PLESIOSAURS FROM THE UPPER CRETACEOUS (CENOMANIAN–TURONIAN) TROPIC SHALE OF SOUTHERN UTAH, PART 2: POLYCOTYLIDAE

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ABSTRACT—Recent fieldwork in the Tropic Shale of southern Utah has resulted in the recovery of several specimens of short-necked plesiosaurs including both polycotylid plesiosauroids and pliosaurids. This report focuses on the former, whereas the latter are discussed in an accompanying paper. Although the Late Cretaceous Cenomanian/Turonian Stage boundary falls within the lower few meters of the Tropic Shale, all but one of the specimens were found in lower Turonian strata based on molluscan assemblages found in direct association with the skeletal material. The plesiosauroid family Polycotylidae is represented by at least three taxa: (1) the 'typical' late Cenomanian/early Turonian *Trinacromerum*; (2) *Eopolycotylus rankini*, gen. et sp. nov., a new genus and species that shares synapomorphies with the late Santonian/early Campanian *Polycotylus latipinnus*; and (3) *Palmula quadratus*, gen. et sp. nov., another new taxon that shares synapomorphies with unnamed taxa from the late Cenomanian of South Dakota and Japan. Cladistic analysis supports the division of the Polycotylidae into two new subfamilies, here designated the Polycotylinae and the Palmulainae. The Turonian plesiosaur fauna of the Tropic Shale, and consequently the large vertebrate fauna of the Cretaceous Western Interior Seaway, is considerably more diverse than previously realized, and there is no indication that this fauna suffered any negative consequences as a result of global scale oceanographic events, including marine extinctions, that transpired during late Cenomanian-early Turonian time.

INTRODUCTION

Nations and Eaton (1991) assembled a variety of independent studies on the Mancos Shale at Black Mesa, northeastern Arizona, encompassing subjects such as lithostratigraphy, invertebrate biostratigraphy, foraminiferal ecology, and paleoceanography, that resulted in significant contributions to our knowledge of the western margin of the Cretaceous Western Interior Seaway (KWIS) during late Cenomanian through early Turonian time. Noticeably absent in their volume, however, are detailed reports of marine vertebrates from this interval. Glimpses of marine vertebrate diversity from the Black Mesa section were later provided by Lucas (1994), who described some plesiosaur remains, and Elliott et al. (1997) who described the remains of a marine turtle.

About 100 km northwest of Black Mesa, in southern Utah, are extensive exposures of equivalent aged deposits that constitute the Tropic Shale, also from which few, if any, vertebrates have been noted in detail. However, recent field work ongoing since 1999 by personnel from the Museum of Northern Arizona (MNA), Flagstaff, and Grand Staircase-Escalante National Monument, Kanab, Utah, has found that there is a diverse and important reptilian fauna in these mainly early Turonian-aged marine deposits. Several specimens of polycotylid plesiosauroids and pliosaurids have been discovered, in addition to marine turtles; the Tropic Shale has even yielded a therizinosaurid dinosaur (Albright et al., 2001; Gillette and Albright, 2003; Gillette et al., 2001a, 2001b). In an accompanying article in this issue

(Albright et al., 2007), we report on the pliosaurs and work on the therizinosaur is currently in progress. In this article, we report on the polycotylid plesiosaurs, two of three of which are new taxa.

FIELD AREA

Details of our study area, including the geological and stratigraphic setting, are provided in the accompanying article in this issue on the pliosaurs (Albright et al., 2007). Briefly, however, this study focused on the vast exposures of Tropic Shale that crop out along the southern escarpment of the Kaiparowits Plateau in southern Utah east and west of the small community of Big Water, west of Lake Powell (Fig. 1). These exposures, which average about 200 m thick, fall within the boundaries of Grand Staircase-Escalante National Monument (GSENM), Utah School and Institutional Trust Lands, and Glen Canyon National Recreation Area (GCNRA). Permits from the pertinent agency (Bureau of Land Management, Utah Geological Survey, or National Park Service, respectively) are required for prospecting and collection of fossils.

Fortunately, the detailed biostratigraphic framework previously constructed for the Mancos Shale at Black Mesa (Kirkland, 1991, 1996; Olesen, 1991) is also applicable to the Tropic Shale in our field area. This, together with the numerous prominent bentonite and limestone concretion marker beds in the Tropic Shale that are correlated across several western states where deposits of the Greenhorn Seaway are exposed (Elder, 1985, 1991; Hattin, 1971, 1985; Obradovich, 1993; Pratt et al., 1985), results in the ability to place all our finds into a high-resolution biochronostratigraphic context. Although the Tropic Shale spans the
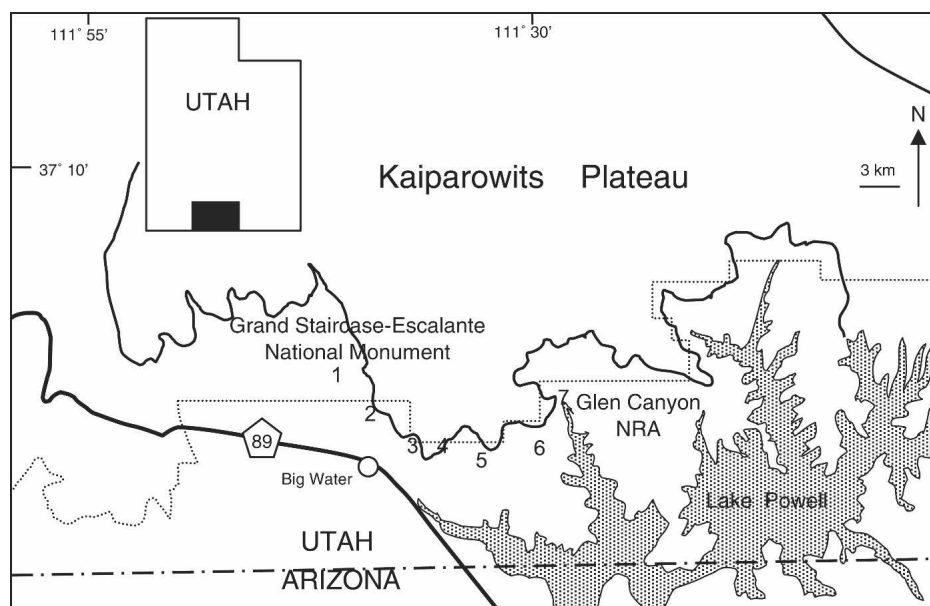
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FIGURE 1.   Area of study, primarily along southern border of Kaiparowits Plateau. Finely dotted line separates Grand Staircase-Escalante National Monument from Glen Canyon National Recreation Area. Note: although not delineated in the figure, there is also a small section of Utah State Institutional and Trust Land immediately north of Big Water and south of the Monument boundary. Numbers refer to approximate locations where stratigraphic columns (Fig. 2) were measured.

late Cenomanian *Sciponoceras gracile* through the middle Turonian *Prionocyclis hyatti* North American Ammonoid Biozones (Cobban and Hook, 1984), or from approximately 94 to 90.5 Ma (Gradstein et al., 1995; Ogg et al., 2004), this study focused primarily on the Lower Turonian part of the section, or from approximately 93.5 to 92 Ma. Figure 2 shows several measured stratigraphic sections in which are placed the vertebrate localities discussed in this report, as well as those noted in the accompanying article on the pliosaurid *Brachauchenius*. Stratigraphic positions of the turtles recovered over the course of this project, as well as the therizinosaur, are also shown. Detailed locality and stratigraphic information is on file at the Department of Geology, Museum of Northern Arizona (MNA), Flagstaff.

ABBREVIATIONS

All specimens described are currently housed at the Museum of Northern Arizona in the vertebrate paleontology collection (**MNA V**), Flagstaff, unless otherwise noted, and all measurements are metric.

Institutional Abbreviations—AMM, Adams Memorial Museum, Deadwood, South Dakota; **FHSM**, Fort Hays Sternberg Museum, Hays, Kansas; **UMUT MV**, University Museum, University of Tokyo, Japan; **USNM**, United States National Museum, Smithsonian Institution, Washington, D.C.

Other Abbreviations—HO, highest stratigraphic occurrence; **LO**, lowest stratigraphic occurrence; **LAD**, last appearance datum follow Aubry (1997).

SYSTEMATIC PALEONTOLOGY

In this report we follow the classification of O'Keefe (2000, 2001, 2004), as well as the conclusions of O'Keefe (2004), Carpenter (1996), Storrs (1999), and Sato and Storrs (2000) that *Trinacromerum* and *Dolichorhynchops* are separate genera. We consider *Trinacromerum bonneri* Adams (1997) a junior synonym of *Polycotylus latipinnus* Cope, 1869.

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943
POLYCOTYLIDAE Williston, 1908
PALMULAINAE, subfam. nov.

Diagnosis—Small to moderate polycotylid plesiosaurs with distinctly polygonal (i.e., nearly equi-dimensional) radius and ulna in the forelimb, and tibia and fibula in the rear limb, in contrast to all other known polycotylids in which the previously noted elements are relatively short and broad.

Type and Only Included Genus—*Palmula*, gen. nov.

Included Unnamed Specimens—AMM 98.1.1, early late Cenomanian of South Dakota (Schumacher and Bell, 1999; Von-Loh and Bell, 1998); UMUT MV 19965, late Cenomanian of Japan (Sato and Storrs, 2000).

PALMULA, gen. nov.

Type and Only Known Species—*Palmula quadratus*, sp. nov.
Diagnosis—As for the type species.

PALMULA QUADRATUS, gen. et sp. nov.
(Figs. 3–6)

Holotype—MNA V9442, anterior part of rostrum, anterior part of mandible, fragment of articular, fragment of occipital condyle, partial right coracoid, partial right scapula, complete right forelimb, right and left ilium, right and left pubis, right and left ischium, complete right hindlimb, one cervical vertebra, 19 dorsal vertebrae, three sacral vertebrae, 11 caudal vertebrae, several ribs.

Type Locality—MNA LOC 1494, Grand Staircase-Escalante National Monument, Kane County, Utah.

