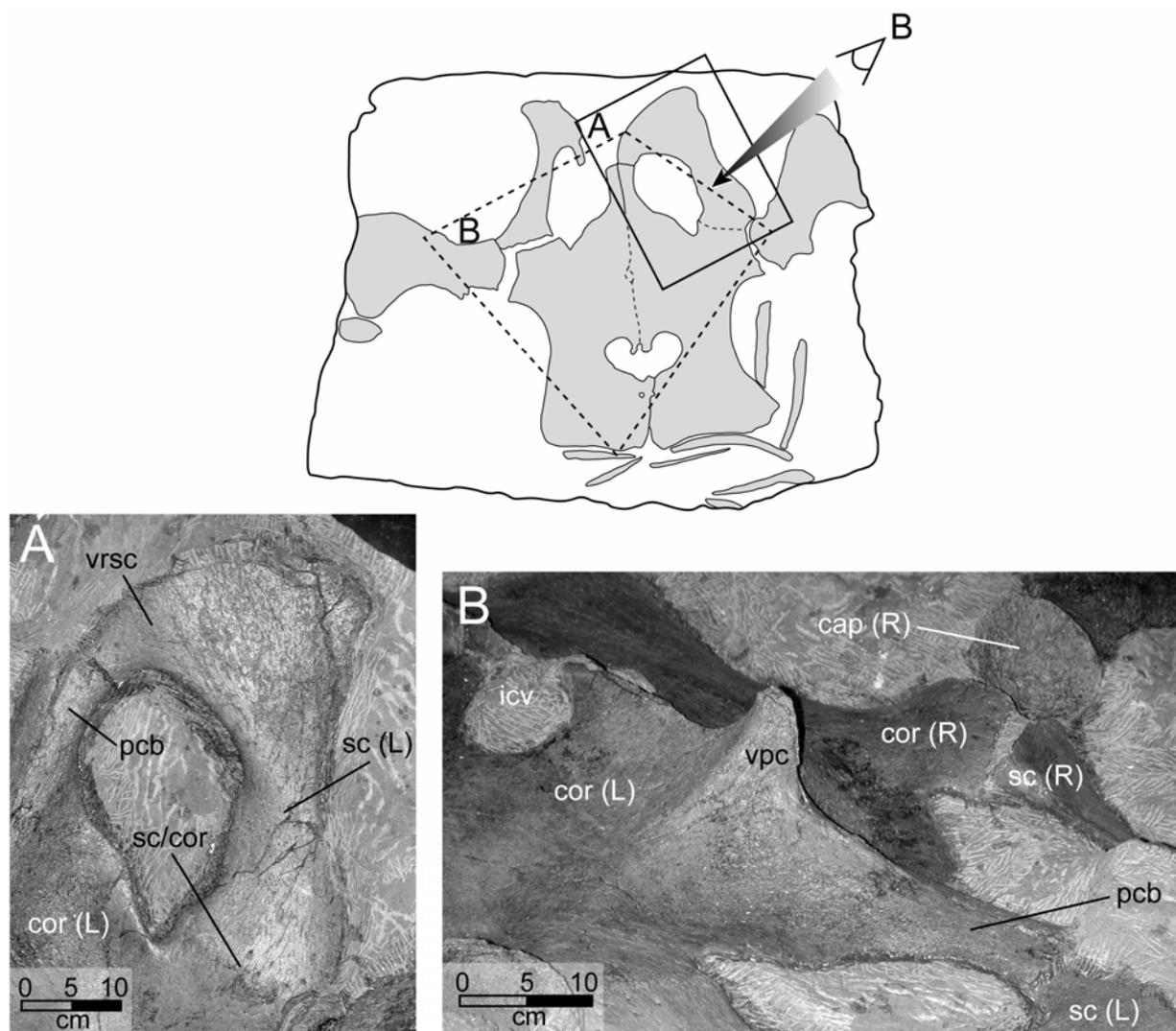
FIGURE 8. Detail of two areas on the ventral surface of TMP 98.49.02, illustrating **A**, the ventral ramus of the left scapula and anterior portion of the left coracoid (anterior is to the top); **B**, oblique, left lateral view of coracoids, showing the prominent ventral coracoid process, and proximal view of the right humerus. **Abbreviations**: **cap**, capitulum; **cor**, coracoid; **icv**, intercoracoid vacuity; **L**, left; **pcb**, pectoral bar; **R**, right; **sc**, scapula; **sc/cor**, scapulocoracoid symphysis; **vpc**, ventral process of the coracoid; **vrsc**, ventral ramus of the scapula.