Stratigraphic Occurrence—Tropic Shale, approximately 18 m above local top of Dakota Formation; approximately 12.3 m above top of Bentonite B; 1.7 m below top of Bentonite C (Fig. 2, column 1); middle to upper part of the *Pseudoaspidoceras flexuosum* Ammonoid Biozone.
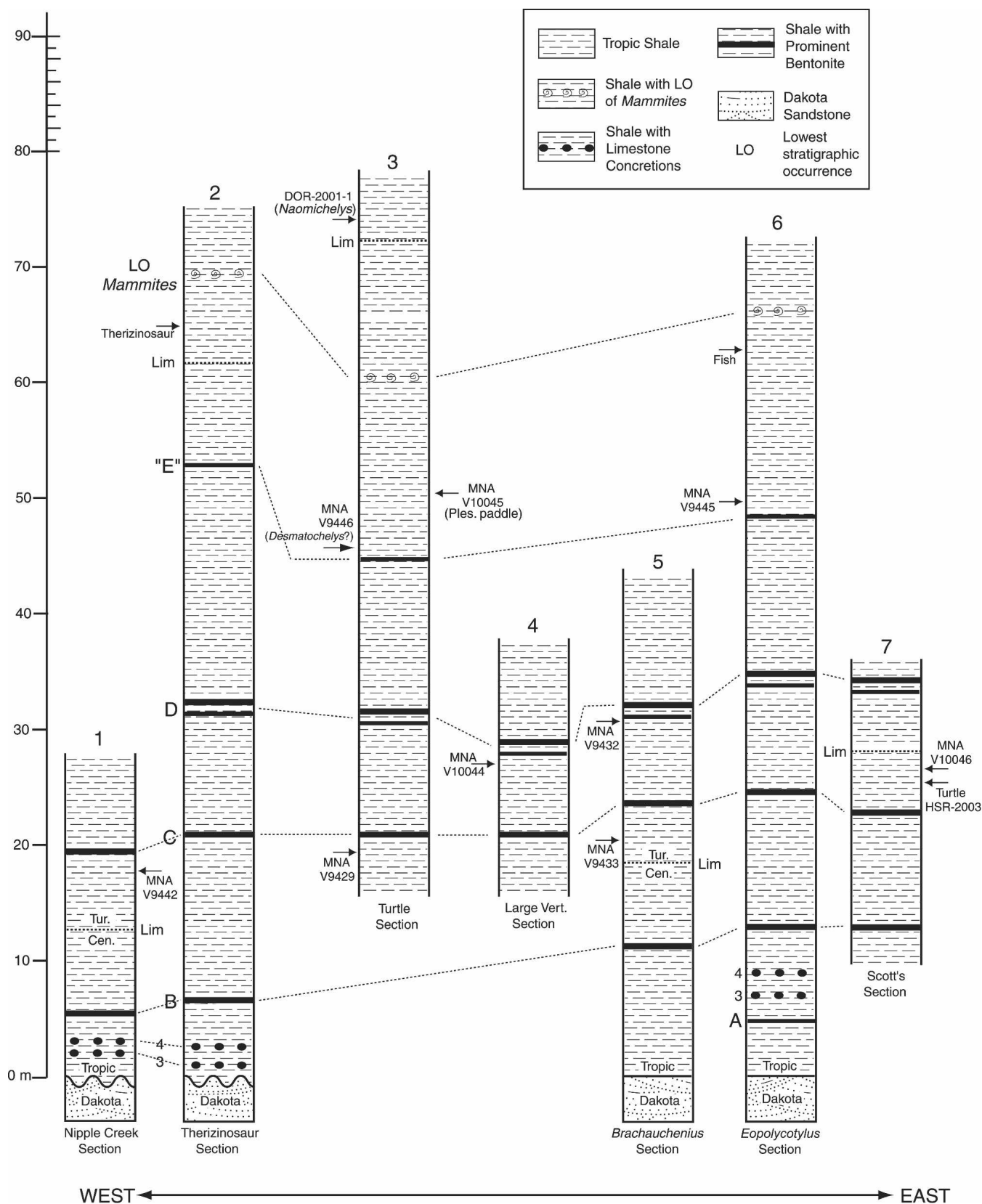
FIGURE 2. Stratigraphic columns of lower Tropic Shale from which selected vertebrate remains (including turtles and therizinosaur) were recovered. Arrows designate vertebrate sites; capital letters **A**–"**E**" designate prominent bentonite marker beds; **Lim** refers to selected limonite marker beds; numbers **3** and **4** designate limestone concretion beds; numbers above each column refer to corresponding localities on index map (Fig. 1). Cenomanian-Turonian boundary in sections 1 and 5 based on in situ biostratigraphic analysis. Distance from west to east approximately 40 km.
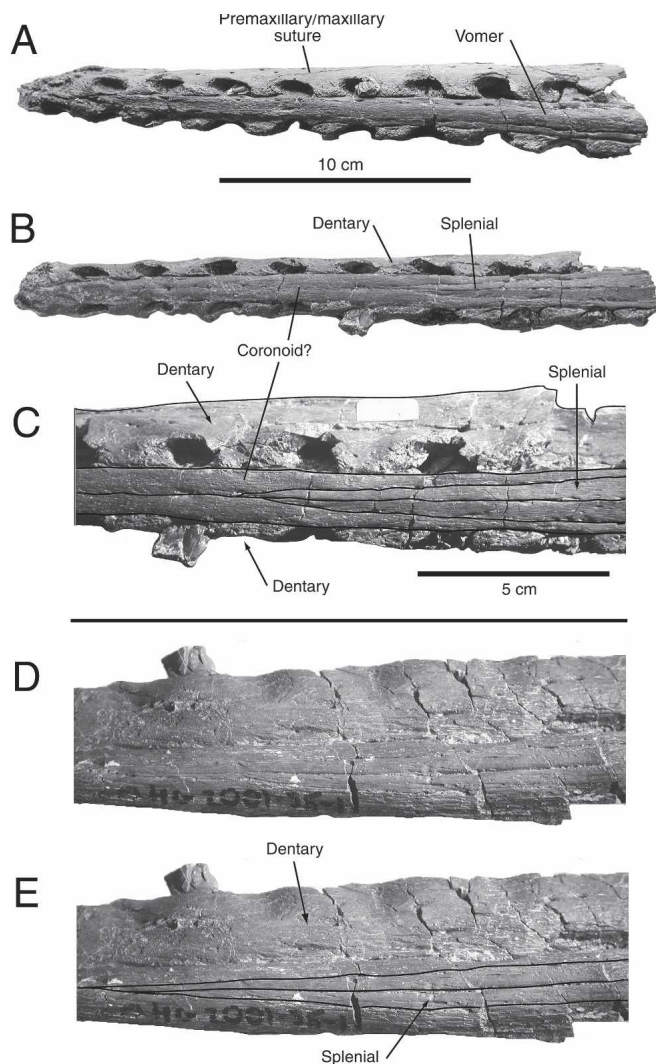
FIGURE 3.   *Palmula quadratus*, sp. nov., MNA V9442. **A**, upper snout showing premaxillary, maxillary, and vomer; **B**, dorsal surface of anterior part of mandible; **C**, close-up view of same with various bones delineated; **D**, ventral surface of anterior part of mandible; **E**, same view with splenial delineated.
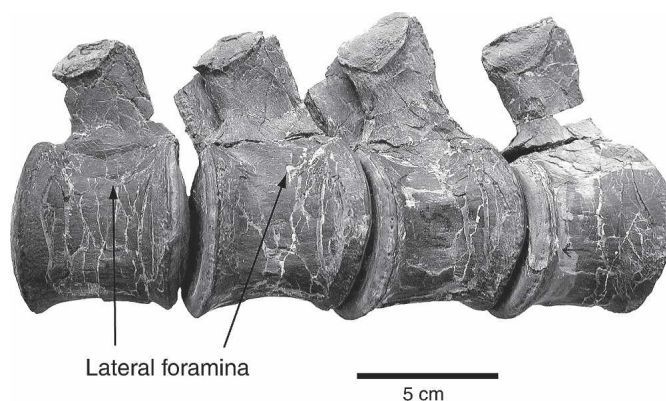

FIGURE 4.   *Palmula quadratus*, sp. nov., MNA V9442. Selected dorsal vertebrae. View is of the ventral surface looking dorsally at transverse process; anterior to right.

Age—Very early Turonian.

Diagnosis—Small as an adult; smaller than AMM 98.1.1 from South Dakota and UMUT MV 19965 from Japan; distinctly polygonal (i.e., nearly equi-dimensional) radius, ulna, tibia, and fibula, unlike short and broad epipodials of all other polycotylids exclusive of Palmulainae, subfam. nov.

Etymology—*Palmula*, Latin for "blade of an oar" in reference to plesiosaur paddles; *quadratus*, Latin for "square" in reference to the equi-dimensional shape of, particularly, the radius and tibia.

Description and Comparisons

Skull and Mandible—Except for a fragment of the occipital condyle and what appears to be a fragment of the articular (recovered as float down-slope from the quarry), the only significant skull elements recovered are the anterior portion of the premaxillary/maxillary and the anterior portion of the mandible; both are distorted by transverse compression. The premaxillary/maxillary suture is immediately anterior to alveolus six, thus the premaxillary contained five teeth (Fig. 3A), as also seen in *Doli-*

chorhynchops osborni Williston, 1903, *Trinacromerum bentonianum* Cragin, 1888, and *Thililua longicollis*, a recently described polycotylid from the Turonian of Morocco (Bardet et al., 2003). From the tip of the snout to the suture measures about 11 cm. The vomer of *Palmula quadratus* extends anteriorly to about the second alveolus.

The mandible fragment is crushed laterally and broken off anterior to the point where the rami diverged; that is, the entire fragment is part of the symphysis (Fig. 3B). This preservation precludes a determination of the number of teeth in the symphysis, although there were at least 10 based on the number of alveoli in the fragment. On the dorsal surface of the mandible the splenial extends anteriorly to a point between alveoli six and seven (Fig. 3C). The distance from the anteriormost extent of this bone to the tip of the snout is 14.4 cm. On the ventral surface, the splenials extend far forward into the symphysis, anteriorly to a point even with the fifth alveolus (Fig. 3D, E); the distance from the anteriormost extent of the splenials to the tip of the snout is about 11.9 cm. This differs significantly from the condition in the paratype of *T. bentonianum* (O'Keefe, 2004), or in MNA V9445 (see below), where the splenials extend only a short distance into the symphysis. In *Thililua longicollis* the splenials extend "anteriorly to the tenth pair of teeth" (Bardet et al., 2003:311), and in *Dolichorhynchops* they extend anteriorly to about the seventh to ninth tooth position based on O'Keefe's (2004) description of FHSM VP404.

Although most teeth are missing, recovered fragments indicate that they closely resemble those of *Dolichorhynchops* and *Thililua*; they are slender, gracile, and striated around the circumference for approximately one third to one half the height of the crown, but smooth to very weakly striated for the distal one half to one third, with a weak posterior carina. The teeth of *Trinacromerum* are also gracile, but with coarser striations. Teeth of *Polycotylus* and the late Albian *Edgarosaurus muddi* Druckenmiller, 2002, are considerably more robust.

The fragment of the occipital condyle, noted previously, would have measured approximately 2.5 cm in diameter.

Vertebrae and Ribs—19 dorsal, three sacral, and 11 caudal vertebrae were recovered in articulation, and one cervical was recovered as float below the quarry, as were other small fragments. Therefore, an accurate vertebral count is not possible because all other cervicals are missing and it is not known how many anterior dorsals or posterior caudals might be missing. The dorsal vertebrae are somewhat deformed by burial, and two of the anterior dorsals are highly deteriorated. The centra are slightly amphicoelous and distinctly concave laterally, as in *Dolichorhynchops* and *Polycotylus* (Fig. 4); but they are not cylinder-
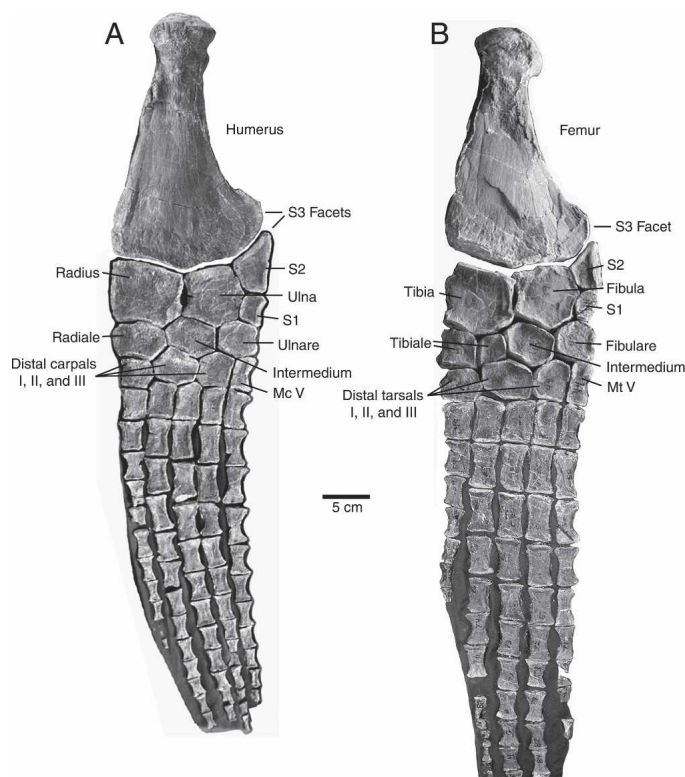
FIGURE 5. *Palmula quadratus*, sp. nov., MNA V9442. **A**, right fore-limb and **B**, right hindlimb; **S** = supernumerary; anterior to left; note epipodial foramen between radius and ulna/tibia and fibula. Photograph of hindlimb is a composite.
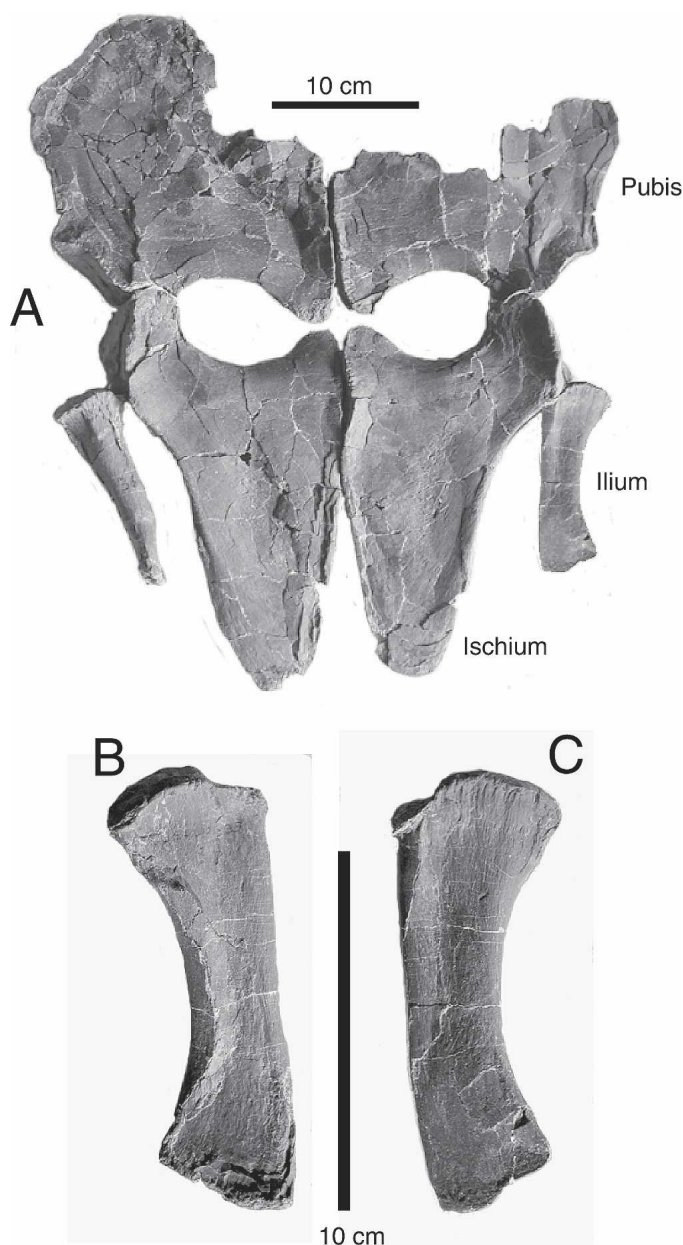

FIGURE 6. *Palmula quadratus*, sp. nov., MNA V9442. Pelvic girdle (dorsal, i.e., internal surface). **A**, left and right pubis, ilium, and ischium; **B** and **C**, right ilium in dorsal and ventral view, respectively.

like "with little constriction around the sides" as described by Carpenter (1996:282) for *Trinacromerum*. On the other hand, these vertebrae resemble those of *Trinacromerum* and *Thililua longicollis* in having a prominent nutritive foramen on each side of the centrum below the transverse process posteriorly to the third caudal. The nearly round articular surfaces of the centra are only slightly broader transversely than the centrum is long anteroposteriorly, and the height is just slightly less than the length. All are consistent in size and shape, and they average approximately 6 cm long by 6.5 cm wide by 5.5 cm tall. The neural arches are crushed and/or missing from most vertebrae, although it can be determined that they were entirely fused to the centra. Two are intact, with neural spines that measure 7.5 cm long on one specimen and about 9 cm long on the other. A pair of distinct facets for articulation of the chevrons first appears on the posterior part of the ventral surface of the sixth caudal vertebra. Although the chevrons are borne solely by one vertebra, as in *Dolichorhynchops*, the articulations differ from the latter taxon in that they do not impinge on the postero-ventral rim of the articulating surface of the centrum, i.e., the facets are only apparent on the postero-ventral surface of the centrum. In *P. lati-pinnus* and *Trinacromerum*, the chevrons are borne equally by adjacent vertebrae as seen by facets on the posterior and anterior edges of the rims of opposing faces (see Carpenter, 1996:fig. 4B, C; Schumacher and Everhart, 2005:fig. 12). All recovered ribs have a single head. Four posterior dorsal vertebrae have ribs directly associated with them. The shortest, posteriormost rib measures approximately 12.5 cm long. The three sacral vertebrae each have ribs that measure approximately 6 cm long.

Pectoral Girdle—The fragmentary portions of the coracoid and scapula bear few if any features of diagnostic utility. The

scapula fragment consists mainly of the process that includes the glenoid fossa and the surface that articulates with the coracoid. The coracoid fragment is distorted but it, too, preserves the humeral facet.

Forelimb—The right front paddle is nearly complete (Fig. 5A). Maximum length of the humerus (propodial) is approximately 28.8 cm; maximum width, measured across the distal end, is approximately 15.5 cm. The humerus does not show the sigmoidal shape typically seen in humeri of other polycotylids (O'Keefe, 2004; B. Schumacher, pers. comm., July 2004). The head, or proximal end, is distinctly demarcated into a relatively large capitulum, measuring 8 cm wide, and smaller tuberosity that measures about 3.5 cm wide; both are strongly pitted. The anterior margin of the humerus is essentially straight, whereas the posterior margin is concave in outline due to broad flaring of

the distal end. The distal margin of the humerus has distinct facets for the radius, ulna, and supernumerary II (the epipodials). There is also a small facet on both the humerus and the proximal end of supernumerary II for articulation with a supernumerary III, which was not recovered.

In marked contrast to all currently described North American polycotylids that have a radius and ulna that are distinctly broader than long (including the late Albian *Edgarosaurus muddi*, the Cenomanian/Turonian *Trinacromerum bentonianum*, the Turonian *T. kirki* Russell [1935], and the early Campanian *D. osborni* and *P. latipinnus*), those of *Palmula quadratus* are nearly as long as they are broad, resulting in a nearly equidimensional shape (Fig. 5A). In this respect, the epipodials closely resemble those of the Japanese polycotylid noted previously and they also resemble those of another new taxon from the early late Cenomanian of South Dakota (AMM 98.1.1) noted by VonLoh and Bell (1998), Schumacher and Bell (1999), and currently under study by Schumacher (B. Schumacher, pers. comm., July 2004).

The five-sided radius has distinct facets for articulation with the humerus, radiale, and intermedium, as well as a prominent antebrachial foramen between the radius and ulna (Fig. 5A). The latter feature also occurs in the South Dakota specimen, but does not appear to be as well developed in the Japanese specimen. The ulna has five facets for articulation with the humerus, intermedium, ulnare, and for supernumeraries I and II. Supernumerary I is roughly rectangular in shape and longer than wide. Supernumerary II is relatively large, subtriangular in shape, with a distinct facet at its proximal termination for articulation with supernumerary III, which was not recovered. Dimensions are provided in Table 1.

The row of proximal carpals, or mesopodials, includes three bones—the radiale, intermedium, and ulnare. The row of distal carpals includes four bones, distal carpals I, II, and III, and metacarpal V, the latter of which is phalangiform and shifted proximally into the distal carpal row as is typical of all plesiosaurs (Owen, 1865; Storrs, 1997:176). All phalanges are dorsoventrally compressed and proximo-distally elongate; all but the proximal row have concave anterior and posterior surfaces. Digit 1 has at least 10 phalanges (one distal phalanx may be missing); digit 2 has at least 13 phalanges (one or two distal phalanges are missing); digit 3 has at least 12 phalanges (one distal phalanx is missing); digit 4 has 13 phalanges; and digit 5 has 11 phalanges (one or two are missing).

Pelvic Girdle—All six elements of the pelvic girdle were found in articulation, although anterior parts of both pubes are missing (Fig. 6A–C). The medial edge of the ilium is nearly straight, the lateral edge is distinctly curved; the sacral end is blunt, slightly convex in outline, significantly broader than the width at mid-shaft, and, unlike that of *Polycotylus,* not at all

tapered (Williston, 1906); the distal end is broader (5.3 cm) than the sacral end (4.4 cm), convex in outline, elliptical in cross section, with a somewhat concave facet for articulation with the ischium (Fig. 6B, C). The left ilium is distorted relative to the undistorted right ilium, resulting in somewhat different measurements, especially for the sacral and distal ends. The length along the medial edge of the right and left ilia, respectively, is 12.4 and 12.2 cm; respective widths of the sacral end are 4.4 and 3.6 cm; respective widths of the distal end are 5.3 and 4.5 cm; and the width at mid-shaft of the right ilium is 2.9 cm. By comparison, the ilia of *Trinacromerum* are nearly straight with a somewhat rounded sacral end and a much narrower, rounder, less compressed shaft. Articulation to the sacrum may have been stronger in *Palmula* than in *Trinacromerum* or *Polycotylus*.

As in all polycotylids, the ischia are much longer than wide and they are longer than the pubes (Williston, 1908). Maximum length of the right ischium is approximately 26 cm, and the width is approximately 16 cm; maximum length of the left ischium is approximately 27.5 cm, and the width is approximately 16 cm (Fig. 6A; see Fig. 7 for points of measurement on specimens). The pubes also resemble those of other polycotylids, but differ in the following traits: there is only a slight concavity or sinuosity along the anterolateral border in *Palmula* (Fig. 6A), in contrast to the distinctly sinuous anterolateral border of *T. kirki* and *P. latipinnus* that results in a prominent, laterally directed extension (compare with Pl. 45 of Russell, 1935, and Pl. 111, fig. 1 of Williston, 1906). In *D. osborni* there is a flared, winglike lateral extension of the pubis that results in a nearly symmetrical spade, or mushroom-shaped outline (see Pl. XVI of Williston, 1903). Width of the left pubis from the anterior termination of the femoral facet to the medial articular suture measures approximately 17.7 cm; the same measurement for the right pubis is approximately 18.7 cm (see Fig. 7).

Hindlimb—The right rear paddle, like the front, is also nearly complete (Fig. 5B). Maximum length of the femur is approximately 27 cm; maximum width, measured across the distal end, is approximately 14 cm. Like the proximal end of the humerus, that of the femur also consists of a relatively large capitulum, measuring approximately 7.4 cm wide, and a smaller trochanter that measures 3.4 cm wide; both are strongly pitted. Also like the humerus, the anterior margin of the femur is nearly straight with a curved posterior margin due to broadening of the distal end. The distal margin of the femur has facets for the tibia, fibula, and supernumerary II, as well as a small facet for supernumerary III.

Like the radius and ulna noted previously, and, again, in contrast to other polycotylids, the tibia and fibula of MNA V9442 are nearly equidimensional rather than short and broad. The tibia is six-sided with distinct facets for articulation with the femur, intermedium, and *two* tarsals that occupy the position of the single tibiale in other polycotylid taxa (Fig. 5B). That is, *four* tarsals are present in the second row of elements (the mesopodials) rather than the three that more typically occur in previ-

TABLE 1. Measurements of forelimb elements for *Palmula quadratus* (cm).

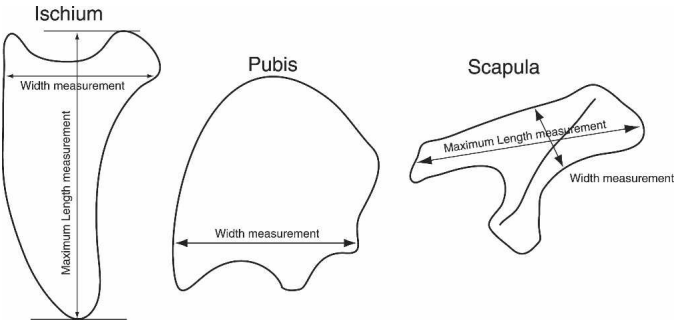| Element	Max. length	Max. width
Radius	7.3	7.9
Ulna	6.9	6.6
Supernumerary I	3.6	2.5
Supernumerary II	6.9	4.3
Radiale	4.3	6.2
Intermedium	4.0	7.7
Ulnare	4.2	4.3
Tibia	6.4	6.5
Fibula	6.4	6.0
Supernumerary I	3.0	2.0
Supernumerary II	5.0	3.0
Tibiale "I"	3.2	3.0
Tibiale "II"	2.5	2.5
Intermedium	4.0	4.5
Fibulare	4.0	3.8

FIGURE 7. Diagrammatic view of selected pectoral and pelvic elements illustrating points of measurement.

ously described North American polycotylids. As with the radius and ulna, there is a well-developed epipodial foramen between the tibia and fibula. Posterior to the two 'tibiale' tarsals is a hexagonal intermedium, slightly smaller than the intermedium of the forelimb, in turn followed by the fibulare. A third row of tarsals includes distal tarsals I, II, and III, and a phalangiform metatarsal V. The phalangeal count for the rear paddle follows: digit 1 has at least seven phalanges with one or two distal phalanges missing; digit 2 has at least 12 phalanges with one or two distal phalanges missing; digit 3 has at least 12 phalanges with at least two distal phalanges missing; digit 4 has 12 phalanges with one or two distal phalanges missing; and digit 5 has nine phalanges with possibly one distal phalanx missing.

Discussion—Although the small size of *Palmula quadratus* suggests a juvenile individual, full ossification of the neural arches to the centra of the vertebrae indicates that the remains belonged to an adult. Additional characters cited by Sato and Storrs (2000:910–911) to support the contention that the taxon they described from Japan was an adult are also present in the Tropic Shale specimen. These include "humerus with clearly defined articular facets, polygon-shaped paddle elements, ... and well preserved supernumeraries." Well-developed facets along the edges of the epi- and mesopodials in MNA V9442, as well as the near absence of intervening space between any of these elements, provides further support of full adult ossification (Storrs, 1997).