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DISCUSSION

Given the incomplete nature of the holotype of *Wapuskanectes*, TMP 98.49.02, and the marked ontogenetic changes that are known to occur in the postcranium of plesiosaurs, it is important to discuss potential problems in comparing and naming a new taxon of elasmosaur. To begin, the holotype specimen of *Wapuskanectes* lacks a skull. Although cranial material is undoubtedly important in the description of any new taxon, it is not necessarily essential for its recognition. Furthermore, we argue that there has been an historical precedence in the use of postcranial characters, and particularly features of the pectoral girdle and propodials, in elasmosaur taxonomy. In part, this is due to the crushed and/or fragmentary nature of skull material often associated with elasmosaurs. Thus, the vast majority of the diagnostic features cited for many recognized species of elasmosaur, such as *Elasmosaurus platyurus* (Cope, 1869), *Hydrotherosaurus alexandrae* (Welles, 1943),
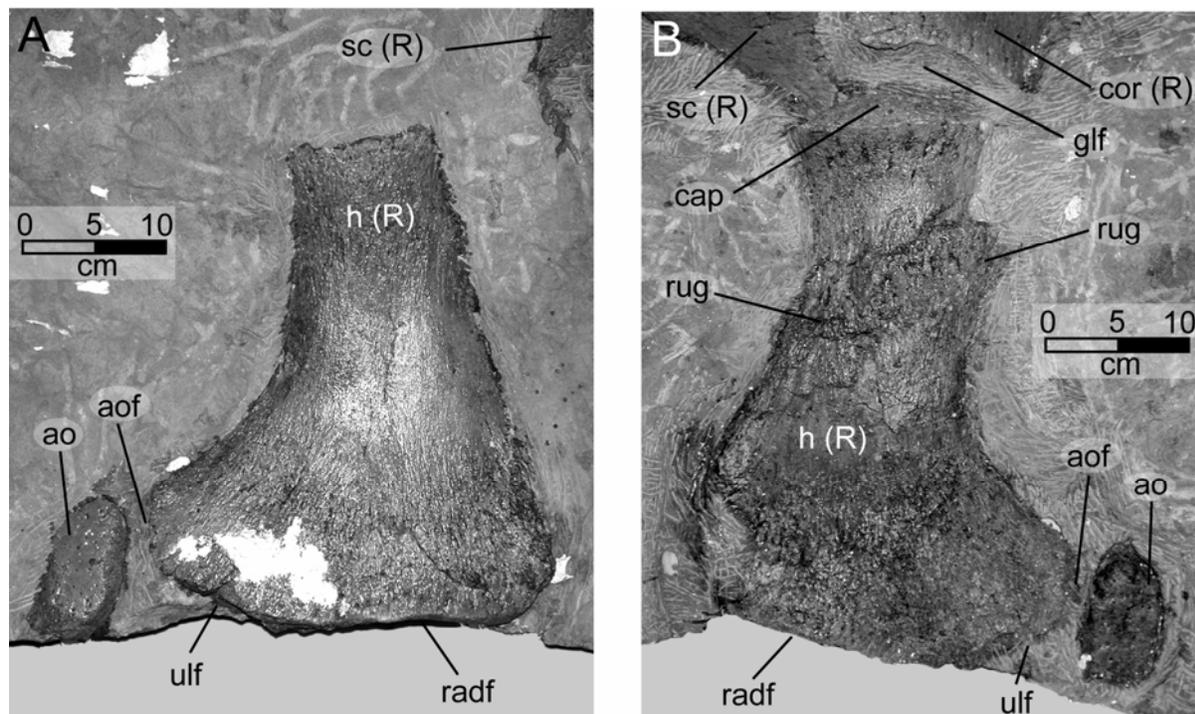
FIGURE 9. Dorsal, **A**, and ventral, **B**, views of the right humerus of TMP 98.49.02. **Abbreviations**: **ao**, accessory ossicle; **aof**, accessory ossicle facet; **cap**, capitulum; **cor**, coracoid; **glf**, glenoid fossa; **h**, humerus; **R**, right; **radf**, radial facet; **rug**, rugosity; **sc**, scapula; **ulf**, ulnar facet.