Palmula quadratus resembles *D. osborni* and *T. longicollis* in size, gracile tooth morphology, and the position of the premaxillary/maxillary suture between the fifth and sixth teeth. With *P. latipinnus*, *P. quadratus* shares the presence of four bones in the epipodial row (O'Keefe, 2004:337). The presence of four facets on the humerus for articulation with the epipodials is a character considered diagnostic of *P. latipinnus* (Storrs, 1999; O'Keefe, 2004), although Sato and Storrs (2000) noted four distinct articular facets on the humerus of the unnamed polycotylid from the Cenomanian of Japan (UMUT MV 19965), as well. (Note: according to B. Schumacher [pers. comm., July 2004], the 'forelimb' of UMUT MV 19965 may actually be a hindlimb, as it appears to lack the sigmoidal curvature typical of polycotylid humeri. On the other hand, lack of sigmoidal curvature may be characteristic of this new subfamily, as it is absent in the humerus of *P. quadratus*.) According to O'Keefe (pers. comm., 2005), however, facets for the supernumerary ossifications may be a function of ontogeny or, perhaps, small body size, as he noted that large individuals of *Trinacromerum* typically have well-developed facets, whereas adults of the smaller *Dolichorhynchops* do not.

The presence of four mesopodials in the hindlimb of MNA V9442 (due to two bones in the position of the tibiale) is a character that could be diagnostic of *Palmula quadratus*, but without a larger sample size to assess variability we currently consider this feature morphologically anomalous and characteristic only of this individual.

POLYCOTYLINAE, subfam. nov.

Diagnosis—Small to large polycotylid plesiosaurs with short and broad radius and ulna in forelimb and tibia and fibula in hindlimb, in contrast to the Palmulainae in which previously noted elements are distinctly polygonal, i.e., nearly equidimensional in length and width.

Included Genera—*Eopolycotylus*, gen. nov., *Polycotylus* Cope 1869, *Trinacromerum* Cragin 1888, *Dolichorhynchops* Williston 1903, and, provisionally, *Edgarosaurus* Druckenmiller 2002; (limbs not known for polycotylids *Georgiasaurus* Otschev 1976, 1977, *Sulcusuchus* Gasparini and Spalletti 1990, or *Thililua* Bardet et al., 2003).

EOPOLYCOTYLUS, gen nov.

Type and Only Known Species—*Eopolycotylus rankini*, sp. nov.

Diagnosis—As for the type species.

EOPOLYCOTYLUS RANKINI, gen. et sp. nov.
(Figs. 8–13)

Holotype—MNA V9445, anterior part of rostrum, anterior part of mandible, right and left clavicle with fused interclavicle, right and left scapula, right and left coracoid, right humerus, right and left ilium, right and left pubis, right and left ischium, right and left femur, most of right rear paddle, most of left rear paddle, three cervical vertebrae, 29 dorsal vertebrae (including three sacrals), one caudal vertebra, and several ribs.

Type Locality—MNA LOC 1496, Glen Canyon National Recreation Area, Kane County, Utah.

Stratigraphic Occurrence—Tropic Shale, approximately 48 m above local top of Dakota Formation, 42.7 m above top of Bentonite A, 14.8 m above top of Bentonite D, 16.5 m below LO of
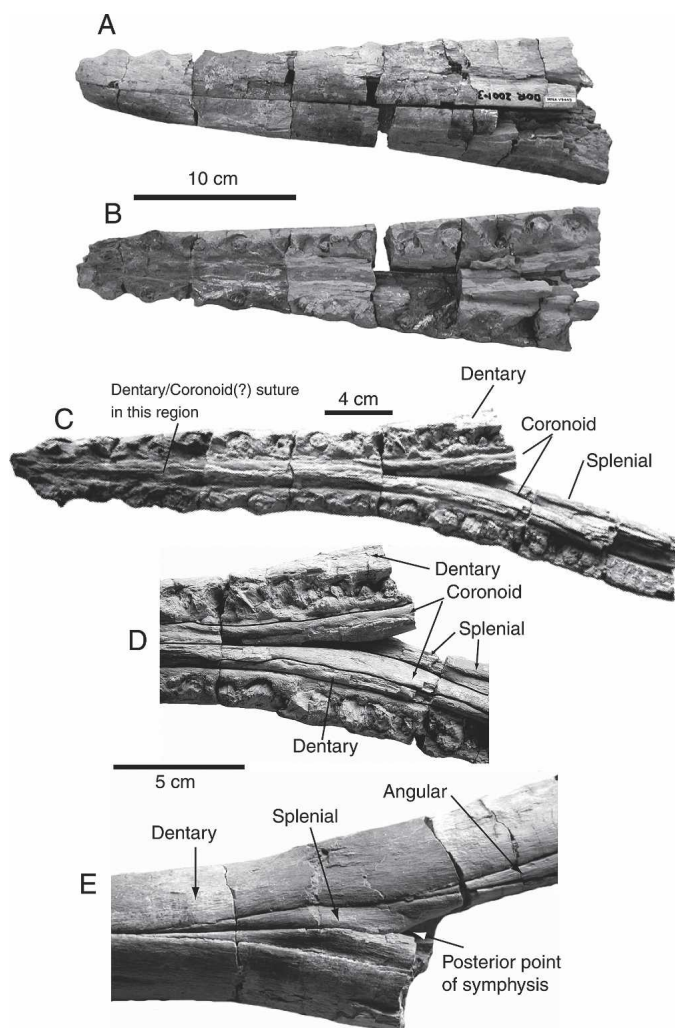

FIGURE 8. *Eopolycotylus rankini*, sp. nov., MNA V9445. **A**, dorsal surface of premaxillary/maxillary; **B**, ventral surface of same; **C**, dorsal surface of mandible; **D**, close up of same showing symphysis and relationship of dentary, coronoid, and splenial; **E**, ventral surface of mandible showing symphysis and relationship of dentary, splenial, and angular.
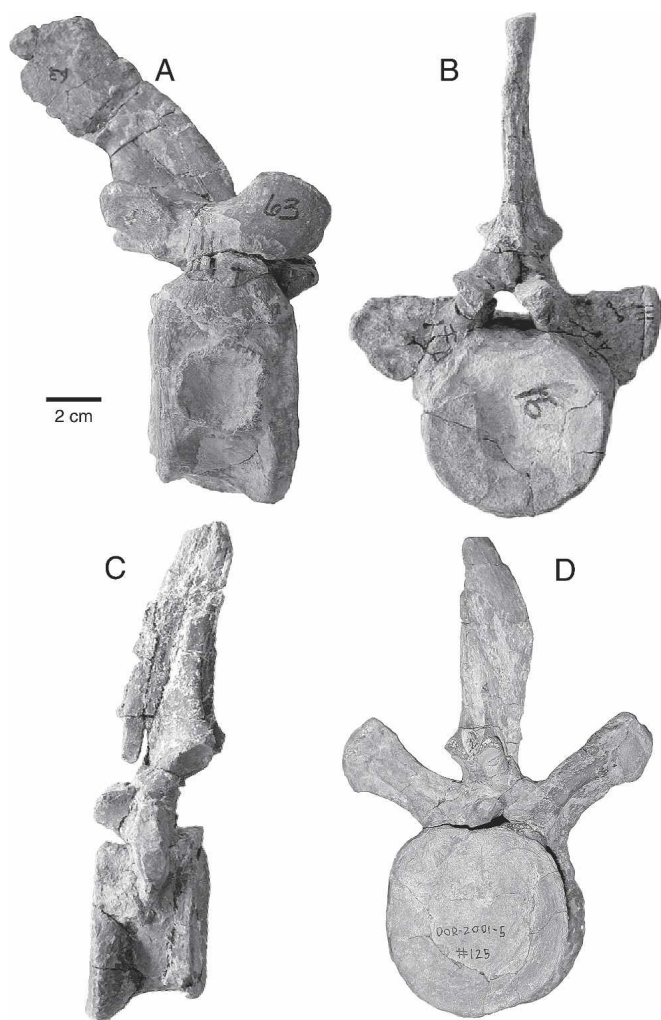
FIGURE 9. *Eopolycotylus rankini*, sp. nov., MNA V9445. **A**, cervical vertebra, lateral view, anterior to right; **B**, pectoral vertebra, anterior view; **C**, same vertebra, lateral view, anterior to left; and **D**, dorsal vertebra, anterior view.
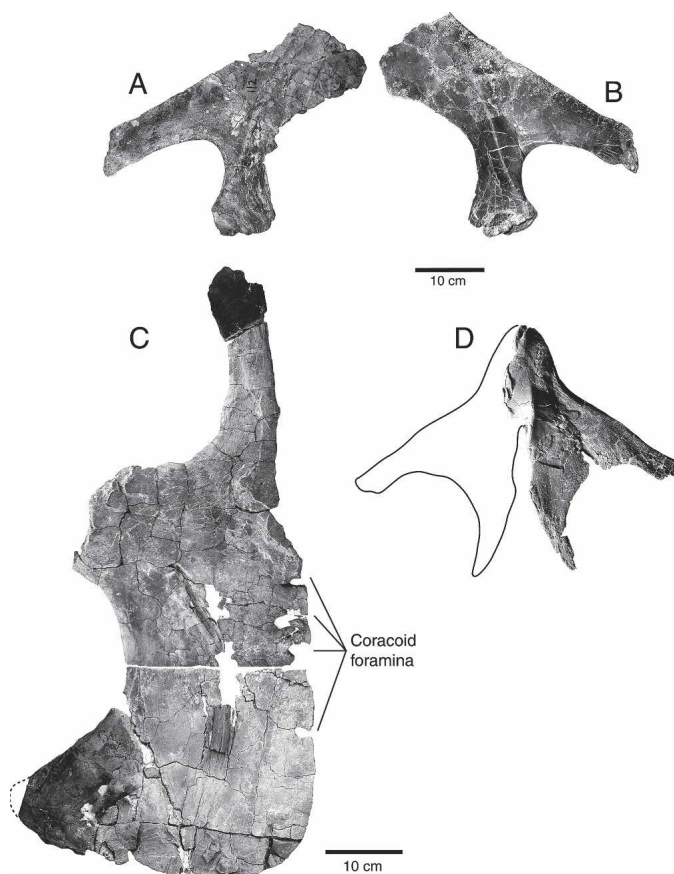

FIGURE 10. *Eopolycotylus rankini*, sp. nov., MNA V9445. Pectoral elements. **A**, right and **B**, left scapula, external view; **C**, right coracoid, external view; **D**, left clavicle and interclavicle, external view, with reconstructed outline of right clavicle.

Mammites; occurs with *Mytiloides mytiloides* and *Morrowites subdepressus*, but not with *Collignoniceras* (Fig. 2, column 6).

Two field locality numbers were originally assigned to this specimen due to the unusual circumstances under which it was found. Briefly, the quarry from which the bulk of the material was recovered is located at the base of a small ridge, and this site was allocated DOR-2001-5 after discoverer David O. Rankin from Big Water, Utah. However, Rankin first found maxilla and mandible fragments sitting exposed atop the ridge immediately above what would become the quarry site, and this ridge-top site was given the field number DOR-2001-3. Snout fragments were also scattered about the base of the ridge. Not until the slope of the ridge was raked by Rankin and M. H. Graffam for additional fragments of the snout was bone found in situ and the quarry opened. Based on additional details of the discovery, it appears that someone found the snout elements as float at the base of the ridge prior to Rankin's discovery, gathered pieces together and placed them atop the ridge where they could be easily relocated. Again, based on details of the discovery, as well as on the nature of preservation of the bones, we have no reservations whatsoever in assigning the snout elements from atop the ridge to the in situ individual recovered from the quarry below.

Age—Late Early Turonian.

Diagnosis—Moderately sized polycotylid plesiosaur; resembles *P. latipinnus* in having stout and coarsely striated teeth unlike *D. osborni* which has slender teeth with fine striations and *T. bentonianum*, which has slender teeth with coarse striations; resembles *P. latipinnus* and *D. osborni*, but differs from *T. bentonianum*, in having non cylinder-like, but laterally and ventrally constricted vertebral centra; resembles *P. latipinnus*, but differs from *D. osborni* and *T. bentonianum*, in having some centra compressed anteroposteriorly, although not to the extent seen in *P. latipinnus*; resembles *T. bentonianum* in having lateral foramina on dorsal vertebrae; interclavicle, clavicle, scapula, and coracoid very similar to *Dolichorhynchops* and *Trinacromerum*; humerus resembles *P. latipinnus* in having four facets for articulation of epipodials, but differs in lacking greatly broadened distal end; humerus also differs from *P. latipinnus* and all other polycotylids in having short, broad, dorsoventrally compressed, less sigmoidal neck; femur differs from *P. latipinnus* in shorter neck and lack of greatly broadened distal end; ilium nearly identical to *P. latipinnus* in curvature and tapered sacral end, unlike the straight ilium with expanded sacral end of *T. bentonianum*; pubis very similar to *T. bentonianum* in lacking scalloped anterolateral edge seen in *T. kirki* and *P. latipinnus*; ischia very similar to *Trinacromerum*, not tapered posteriorly as in *P. latipinnus*, not as broad anteriorly as in *D. osborni*.