and *Callawayasaurus colombiensis* (Welles, 1962) are from the postcranium.

　　Secondly, *Wapuskanectes* lacks its cervical series in its entirety. The cervical series, and especially their total number, have traditionally played an important role in distinguishing elasmosaur taxa. Additionally, the dorsal vertebrae, which are incompletely exposed in this specimen, exhibit few diagnostic characters among elasmosaurs in general, making comparisons with other taxa difficult. For these reasons, characters of the pectoral girdle are emphasized in the diagnosis of *Wapuskanectes*.

　　Finally, a potential problem in comparing *Wapuskanectes* to other taxa relates to its ontogenetic status, especially with respect to its pectoral girdle. As discussed by Brown (1981) and Carpenter (1999), the morphology of the plesiosaur pectoral and pelvic girdles may change dramatically during ontogeny. Nearly complete ontogenetic series for *Cryptoclidus eurymerus* demonstrate that the presence of certain characters, such as the union of the scapulae along the ventral midline, the development of a pectoral bar, and the morphology of the posterior coracoids, are ontogenetically changeable in this species. However, these characters may still have taxonomic utility (Welles, 1952), provided several independent lines of evidence are used to infer ontogenetic state. For

example, Carpenter (1999) documented a growth series for *Styxosaurus snowii*, based on several specimens, in which he demonstrated the absence of a pectoral bar, even in fully mature individuals. Furthermore, even when comparisons are made with taxa represented by adult specimens, most individuals have probably not reached as advanced an ontogenetic state as that of *Wapuskanectes*. However, given the predictable morphological trajectories consistent with that observed in other plesiosaurs, including *Cryptoclidus* (Brown, 1981) and *Styxosaurus* (Carpenter, 1999), important comparisons may still be made with other taxa that differ in their morphology. In sum, although the holotype specimen of *Wapuskanectes* lacks a skull and cervical vertebral series, we believe that the very-well preserved portions of the postcranial skeleton described above are diagnostic and representative of a new taxon of elasmosaur.

　　Comparisons　　with　　Other　　Taxa—*Wapuskanectes* shares many characters of the vertebral column, pectoral girdle, and limbs with other described long-necked, small-skulled Cretaceous plesiosaurs (Elasmosauridae *sensu* O'Keefe, 2001 and Clade "X" Sato, 2002). These include: anterior dorsal vertebral centra ("pectorals") that are broader than tall; medial expansion of the ventral ramus of the scapulae; a

cordiform, intercoracoid vacuity; and short, massive propodials. Thus, hereafter *Wapuskanectes* is compared to the following Cretaceous elasmosaurids: *Brancasaurus brancai* Wegner, 1914; *Callawayasaurus colombiensis* (Welles, 1962); *Styxosaurus glendowerensis* (Persson, 1960); *Aphrosaurus furlongi* Welles, 1943; *Elasmosaurus platyurus* Cope, 1869; *Hydralmosaurus serpentinus* (Cope, 1877); *Hydrotherosaurus alexandrae* Welles, 1943; *Libonectes morgani* (Welles, 1949); *Morenosaurus stocki* Welles, 1943; *Styxosaurus snowii* (Williston, 1890); *Terminonatator ponteixensis* Sato, 2003; *Thalassomedon haningtoni* Welles, 1943; and a recently described, but unnamed, New Zealand taxon, CM Zfr 145, housed in the collections of the Canterbury Museum, Christchurch (Hiller and Mannering, 2005). It should be noted that our knowledge of the pectoral and pelvic girdles of *Elasmosaurus platyurus* is wholly based on Cope's (1869) original (and confusing) description and illustrations, as these elements cannot be relocated and have been missing since at least the beginning of the Twentieth Century (Williston, 1906; Carpenter, 1999). A confusing number of other nominal elasmosaur taxa exist in the literature; we follow the synonymies given most recently by Carpenter (1999) in his review of Western Interior forms**.**

Elasmosaur interclavicles are infrequently discussed in the literature. Among Cretaceous elasmosaurs, interclavicles have been described for *Brancasaurus* (Wegner, 1914), *Thalassomedon* (Welles, 1943), *Morenosaurus* (Welles, 1943), *Aphrosaurus* (Welles, 1943), *Styxosaurus snowii* (formerly *Alzadasaurus pembertoni*) (Welles and Bump, 1949; Carpenter, 1999), and *Libonectes morgani* (formerly *Elasmosaurus morgani*) (Welles, 1949; Carpenter, 1997). The interclavicle of *L. morgani* was interpreted from an element isolated from the rest of the clavicular arch, but its morphology was not described (Welles, 1949). Although the interclavicles of *Thalassomedon* and *Morenosaurus* are similar to that of *Wapuskanectes* in having a dorsally concave surface, they differ in all other respects. In terms of overall morphology, the interclavicles of *Thalassomedon*, *Morenosaurus*, and *Libonectes* all bear prominent anterior projections and straight to slightly convex posterior margins. *Thalassomedon* further differs in its proportions, being approximately as wide as long. In contrast, the anterior margin of the interclavicle of *Aphrosaurus* and *Brancasaurus* is concave, and its lateral margins taper to wing-like projections. Finally, the interclavicle of *Thalassomedon* and *Morenosaurus* bears a keel on its ventral surface, although this area is not visible in *Wapuskanectes*.

The structure of the ventral rami of the scapulae in *Wapuskanectes* is unique among described Cretaceous elasmosaurs, whereby they contact the coracoids (the pectoral bar) without the development of a broad, medial scapula-scapula contact. In *Hydralmosaurus*, *Styxosaurus*, *Thalassomedon*, and *Morenosaurus* the ventral rami all share a broad contact along the midline, but lack a posterior process that contacts the coracoids. In *Libonectes* and *Elasmosaurus*, a broad, medial scapula-scapula contact is present, in addition to a complete pectoral bar. In other taxa for which appropriate material is available and described, including *Aphrosaurus* and *Hydrotherosaurus*, the pectoral bar is entirely absent and the scapulae share little or no medial contact. The ventral rami of the scapulae of *Brancasaurus* are too poorly preserved to enable reconstruction of their original morphology, but the dorsal process is narrower anteroposteriorly, and is more horizontally inclined relative to the ventral ramus, than is the case in *Wapuskanectes*.

In general, the scapulae and coracoids of *Wapuskanectes* most closely resemble those of the Early Cretaceous elasmosaur *Callawayasaurus* (Figure 10). The holotype specimen of *Callawayasaurus*, UCMP 38349, like TMP 98.49.02, was an adult individual at the time of death. In addition to its large size (comparable to TMP 98.49.02 in the dimensions of its vertebrae and coracoids), many of the sutures in the skull of the holotype of *Callawayasaurus* are fused, and many of the cervical ribs and all of the cervical neural arches are fused to the centrum, without any trace of original lines of suture. The original relationships of the scapulae and coracoids of UCMP 38349 are somewhat difficult to determine as preserved, due to postmortem displacement that apparently occurred at the time of deposition. To clarify their original life positions, several blocks containing the pectoral girdle were rearticulated, photographed, and illustrated. The illustrations allow the scapula and coracoid to be rearticulated graphically, the reconstruction of which is presented in Figure 10B.