Etymology—Eo, from eos, Greek for dawn, earliest, oldest; *rankini*, for David O. Rankin of Big Water, Utah, discoverer of this and several other important specimens from the Tropic Shale (see acknowledgments).
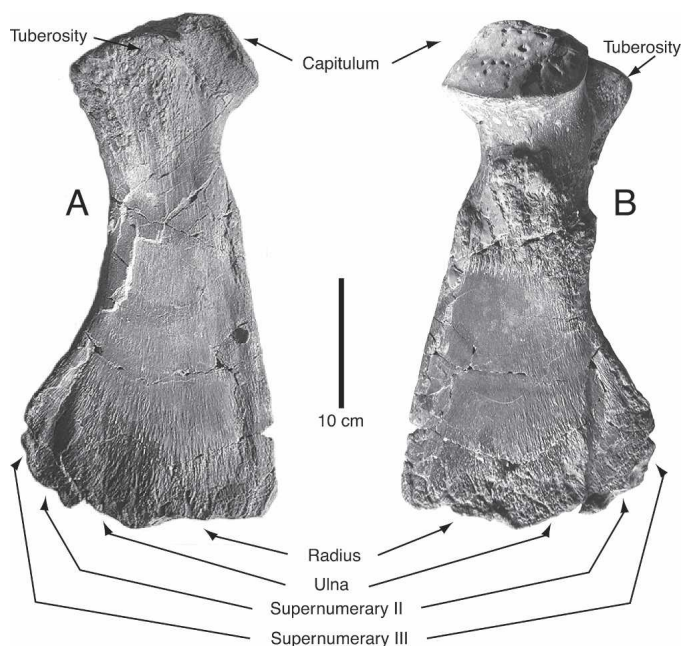
FIGURE 11. *Eopolycotylus rankini*, sp. nov., MNA V9445. Right humerus in **A**, dorsal, and **B**, ventral view.

Description and Comparison

Skull—Remains of the skull of MNA V9445 include only the anterior portion of the snout. The upper bones of the snout include the premaxillary, maxillary, and vomer, and they are broken posterior to about the 15th tooth position. The premaxillary/maxillary suture, as seen on the left side, occurs immediately anterior to alveolus six, resulting in five premaxillary teeth per side (Fig. 8A, B). The length from the tip of the snout to the premaxillary/maxillary suture is about 12 cm. Although this is only 1 cm longer than that of MNA V9442, MNA V9445 is a much larger, more robust individual.

The mandible includes the entire symphysis rather than just the anterior portion as was the case with *P. quadratus*. The rami begin to diverge (as seen from the dorsal aspect; Fig. 8C, D) at about the 12th tooth position, but the symphysis actually ends (as seen ventrally; Fig. 8E) at about the 14th to 15th tooth position (the symphysis bears 15 teeth), similar to *Thililua* and *Dolichorhynchops*. The length of the symphysis as measured along the ventral surface is about 28.4 cm. On the ventral surface, the splenials extend anteriorly to a point immediately posterior to alveolus eight, which is about 10 cm anterior to the posterior point of the symphysis. This is a much greater anterior extension than seen in the mandible fragment of the paratype of *T. bentonianum*, USNM 10946, but not nearly as far forward as the splenials extend in *P. quadratus*. The angular, on the other hand, which separates the dentary from the splenial, extends anteriorly only as far as the posterior point of the symphysis. In all other polycotylids, the angular extends into the symphysis, if even only minimally.

A cross-sectional view of the anterior part of the mandible of MNA V9445 shows what we think is a pair of bones separate from the dentaries that can only be anterior extensions of the coronoids (Fig. 8C, D). On the dorsal surface of the symphysis, at the anteriormost extent of these bones between the fourth and fifth alveoli, is a forked suture with the medial part of the dentaries that meet and extend to the tip of the mandible, not unlike that figured by Carpenter (1996:fig. 7D; 1997:fig. 3E, 6B) for the mandible of *Dolichorhynchops* (further discussion subsequently).
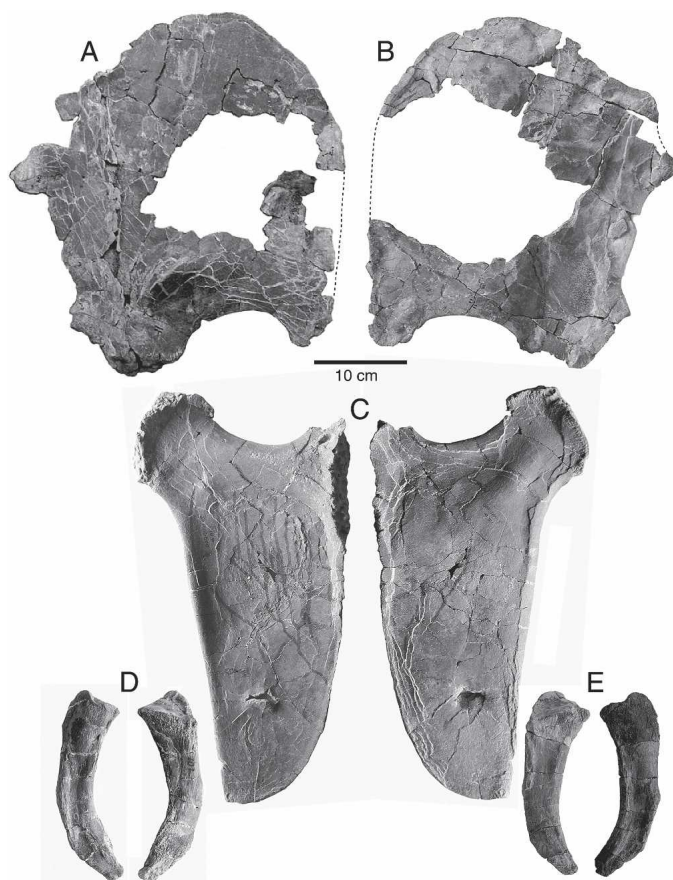

FIGURE 12. *Eopolycotylus rankini*, sp. nov., MNA V9445. Pelvic elements. **A**, right and **B**, left pubis, ventral view; **C**, left ischium in dorsal view (left) and ventral view (right); **D**, left ilium in dorsal view (left) and ventral view (right); **E**, right ilium in dorsal view (right) and ventral view (left).

Most of the teeth in both the upper and lower jaws are damaged and/or missing, but fragments indicate that they are considerably more robust (stout) than the gracile teeth of *Palmula*, *Dolichorhynchops*, *Trinacromerum*, and *Thililua*. On the lingual surface they are coarsely striated for about one-half the crown height, then very weakly striated, if at all, for the distal half; labially the enamel is smooth; there is also a weak posterior carina. This description closely matches that of Carpenter's (1996:268) for the teeth of *P. latipinnus*, although O'Keefe (2004:334), in his revised description of *P. latipinnus*, noted that the crowns of the teeth were "heavily striated all around."

Vertebrae and Ribs—Three cervical, 26 dorsal (including pectorals), three sacral, and one caudal vertebrae were recovered. All vertebrae are slightly amphoecoelus. Two of the cervicals include only the centra, which are slightly wider than tall and shorter than wide. One has a centrum that measures 7.0 cm wide, 6.3 cm tall, and 4.5 cm long. There are two small nutritive foramina on the dorsal surface of the centrum (the floor of the neural canal) and two larger foramina on the ventral surface that are separated by an anteroposteriorly oriented ridge. There are two large facets on the dorsolateral surface for articulation of the neural arch, which is missing, indicating that it was not yet fused to the centrum. Another cervical vertebra, however, has a fused neural arch (Fig. 9A), but the sutures are still clearly visible thus indicating that the individual was likely a late juvenile/early adult. Facets on the lower part of each side of the centrum indicate that the single-headed cervical ribs also were not fused.
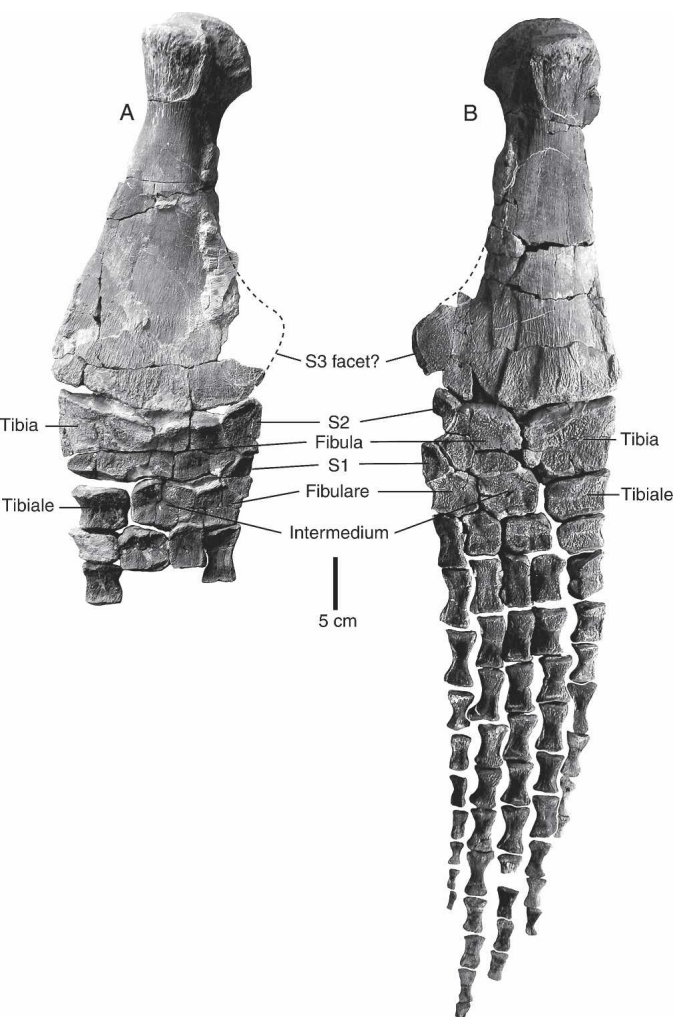
FIGURE 13. *Eopolycotylus rankini*, sp. nov., MNA V9445. **A**, left femur with epi- and mesopodials; **B**, right femur with podials and phalanges.

description, however, these centra are not "approximately half as long as high," nor would they be considered "extremely short." Neural spines are relatively narrow anteroposteriorly, slightly slanted posteriorly, and taper toward the tip, very similar to that illustrated by Storrs (1999:fig. 3) for *P. latipinnus*. Table 2 provides measurements for the dorsal centra that could be measured relatively accurately.

Two articulated series of dorsal vertebrae were recovered (one of 13, the other of 5, including the sacrals). Although laterally distorted, the centra appear restricted rather than cylinder-like, and all are about as long as they are wide. They measure between approximately 5.5 to 6.5 cm long by approximately 6 cm wide by 7.5 to 8.5 cm tall. What may be a single caudal vertebra represents the last of this articulated series, but the nature of chevron articulation cannot be determined.

Pectoral Girdle—All elements of the pectoral girdle were recovered (Fig. 10A–D). The clavicles were preserved folded together, one on top of the other. Although separated in preparation, the right clavicle and the right part of the interclavicle are distorted. The clavicles and interclavicle are strongly fused, but the suture between them remains visible. The clavicles closely resemble those of *Dolichorhynchops* and *Trinacromerum* in general morphology, as does the interclavicle in having an "anterior and posterior emargination, the latter forming part of a large interclavicular fenestra" (Storrs, 1999:11). From the anterior tip of the interclavicle to the distal tip of the coracoid process measures approximately 36.5 cm; from the anterior tip of the interclavicle to the distal tip of the scapular process measures approximately 32.3 cm.

The scapulae of MNA V9445, like the clavicles and interclavicle, closely resemble those of *Dolichorhynchops* and *Trinacromerum*. Maximum length from the end of the clavicular process to the end of the lateral process is approximately 42 cm for the right scapula and approximately 41 cm for the left. Maximum width as measured across the widest point of the clavicular process is 11 cm for the right and 12 cm for the left (see Fig. 7). There is a prominent scapular spine on the ventral (exterior) surface.