Based on this reconstruction, which largely agrees with that given by Welles (1962:fig. 5), the ventral rami of the scapulae are interpreted as lacking any contact along the ventral midline. The rami also lack a prominent, posteriorly directed prong that extends towards, or makes contact with, the coracoids. Thus, a pectoral bar is clearly absent in *Callawayasaurus*.

The coracoids of *Wapuskanectes* display a unique combination of characters, including the presence of a complete pectoral bar, a well-developed anterior process along the midline, a prominent ventral midline process, and a fully enclosed intercoracoid vacuity. Among Cretaceous elasmosaurs, only *Elasmosaurus*
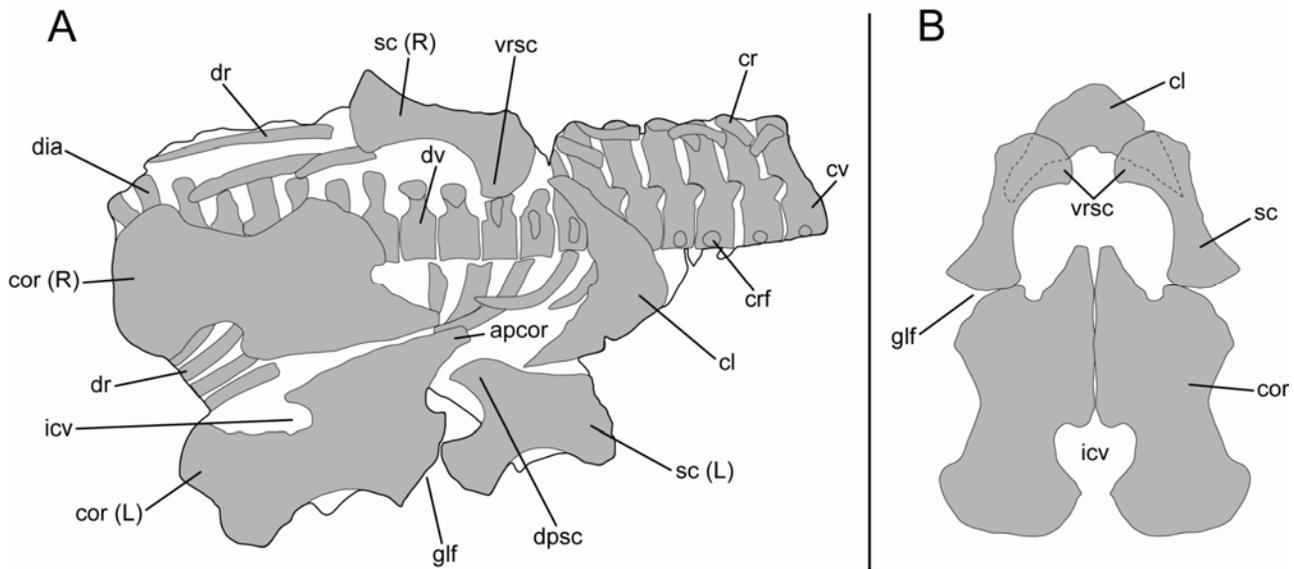
FIGURE 10. Assembled blocks of UCMP 38349, holotype specimen of *Callawayasaurus colombiensis*, **A**, showing a ventral view of the semi-articulated pectoral girdle, articulated posterior cervical and dorsal vertebrae, and associated ribs. Anterior is to the right and unshaded areas represent matrix. Reconstruction, **B**, of the pectoral girdle of *Callawayasaurus colombiensis*, in ventral view. Anterior is to the top. **Abbreviations**: **apcor**, anterior process of coracoid; **cl**, clavicle; **cor**, coracoid; **cr**, cervical rib; **crf**, cervical rib facet; **cv**, cervical vertebra; **dia**, diapophysis; **dpsc**, dorsal process of scapula; **dr**, dorsal rib; **dv**, dorsal vertebra; **icv**, intercoracoid vacuity; **L**, left; **R**, right; **sc**, scapula; **vrsc**, ventral ramus of the scapula.

and *Libonectes* have a complete pectoral bar. Several taxa, including *Callawayasaurus*, *Aphrosaurus*, *Morenosaurus*, *Styxosaurus glendowerensis*, and CM Zfr 145 possess a well-developed anterior process of the coracoid along the midline, but lack a pectoral bar. It should be noted that the presence of this process may be precursory to the formation of a complete pectoral bar in older adults of some taxa, but can also exist, at least hypothetically, in the absence of a pectoral bar. This process is absent in *Hydrotherosaurus*, *Hydralmosaurus*, *Styxosaurus snowii*, and *Thalassomedon*. The presence of this feature in *Brancasaurus* is uncertain.

Probably the most conspicuous and unique feature of the ventral surface of the coracoids of *Wapuskanectes* is the very pronounced ventral process along the midline. A process of similar size and shape is not found in any other described elasmosaur, although most elasmosaurs do possess a thickening of the coracoids along the midline symphysis in this region. The holotype of *Hydralmosaurus serpentinus*, AMNH 1495, shows "… extreme thickening in the midline and consequent development of a great ventral keel 13 cm deep. I know of no other comparable structure in any other elasmosaur." (Welles, 1952:64–65). Welles' characterization of this structure as a "keel", rather than a distinct process, suggests morphological dissimilarity to *Wapuskanectes*. The coracoids of CM Zfr 145 most closely resemble those

of *Wapuskanectes* in possessing a more discrete process, or "spike" along the ventral midline. However, the coracoid process of this temporally much younger specimen (late Maastrichtian) is not as large as that of *Wapuskanectes*, and the appendicular skeleton also differs markedly in a variety of other aspects, especially in its scapular and humeral morphology.

Cretaceous elasmosaurs, at least for taxa represented by adequate material, all possess a cordiform intercoracoid vacuity, in contrast to Cretaceous short-necked polycotylids that lack large openings along the midline (although they often have much smaller perforations). The overall morphology of the intercoracoid vacuity is relatively consistent among taxa; the greatest variation exists with respect to its posterior border. Some taxa, including *Aphrosaurus* and *Hydrotherosaurus*, possess an open intercoracoid vacuity, in which the coracoids do not meet along the midline posterior to the vacuity. In other taxa the coracoids nearly meet caudad to the vacuity, as in *Callawayasaurus*, *Libonectes*, and possibly CM Zfr 145. Only in *Brancasaurus* and an adult specimen of *Styxosaurus snowii*, SDSM 451, do the coracoids appear to meet fully along the midline and completely close the vacuity. However, in *Brancasaurus*, the midline contact of the coracoids posterior to the vacuity is much shorter than that of *Wapuskanectes*, and the posterior portions of the coracoids are also considerably narrower, mediolaterally. Undoubtedly,

the extent to which the coracoids bound the posterior margin of the intercoracoid vacuity is subject to ontogenetic variation; however, in no taxa do the coracoids enclose the vacuity to the same extent as they do in *Wapuskanectes*.

Finally, a unique character of the coracoids of *Wapuskanectes* is the presence of perforations along the posterior midline. One of the characters cited by O'Keefe (2001:22) as being diagnostic of the Polycotylidae is the presence of "…posterior perforations in the coracoid." The taxonomic utility and ontogenetic variation exhibited by this character within Plesiosauria needs reassessment in future phylogenetic analyses.