The coracoids have the general polycotylid morphology as seen in *Dolichorhynchops* and *Trinacromerum*, including an anterior, or clavicular, extension, as well as a prominent, smoothly rounded posterolateral flare, or extension. They do not, however, have the "tooth-like projections" on the anterior margin of the posterolateral extension described and illustrated by Williston (1903:42) for *Dolichorhynchops* and by Adams (1997) for 'Trinacromerum bonneri'; nor do they have the prominent posterior extension seen in *P. latipinnus* or *T. kirki*. This may, however, be a function of ontogeny. There are four large foramina located along the medial border. Total length of both coracoids is approximately 80 cm (preparation was not yet complete at the time of this writing) and maximum width (measured at the posterolateral extension) is approximately 39 cm.

The dorsal vertebrae, in contrast to those of *Trinacromerum*, are not cylinder-like (Carpenter, 1996), although like *Trinacromerum*, lateral foramina are apparent on the better preserved specimens. The centra are constricted laterally and ventrally, they are only slightly wider than tall, and some, but not all, resemble those illustrated by Storrs (1999:fig. 3) and noted by Williston (1906) and O'Keefe (2004) for *P. latipinnus* in being much shorter than wide (Fig. 9B–D). Unlike Storrs' (1999:12)

TABLE 2. Measurements of selected dorsal vertebrae (15–115, anterior dorsals) for *Eopolycotylus rankini*.

Field number of specimen	Max. width of centrum (cm)	Max. height of centrum (cm)	Max. length of centrum (cm)	Approx. height of neural spine (cm)
Vertebra no. 15	7.3	6.6	4.3	9.5
Vertebra no. 16	7.5	6.7	4.7	11.5
Vertebra no. 26	7.4	7.2	4.5–5.0	—
Vertebra no. 64	7.7	7.5	4.9	12.5
Vertebra no. 113	7.4	7.2	5.2	—
Vertebra no. 114	7.5	7.5	5.0	12.5
Vertebra no. 115	6.0	6.4	4.2	12.0
Vertebra no. 123	8.0	7.9	4.3	—
Vertebra no. 125	7.9	7.9	5.2	—
Vertebra no. 00	7.5	7.5	4.8	5.5

Height of neural spines is measured from the top of the neural arch between pre-zygopopheses.

Forelimb—The humerus measures approximately 37.5 cm long by approximately 18.4 cm wide. The proximal end differs from that of other polycotylids in several aspects. First, the neck of this element is very broad (approximately 10 cm) and distinctly non–shaft-like (Fig. 11) in contrast to the long, slender, relatively oval to rounded shaft more typical of other polycotylids. (Note: this does not appear to be due to dorsoventral compression; no other bones associated with this specimen were noticeably compressed, nor were limb elements from any of the other many specimens found in the Tropic Shale.) Second, the dorsal surface of the tuberosity is broad anteroposteriorly, compressed dorsoventrally, and shifted caudally to the extent that it forms the entire posterior margin of the proximal end when viewed from a dorsal or ventral aspect. The dorsal surface of the tuberosity is strongly textured for muscle attachment. The capitulum, on the ventral surface, is pitted and shifted anteriorly, opposite that of the tuberosity, such that only it forms the outline of the anterior surface at the proximal end. This anterior shift gives rise to a very subtle sigmoidal curvature in contrast to the significant curvature seen in *P. latipinnus*. Just distal to the capitulum, on the neck of the humerus, is a broad region of massive rugosities for muscle insertion.

On the distal end of the humerus are four distinct surfaces for articulation with the epipodials (Fig. 11A, B). The facet for articulation with the radius is nearly 10 cm long and that for the ulna about 6.5 cm. Those for articulation with supernumeraries II and III measure about 3 cm and 2.5 cm long, respectively. None of the epi- or mesopodials of the forelimb were recovered, although a few phalanges that likely belong to this paddle were found in the vicinity of the humerus in a random, disarticulated state.

Pelvic Girdle—All elements of the pelvic girdle were recovered (Fig. 12A–E). The left and right ilia have a maximum length of about 23 cm and 21.4 cm, respectively, and the entire element is curved; this contrasts with that of *Palmula*, which has a distinctly curved lateral edge, but a nearly straight medial edge. The proximal half of the element abruptly narrows to a tapered sacral end, which likely resulted in minimal articulation with the sacrum; in *Palmula* the sacral end is broad and blunt with an obvious facet for articulation with the sacrum (Fig. 12 D, E).

With its curved profile and tapered sacral end, the ilium of MNA V9445 is nearly identical to that of *P. latipinnus* (Williston, 1906:pl. III, fig. 1c). It also resembles the ilium of *T. kirki* in size and curvature (Russell, 1935:pl. 45), but the sacral end of *T. kirki* is not tapered. The ilia of *T. bentonianum* differ significantly in being straight rather than curved, in having a narrow, relatively rounded rather than compressed mid-shaft, and in having a blunt sacral end that is wider than the shaft.

The pubes are of general polycotylid shape as exemplified by *T. bentonianum*. Although the anterolateral edge is weakly scalloped, similar to *Palmula*, they lack the deeply scalloped edge of *T. kirki* and *P. latipinnus* (Fig. 12A, B). Maximum transverse width of the right and left pubes, respectively, is approximately 41 cm and 40 cm. Respective measurements for the femoral facets of both are 9 cm and 7 cm, and for the ischial facets, 6.5 cm and 7 cm.

The ischia are nearly identical to those of *T. kirki* in overall morphology and they differ from those of *P. latipinnus* in being less tapered posteriorly (Fig. 12C). They differ from ischia of *Dolichorhynchops* in being relatively narrower anteriorly, rather than distinctly broad. The left ischium measures 47.6 cm long by 24.0 cm wide (the right is distorted).

Hindlimb—Maximum lengths of the left and right femora are approximately 37.5 cm and 38 cm, respectively; respective measurements for the maximum width of the distal ends are about 20.8 cm and 20.3 cm. The width of the capitulum and trochanter of both femora is about 11 cm and 7 cm, respectively, and they are not offset to the extent seen in the humerus, nor is the femur as dorso-ventrally compressed (Fig. 13). The length of the shaft is proportionally shorter than in the femur of *P. latipinnus* or *T. kirki*. Interestingly, the left femur appears to have only three facets (for the tibia, fibula, and supernumerary II), whereas the right femur has four (the fourth for supernumerary III). Respective measurements for the tibia, fibula, and supernumerary II facets are approximately 9.5 cm, 7 cm, and 4 cm (left) and 9 cm, 6.5 cm, and 4 cm (right). Table 3 provides additional measurements for the epi- and mesopodials of the rear paddles.

The tibia of *E. rankini* is not nearly as short and broad as in *Dolichorhynchops*, *Trinacromerum*, or *P. latipinnus*, nor is it equi-dimensional as in *Palmula*. The fibula, too, differs from *Dolichorhynchops* and *Trinacromerum*, but resembles *P. latipinnus,* in its nearly equi-dimensional length and width (see Williston, 1903:Pl. XXI). The tibiale is broader than long and it has a slight proximally-directed extension at its antero-proximal corner (Fig. 13A, B). In addition to having prominent articular facets for the tibia, intermedium, and distal tarsal I, it also has a minor facet for articulation with distal tarsal II. The intermedium is also broader than long, hexagonally shaped, with facets for the tibiale, tibia, fibula, fibulare, and distal tarsals II and III. The length and width of the fibulare are nearly the same, in contrast to the tibiale and intermedium, and it has facets for the fibula, supernumerary I, distal tarsal III, and metatarsal V. The third row of tarsals includes distal tarsals I, II, and III, and a phalangiform metatarsal V. Distal tarsals I and II are broader than long, whereas distal tarsal III is longer than wide. Distal tarsal II has a prominent, rounded boss on the proximal articular surface that fits between the tibiale and the intermedium. The phalanges, particularly the proximal series, are relatively more elongate than those of *P. latipinnus*.

Discussion—Neither Carpenter (1996, 1997) nor O'Keefe (2004:fig. 4), in their reconstructions/discussions of the mandible of *Dolichorhynchops*, mention the coronoid extending anteriorly

TABLE 3. Measurements of hindlimb elements for *Eopolycotylus rankini* (cm).

Element	Max. length	Max. width	Element	Max. length	Max. width
L. femur	37.5	20.8	R. femur	38.0	20.3
L. tibia	8.0	9.5	R. tibia	7.3	10.0
L. fibula	7.0	7.2	R. fibula	7.3	8.0
L. supernumerary I	4.0	2.9	R. supernumerary I	4.1	2.2
L. supernumerary II	5.5	~4	R. supernumerary II	—	—
L. tibiale	4.0	5.3	R. tibiale	4.0	6.7
L. intermedium	5.0	6.0	R. intermedium	4.5	5.8
L. fibulare	4.2	4.4	R. fibulare	4.5	4.6
L. distal tarsal I	3.0	4.9	R. distal tarsal I	—	—
L. distal tarsal II	4.4	4.6	R. distal tarsal II	—	—
L. distal tarsal III	4.1	3.5	R. distal tarsal III	—	—
L. metatarsal V	6.0	3.4	R. metatarsal V	5.3	—

as a contribution to the symphysis. O'Keefe (pers. comm., 2005), in fact, maintains the more traditional view that what we perceive as anterior extensions of the coronoids into the symphysis are "flanges of the dentary." Although Druckenmiller (2002:36) noted that the coronoid of *Edgarosaurus* extended "along the dorsomedial surface of the dentary for most of its length," he could not determine if the coronoid extended into the symphysis. However, he did note a "well developed . . . large, single median ridge" on the dorsal surface of the anterior symphysis that he considered dentary. We provisionally consider this ridge the anterior extension of the coronoids. The main references alluding to this morphological feature are those from Williston's early 20th-century work on *D. osborni* and *T. bentonianum*. Referring to *Dolichorhynchops*, Williston (1903:31) stated, "The bone which I determine as the coronoid is most peculiar, remarkably unlike that in any other animal which I know. It is a long, slender, flattened, trihedral bone, extending far forward, and like the splenial, meeting its mate in the median symphysis. It follows the inner margin of the dental border of the dentary, apparently at least as far as the middle of the symphysis." Later, referring to *Trinacromerum*, Williston (1908:721) re-emphasized, "The great elongation of the coronary [sic], and its union in a median symphysis is the most striking characteristic of the plesiosaur mandible."

TRINACROMERUM Cragin, 1888
TRINACROMERUM ?*BENTONIANUM* Cragin, 1888
(see Carpenter, 1996, for synonymy)
(Fig. 14)

Holotype—USNM 10945, fragmentary skull and post-crania. Paratype: USNM 10946, skull and atlas/axis complex (Carpenter, 1996; O'Keefe, 2004).

Type Locality, Horizon, and Age—Fairport Chalk Member of the Carlile Shale, Osborne County, Kansas (Schumacher and Everhart, 2005), contra Fencepost Limestone, Pfeiffer Shale Member of the Greenhorn Limestone (Carpenter, 1996); early middle Turonian.

Referred Specimens—UMNH Accession Number 96.10, "partial skeleton from the tail and trunk region, consisting of two sections of vertebrae in articulation, one with approximately 18 vertebrae, the other with approximately 30 vertebrae; isolated vertebrae, two teeth, a paddle bone, and additional unidentified

FIGURE 14. *Trinacromerum* ?*bentonianum*. **A**, **B**, MNA V10044, cervical vertebrae; **C**, MNA V10045, right femur with proximal paddle elements.

elements" (Gillette et al., 1999:270); MNA V10044, two cervical vertebrae; MNA V10045, right femur with proximal paddle elements.

Locality—UMNH Accession Number 96.10: Utah Geological Survey Locality 42Ka008VI, near Muddy Creek, Orderville, Kane County, Utah; MNA V10044: MNA LOC 1607, Glen Canyon National Recreation Area, Kane County, Utah; MNA V10045: MNA LOC 1610, Glen Canyon National Recreation Area, Kane County, Utah.

Stratigraphic Occurrence and Age—UMNH Accession Number 96.10: Tropic Shale, upper part of the *Sciponoceras gracile* Ammonoid Biozone, late Cenomanian; MNA V10044: Tropic Shale, approximately 6 m above top of Bentonite C, approximately 2 m below top of Bentonite D (Fig. 2, column 5), early Turonian; MNA V10045: Tropic Shale, approximately 18.75 m above top of Bentonite D, approximately 10.0 m below LO of *Mammites* (Fig. 2, column 4), early Turonian.