Salient features of the humeri are often subtle, making comparisons between taxa difficult. However, the humerus of *Wapuskanectes* clearly differs from that of *Hydralmosaurus*, *Morenosaurus*, and, to a lesser degree, *Libonectes*, which possess a marked postaxial extension at its distal end. Unlike *Wapuskanectes*, *Styxosaurus snowii* (represented by SDSM 451) and *Hydrotherosaurus* lack postaxial accessory facets and bear much more pronounced anterior knees (a convexity along the distal, preaxial margin of the propodial, which does not participate in the articular surface). The humerus of *Brancasaurus* is relatively elongate and gracile when compared to that of *Wapuskanectes*, and also lacks a postaxial accessory facet. Although more similar in overall morphology, both the holotype and paratype specimens of *Callawayasaurus* also lack distinct postaxial accessory facets, as does *Terminonatator*. Although well-developed rugosities on the ventral surface of the humerus have been noted for a number of elasmosaurid taxa, including *Callawayasaurus*, the large postaxial extension seen in *Wapuskanectes* is also unique.

In summary, *Wapuskanectes* most closely resembles *Callawayasaurus*, especially in regard to the structure of the pectoral girdle, but the taxa also differ in a number of features. It is also significant that *Callawayasaurus*, recovered from a lower Aptian succession in Colombia, shares a relatively close temporal distribution with *Wapuskanectes* (lower Albian), a separation of approximately nine million years.

Comparison with TMP 99.68.01—Special consideration is given here to a comparison between the holotype of *Wapuskanectes*, TMP 98.49.02, and TMP 99.68.01. TMP 99.68.01 (Figure 11) comprises the incomplete, partially articulated remains of an elasmosaurid plesiosaur found approximately 1.5 km south of TMP 98.49.02, and within the same 2.5 meter thick stratigraphic unit. With reference to elements preserved, the two specimens overlap in several areas, including dorsal vertebrae and ribs, gastralia, coracoids, and to a lesser extent scapulae and possibly

humeri. The primary difference between the two taxa is their relative ontogenetic state; TMP 98.49.02 represents a much larger, fully mature individual than TMP 99.68.01, which is relatively small and osteologically immature. A full description of TMP 99.68.01 will be presented elsewhere.

ELASMOSAURIDAE Cope, 1869
gen. et sp. indet.

Referred Material—TMP 99.68.01 (Figure 11).
Locality and Horizon—West side of the Syncrude Base Mine, near Ft. McMurray, Alberta, Canada (Lat. 57° 02′ 13.17′′ N, Long. 111° 66′ 78.59′′ W); Wabiskaw Member of the Clearwater Formation, lowermost Albian, Lower Cretaceous.

Discussion—Despite their age differences, TMP 98.49.02 and TMP 99.68.01 share a number of morphological similarities suggesting that they are possibly conspecific. The general proportions of their dorsal vertebrae are similar and differ primarily in the size of their neural spines. With respect to dorsal ribs, TMP 99.68.01 possesses a unique blade-like expansion along the distal margin of the shaft; unfortunately, TMP 98.49.02 does not expose the equivalent anterior dorsal ribs. Differences in the more posterior dorsal ribs were not evident.

The most significant similarities are in the morphology of the coracoids. Similarly to TMP 98.49.02, TMP 99.68.01 possesses a prominent anterior expansion of the coracoids along the midline. TMP 99.68.01 also exhibits a pronounced thickening of the coracoid along the ventral midline, although it does not culminate in as prominent a process as that seen in TMP 98.49.02. Both share a cordiform intercoracoid vacuity, although that of TMP 99.68.01 is proportionately larger. Considering its relatively young ontogenetic state, the posterior end of the coracoid of TMP 99.68.01 also shows a considerable degree of medial expansion compared to that of most elasmosaur taxa, nearly closing the intercoracoid vacuity caudad. The preserved portion of the scapula in TMP 99.68.01 most closely resembles the dorsal process of TMP 98.49.02, but is broader anteroposteriorly. In the absence of a positive identification of the poorly preserved propodial of TMP 99.68.01, comparisons are not possible.