Description and Discussion—In light of the abundance of plesiosaur material from the Tropic Shale reported herein, a re-evaluation of the Muddy Creek specimen reported by Gillette and colleagues (1999) was undertaken. Only the vertebrae were examined, but they are very large, distinctly cylindrical, and they show lateral nutritive foramina. M. Getty (pers. comm., 2006) of the Utah Museum of Natural History described the teeth as fairly robust with a weakly to moderately striated crown. Although not conclusive, the cylinder-like shape of these vertebrae, with little lateral or ventral constriction, supports tentative referral to a large specimen of *T. bentonianum*.

MNA V10044 includes two cervical vertebrae that are tentatively referred to *T. bentonianum* on the basis of their large size and cylinder-like morphology (Fig. 14A, B). The centra are wider than they are tall, and also wider than long. Similar in size, they both measure approximately 13 cm wide by 10 cm tall by 9.5 cm long. There is a distinct nipple-like structure at the center of the articulating surface of the centrum, and they have dorsoventrally compressed, somewhat downwardly directed processes (broken) for cervical rib articulation low on the side of the centrum. One vertebra has a neural spine, although broken and not attached, which is tall, transversely flattened, and anteroposteriorly broad. The proximity of the two ventral foramina indicates that these vertebrae are likely from the anterior part of the neck rather than the posterior.

Referral of MNA V10045 to *Trinacromerum* is based primarily on the short and wide aspect of the tibia and fibula (Fig. 14C). The femur, identified as such by the lack of sigmoidal curvature typically seen in plesiosaur humeri, measures 25.5 cm long by 12.8 cm wide at its distal end. The trochanter measures approximately 4 cm wide and the capitulum is approximately 6.5 cm wide. Additional elements include supernumeraries I and II, the tibiale, intermedium, fibulare, distal tarsals I, II, and III, and metatarsals I–IV. There does not appear to have been a supernumerary III; metatarsal V is missing, although several disarticulated phalanges were recovered.

The individual was likely a juvenile as indicated by the weakly developed facets along the edges of the epi- and mesopodials and the relatively broad spaces between these elements (compare with *Palmula quadratus*). Also, the facets along the distal margin of the femur, for the tibia, fibula, and supernumerary II, are weakly developed.

DISCUSSION

Providing brief summaries of problems that have long plagued polycotylid classification, both Sato and Storrs (2000) and Druckenmiller (2002) noted the absence of detailed cladistic analyses. Bardet and Godefroit (1998), however, and more recently O'Keefe (2000, 2001, 2004), presented a series of cladistic analyses and taxonomic revisions that shed considerable light on
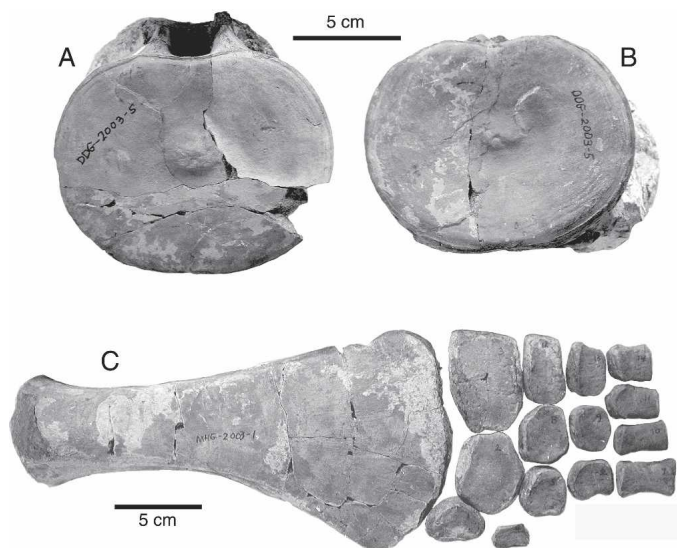
these problems, and additionally confirmed previous hypotheses proposing that polycotylids are more closely related to the long-necked elasmosaurids than they are to the short-necked pliosaurids (e.g., Bakker, 1993; Carpenter, 1996, 1997). O'Keefe's analyses also supported the monophyly of the Polycotylidae.

Phylogenetic Analysis

To ascertain the relationships of *Palmula quadratus* and *Eopolycotylus rankini* relative to other polycotylids, a cladistic analysis was performed using PAUP* 4.0b10 (Swofford, 2001) and McClade 4.0. It is important to note, however, that the lack of abundant or well-preserved cranial material for the Tropic Shale specimens somewhat compromises the level of confidence that can be placed in the analysis, because it is these characters, particularly those of the palate and basicranium, that appear most diagnostic for the Polycotylidae (i.e., Carpenter, 1997; O'Keefe, 2004). Therefore, mostly post-cranial characters were used, although the few cranial and dental characters that could be obtained were included.

Appendix 1 shows the characters and character states, and Appendix 2 the character-taxon matrices, used for this analysis. Thirty-one characters for 10 taxa were scored, with *Plesiosaurus dolichodeirus* Conybeare (1824) and *Tricleidus seeleyi* Andrews (1909) comprising the outgroups (see O'Keefe, 2004). Characters for all taxa except *Palmula quadratus* and *Eopolycotylus rankini* were scored from the literature and previously developed matrices (primarily O'Keefe, 2000, 2004, and Schumacher, unpublished ms; but also Bardet et al., 2003; Carpenter, 1996, 1997; Druckenmiller, 2002; and Sato and Storrs, 2000). Cranial characters for *P. latipinnus* were scored from Adams (1997) because, as noted previously, we consider *Trinacromerum bonneri* Adams (1997) a junior synonym of *Polycotylus latipinnus* Cope (1869), from Schumacher and Martin (1995), and from an unpublished manuscript generously provided by B. Schumacher. All multistate characters are unordered. Heuristic searches used 1000 random input orders, equal weights for all characters. Bootstrap analyses included 100 replications and 10 random input orders per replicate.

Figure 15 shows the results of strict consensus analysis that yielded 12 equally parsimonious trees (MPTs) with a tree length (TL) of 50, a consistency index (CI) of 0.840, a retention index (RI) of 0.733, and a homoplasy index (HI) of 0.160. Majority Rule analysis yielded identical results. Bootstrap percentages were very high (97%) for the ingroup clade, including *Edgarosaurus*, and for the *Polycotylus/Eopolycotylus* clade (83%). The clade exclusive of *Edgarosaurus* resulted in a lower bootstrap percentage of 59, likely due to the absence of many characters for *Palmula*, the Japanese specimen (UMUT MV 19965), and particularly *Thililua*.

Results support the monophyly of the Polycotylidae, as concluded by O'Keefe (2004), which is united primarily on the basis of the extension of the splenial and angular into the symphysis (9) and cervical vertebrae that are more short than tall (12). Although the analysis resulted in an unresolved outgroup polytomy, it supports a clade in which *Edgarosaurus*, as the most plesiomorphic member of the family, is the sister taxon to the clade containing all other polycotylids. The clade comprised of all polycotylids except *Edgarosaurus* is supported by the absence of a pineal foramen (6) and a long mandibular symphysis (8).

In an earlier analysis in which some characters were scored differently due to incomplete preparation of key specimens and minor ambiguities in the literature, the clade comprised of all polycotylids except *Edgarosaurus* was supported by several additional characters. These included supernumerary ossifications in the propodial and epipodial rows (20), interlocking distal phalanges (22), elongate clavo-coracoid process (25), one or more medial coracoid foramina (27), a pubis shorter than the ischium
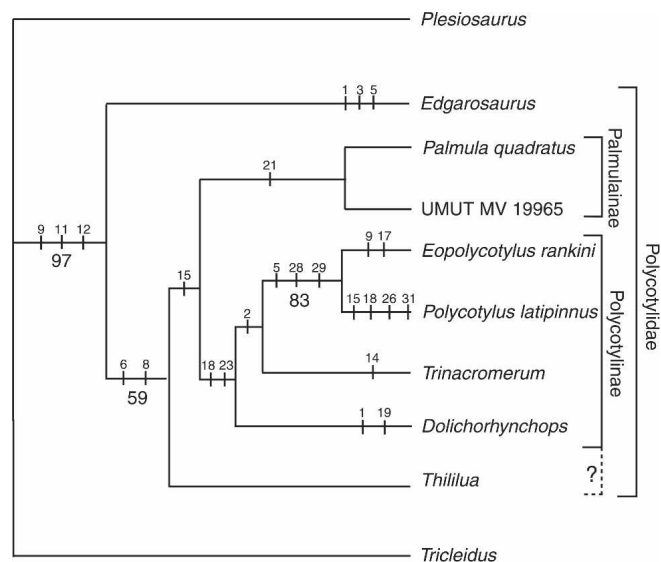

FIGURE 15. Strict consensus of twelve MPTs showing relationships within Polycotylidae; both *Plesiosaurus* and *Tricleidus* as outgroup (TL = 50, CI = 0.840, RI = 0.733, HI = 0.160). See text for discussion and Appendices 1 and 2 for characters, character states, and character/taxon matrix. Larger numbers denote bootstrap percentages, small numbers are those derived states characterizing each node. Nodes without bootstrap percentages indicate less than 50%.

(30), and very long ischia relative to width (31). This earlier analysis differed from the current one in the following: characters 1 and 4 were scored differently for *Dolichorhynchops* (0 vs 1, 3 vs 2, respectively); characters 5 and 19 were scored differently for *Trinacromerum* (1 vs 0, 0 vs 1, respectively); characters 6 and 31 were scored differently for *Polycotylus* (0 vs 1, 2 vs 1, respectively); and characters 15, 16, and 18 were scored differently for *Palmula* (0 vs 1, ? vs 2, and 1 vs 0, respectively). (Note: this earlier analysis yielded a single MPT with a TL = 51, CI = 0.804, RI = 0.756, and HI = 0.196.)

Like our present analysis, however, the earlier one also divided the Polycotylidae into two clades. *Palmula* and the Japanese taxon (UMUT MV 19965) form a clade separate from all other members of the Polycotylidae exclusive of *Edgarosaurus* based on the synapomorphy of the distinctly equi-dimensional radius/ulna and tibia/fibula (character 21); we refer these taxa to the new subfamily-level clade, the Palmulainae. The second clade includes *Dolichorhynchops*, *Trinacromerum*, *Polycotylus*, and *Eopolycotylus*, which share the more typical short and broad epipodial morphology; we refer this second subfamily-level clade to the Polycotylinae. This group is further united by a sigmoidally shaped humerus (18) and the absence of an antebrachial foramen (23). Although *Thililua* falls outside the clade including the Polycotylinae and the Palmulainae, because limbs are not yet known for this taxon, we provisionally include it within the Polycotylinae (Fig. 15). On the other hand, we consider the specimen from South Dakota (AMM 98.1.1) a member of the Palmulainae due to its distinct epipodial morphology (more equi-dimensional than short and wide), although it is not included in the present analysis because it is currently under study by Schumacher.

Unlike previous analyses in which *Dolichorhynchops* and *Trinacromerum* appear most closely related to one another, our analysis resulted in *Trinacromerum* as the sister taxon to the *Polycotylus/Eopolycotylus* clade, based primarily on the number of maxillary teeth (>30) and chevron placement; and *Dolichorhynchops* is the sister taxon to that clade. We note again, however, that this result may be due to the limited number of characters used in our analysis, and our reliance on mainly post-

cranial traits. The *Polycotylus/Eopolycotylus* clade is united by the derived states of characters 5, 28, and 29 (relatively robust teeth and ilium morphology). Autapomorphies further diagnose both *Polycotylus* and *Eopolycotylus*. In the former are the much shorter than wide dorsal vertebrae (15), the highly sigmoidal humerus (18), a posterior extension of the coracoid (26, although possibly ontogenetic), and the very long length of the ischium relative to width (31). In *Eopolycotylus*, the angular does not extend into the symphysis as it does in other known polycotylids (9), and the shaft of the humerus and femur is very broad relative to the length (17).

Notes on New Taxa

Palmula quadratus—Of the characters noted by Carpenter (1996) as diagnostic of the Polycotylidae, those discernable from the recovered material of *Palmula quadratus* include four to seven pairs of premaxillary teeth (five in MNA V9442), no caniniform teeth, and a long mandibular symphysis. Discernable diagnostic characters noted by O'Keefe (2004) include ischium longer than pubis, splenial included in mandibular symphysis, and supernumerary ossifications in propodial and epipodial rows. One character Carpenter (1996:267) listed as diagnostic at the family level that is different in the Tropic Shale specimen, however, is "epipodials short and wide." As noted in Sato and Storrs (2000), Brown (1981) and Storrs (1997) considered long epipodials to be plesiomorphic. The derived condition of short and wide epipodials, considered characteristic of the Polycotylidae (Carpenter, 1996), occurs in the family's oldest member, the late Albian *Edgarosaurus*, as well as in the most recent, Campanian members, *D. osborni* and *P. latipinnus*. The polygonal epipodials of the Tropic Shale, Japanese, and South Dakota specimens are not here considered 'long,' i.e., they are not considered representative of the plesiomorphic condition, but instead appear to be synapomorphies diagnostic of a new clade of plesiosaurs nested within the Polycotylidae. In light of the new Tropic Shale, Japanese, and South Dakota specimens, short and wide epipodials can no longer be considered a diagnostic character of the Polycotylidae as presently understood. Thus, a new subfamily of the Polycotylidae, the Palmulainae, is erected for those taxa that have distinctly polygonal, rather than short and broad, epipodials.