When comparing the two specimens, it is evident that most of the morphological disparity is explainable by ontogenetic, and possibly sexual, differences. This includes: an increase in the height of the neural spines of dorsal vertebrae; an expansion of the anterior process of the coracoid, ultimately resulting in the formation of a complete pectoral bar; the development of a prominent ventral coracoid process; complete posterior closure of the intercoracoid vacuity; and
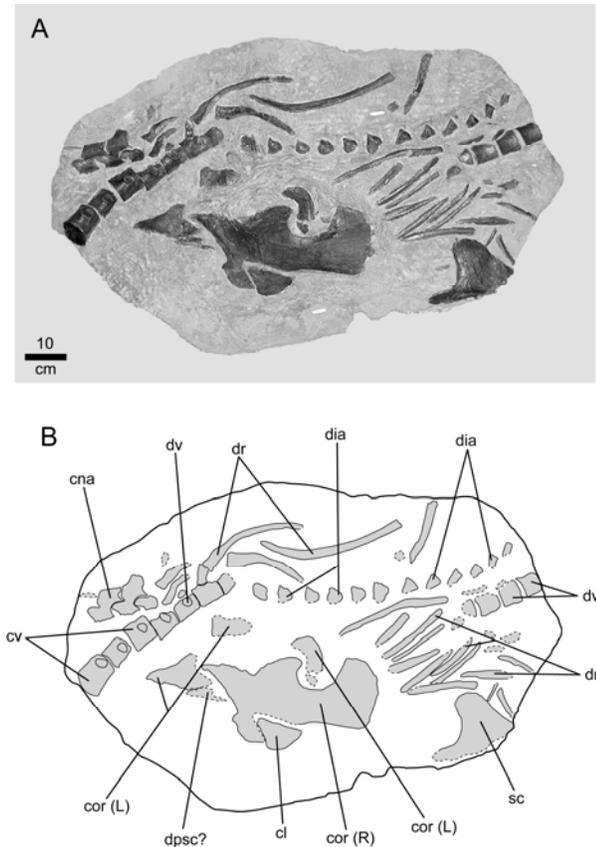
FIGURE 11. Photograph, **A**, and interpretation, **B**, of the dorsal surface of TMP 99.68.01. Anterior is to the left in both figures; dashed lines represent elements that extend into the matrix. **Abbreviations**: **cl**, clavicle; **cna**, cervical neural arch; **cor**, coracoid; **cv**, cervical vertebra; **dia**, diapophysis; **dpsc**, dorsal process of scapula; **dr**, dorsal rib; **dv**, dorsal vertebra; **L**, left; **R**, right; **sc**, scapula.

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possibly the development of perforations posteriorly along the coracoid midline. Many of these morphological modifications, especially those of the coracoids, are consistent with those observed in other plesiosaur taxa (Brown, 1981; Carpenter, 1999). However, pending more discoveries from the Wabiskaw Member and a better understanding of ontogenetic changes in the plesiosaur skeleton, we defer from formally referring TMP 99.68.01 to *Wapuskanectes*.

In addition to these morphological similarities, it is also notable that the fossiliferous unit of the Wabiskaw Member has produced a total of at least three reasonably complete elasmosaurid plesiosaurs, TMP 96.97.01 (Druckenmiller and Russell, 2003), TMP 98.49.02, and TMP 99.68.01. Given the highly restricted temporal and geographic distribution of the fossiliferous unit, it seems unlikely that all three specimens represent separate elasmosaurid taxa.

CONCLUSIONS

Elasmosaurs were a prominent and diverse group of marine vertebrates in the Late Cretaceous seas, but their distribution and diversity in the Early Cretaceous remains poorly known. In addition to being the oldest Cretaceous elasmosaur described to date from North America, *Wapuskanectes betsynichollsae* sheds new light on the composition of the vertebrate fauna of the Boreal Sea, prior to the establishment of the Late Cretaceous Western Interior Seaway. New elasmosaur material from the Wabiskaw Member may also provide a basis for a better understanding of ontogenetic changes within Plesiosauria. Although *Wapuskanectes* expresses features diagnostic of Cretaceous Elasmosauridae, its systematic position relative to other elasmosaurids, as well as a more precise definition of this clade, is left open pending a broader consensus of plesiosaur phylogeny.

ACKNOWLEDGEMENTS

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