Eopolycotylus rankini—Referral of MNA V9445 to the new genus *Eopolycotylus* is based on what is here considered a series of synapomorphies shared with *Polycotylus latipinnus*, as well as several autapomorphies. Synapomorphies include: (1) stout, striated teeth; (2) some anteroposteriorly compressed vertebrae, although not to the extent seen in *P. latipinnus*; (3) narrow, swept back neural spines; (4) four bones in the epipodial row; (5) and, particularly, curved ilia with a tapered sacral end. Although Schumacher (pers. comm., 2005) suggests that ilium morphology may be sexually dimorphic, it is difficult to test this hypothesis with such limited material. Currently, it can only be determined that the ilia of *Eopolycotylus rankini* are nearly identical to those of *Polycotylus latipinnus* and entirely distinct from those of *Trinacromerum bentonianum*. But MNA V9445 differs from *Polycotylus*, as well, particularly in the robust morphology of its humerus and femur. Those of *Polycotylus* are relatively longer, more gracile, and are more distally expanded than in *Eopolycotylus*; the former also has a much greater degree of sigmoidal curvature in the humerus. These features therefore preclude referral of MNA V9445 to *Polycotylus* and support its placement into a new taxon.

SUMMARY AND CONCLUSIONS

Recent research within Turonian marine sediments of the Tropic Shale deposited in southern Utah indicates that the Cretaceous Western Interior Seaway, at least along its western margin, harbored a more diverse reptilian fauna than previously realized. In addition to the presence of the pliosaurid *Brachauchenius lucasi* and the polycotylid *Trinacromerum bentonianum*, the Tropic Shale has also yielded two new plesiosaur taxa, *Palmula quadratus* and *Eopolycotylus rankini*. Cladistic analysis indicates that *Palmula quadratus*, together with new, unnamed taxa from South Dakota and Japan, represent a new clade of polycotylid plesiosaurs diagnosed by distinctly polygonal epipodial elements. We designate this new clade of polycotylids the Palmulainae. Those polycotylids that have the more typical short and broad epipodial morphology, including *Eopolycotylus*, *Polycotylus*, *Trinacromerum*, *Dolichorhynchops*, and provisionally *Thililua*, comprise the new clade Polycotylinae.

Numerous workers have long noted the profound faunal changes that occurred in the marine realm, on a global scale, near the Cenomanian-Turonian (C-T) Stage boundary as a result of significant oceanographic events during the late Cenomanian, specifically ocean anoxic event II (OAE II). Changes during OAE II included the extinction of 24% of all marine genera (Raup and Sepkoski, 1986; but see discussion by Kerr, 2001, of "Lazarus taxa" with respect to the C-T extinction event), the worldwide occurrence of organic-rich anoxic sediments (Schlanger and Jenkyns, 1976), a positive ∂^{13} C excursion (Schlanger et al., 1987), and an expansion of the oxygen minimum zone onto shelf areas that led to extinction of deep water faunas (e.g., Leckie et al., 1991, 1998; Keller and Pardo, 2004; and Prokoph et al., 2001, and references within). Although the timing of OAE II is currently in a state of flux (for example: Keller and Pardo [2004] place OAE II entirely within the late Cenomanian, whereas Prokoph et al. (2001) show OAE II straddling the C-T boundary), there is no disputing that marine extinctions and faunal turnover occurred at the C-T boundary.

In contrast to the marine realm, on the other hand, Eaton and colleagues (1997) showed that there was little if any extinction of brackish-water species across the C-T boundary and that there was an actual increase in diversity of fully terrestrial organisms, including mammals and dinosaurs. However, they found significant extinction of freshwater aquatic species, such as fish and turtles, and attributed this to the drowning of coastal floodplains along the western margin of the KWIS during maximum transgression during the early Turonian. This major sea level transgression also resulted in the return of marine diversity as the northward flow of normal, saline, subtropical marine waters into the KWIS significantly altered the previous late Cenomanian conditions of relatively low sea level and low salinity (e.g., Elder, 1991; Keller and Pardo, 2004; Leckie et al., 1998).

With the C-T boundary marine extinctions in mind, we carefully and accurately recorded stratigraphic data at each vertebrate locality realizing that these data might harbor information that could bear on the boundary events noted previously. Based on the evidence from the marine vertebrate record derived from this study, there is no indication that the oceanographic events of the late Cenomanian-early Turonian responsible for the variety of responses noted previously had a significant, discernable impact on the plesiosaur fauna of the KWIS. As indicated in Figure 2, no marine vertebrates, plesiosaurs or otherwise, were found immediately at, or adjacent to, the C-T boundary, easily located in the field by examination of molluscan faunas (especially an influx of *Mytiloides hattini*) in concert with a locally persistent limonite horizon that closely approximates the stage boundary. Additional results follow: (1) the most productive interval yielding specimens of plesiosaurs is that in lower Turonian sediments from just below Bentonite D stratigraphically down to approximately 4 m below Bentonite C (polycotylids and *Brachauchenius* occur in this interval); (2) no plesiosaur remains were recovered from the stratigraphic interval between bentonites D and "E"; (3) articulated remains of plesiosaurs (but only polycotylids)

were recovered from the interval between bentonite "E" and the LO of *Mammites*; and (4) only very rare remains of plesiosaurs were found above the LO of *Mammites*.

Regarding items (1) and (2), it is both interesting and difficult to explain the abundance of material below bentonite D, in concert with the absence of vertebrate remains in the stratigraphic interval between bentonites D and "E." First, our field work over the course of this relatively long-term study was both extensive and intensive in nature, and no less time was spent surveying this stratigraphic interval than any other. Second, it is unlikely that the absence of vertebrates over this interval is due to conditions non-conducive to preservation, because there are no apparent changes in lithology, obvious unconformities, or indications of dramatically changing sedimentation rates when compared with the other stratigraphic intervals in which large vertebrates were found. In fact, Olesen (1991) noted an increase in diversity and abundance of planktonic foraminifera over this interval reflecting normal oceanic salinities and increasing depth. Increasing depth would not hinder preservation either, as vertebrate remains (plesiosaur, turtle, dinosaur, and fish) were found in the overlying interval between bentonite "E" and the LO of *Mammites* within which depth continued to increase. One explanation, however, may be that this interval crops out as slightly steeper slopes than the more productive interval below, thereby reducing the amount of surface area exposed. Above the *Mammites* zone, on the other hand, slopes in most places are even steeper and very rare fragments were recovered, one of which was the proximal portion of a very large, highly eroded, propodial (MNA V9457). Although not shown on the stratigraphic columns of Figure 2, it was found several tens of meters above site DOR-2001-1 in the "Turtle Section" (column 3).

Additional specimens from our field area not described in this report, but shown in Figure 2, include: (1) a series of several dorsal vertebrae discovered by M. Graffam (MNA V9429, Fig. 2, column 3) that apparently belonged to a juvenile individual based on the unfused nature of the neural arches; (2) a nearly complete skeleton, including skull, of a polycotylid (MNA V10046; Fig. 2, column 7) discovered by S. Richardson and currently under study by R. Schmeisser, a graduate student in the Department of Geology at Northern Arizona University; and (3) a partial skeleton of a very small individual discovered by Rankin, just as this paper was being completed, northeast of Kanab, Utah, about 85 km west of our main study area near Big Water. These tantalizing specimens provide even more evidence for what may be a considerably higher level of plesiosaur diversity in the KWIS during the late Cenomanian-early Turonian than previously realized, and indicate that continued prospecting of the Tropic Shale will yield further surprises. The Tropic Shale affords an excellent, previously unexploited window through which this important interval of time for North American, even global, biotic diversity and evolution can be viewed.

ACKNOWLEDGMENTS

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APPENDIX 1. Characters and character states used in phylogenetic analysis.

1. Number of premaxillary teeth: 0) ≤5, 1) ≥6. For *Polycotylus latipinnus*, O'Keefe (2004) indicated that this character is unknown; Schumacher (unpublished manuscript, 2004), on the other hand, scored this character as ≤5; for *Dolichorhynchops*, Carpenter (1996) reported this character variable (5 to 7), but in 1997, he reported 6, as does Schumacher (unpublished manuscript, 2004); O'Keefe (2004) reported 5 for *Dolichorhynchops*.
2. Number of maxillary teeth: 0) ≤20, 1) 21–30, 2) >30 (Carpenter, 1997; Bardet et al., 2003; Druckenmiller, 2002; O'Keefe, 2004; Schumacher and Martin, 1995).
3. Caniniform teeth on maxilla: 0) absent, 1) present (O'Keefe, 2004, char. 54).
4. Number of dentary teeth: 0) ≤20, 1) 21–25, 2) 26–30, 3) >30 (Bardet et al., 2003; Druckenmiller, 2002; Schumacher, unpublished manuscript, 2004; Schumacher and Martin, 1995).
5. Tooth form: 0) gracile (slender), 1) robust (stout).
6. Pineal foramen: 0) present, 1) absent (Schumacher, unpublished manuscript, 2004).
7. Elongate rostrum: 0) absent, 1) premaxilla only, 2) elongate premaxilla and maxilla (modified from O'Keefe, 2004, char. 7).
8. Mandibular symphysis: 0) short, 1) long. (O'Keefe, 2004, [char. 48] included 2 additional states ["somewhat enforced" and "scooplike"] to allow for morphologies found outside the Polycotylidae).
9. Splenial participates in symphysis: 0) no, 1) yes, but not angular, 2) splenial and angular extend into symphysis (Adams, 1997; modified from O'Keefe, 2004, char. 49).
10. Coronoid extends into symphysis: 0) does not, 1) does.
11. Neck length: 0) primitive, 1) long, 2) intermediate, 3) short (modified from O'Keefe, 2004, char. 2).
12. Cervical vertebrae proportions: 0) length ≥ height, 1) length < height (modified from O'Keefe, 2004, char. 61).
13. Number of cervical vertebrae: 0) 28-32, 1) >32, 2) <28 (modified from Bardet et al., 2003, Carpenter, 1996, and O'Keefe, 2004).
14. Dorsal vertebrae: 0) lateral walls of centrum constricted, 1) cylinder-like centrum (modified from Schumacher, unpublished manuscript, char. 25).
15. Dorsal vertebrae: 0) longer than wide, 1) shorter than wide, 2) much shorter than wide.
16. Caudal chevron facets: 0) on anterior and posterior face of centrum, 1) mainly on posterior face of centrum (Carpenter, 1996, 1997; Storrs, 1997), 2) on ventral surface of centrum.
17. Humerus: 0) narrow shaft, 1) broad shaft.
18. Humerus: 0) shaft not sigmoidal, 1) shaft weakly sigmoidal, 2) shaft strongly sigmoidal (modified from O'Keefe, 2004, char 95, who noted only absence or presence of sigmoidal humeral shaft).
19. Distinct facets on distal humerus for supernumeraries: 0) absent, 1) present (modified from O'Keefe, 2004, char. 84).
20. Supernumerary ossifications: 0) epipodial row, 1) propodial and epipodial row (modified from O'Keefe, 2004, char. 87).
21. Epipodial dimensions: 0) longer than wide, 1) shorter than wide, 2) approximately equi-dimensional (modified from O'Keefe, 2004, char. 86, and Schumacher, unpublished manuscript, char. 20).
22. Interlocking distal phalanges: 0) absent, 1) present (modified from O'Keefe, 2004, char. 88).
23. Antebrachial foramen: 0) present, 1) absent (modified from Schumacher, unpublished manuscript, char. 22).
24. Interclavicle: 0) present, 1) absent.
25. Anterior process of coracoid (clavo-coracoid process): 0) short or absent, 1) intermediate, 2) elongate (modified from Schumacher, unpublished manuscript, char. 26; in *Tricleidus* the longitudinal pectoral bar is formed by the scapula and coracoid [O'Keefe, 2004]).
26. Posterior extension of coracoid: 0) absent, 1) present (as seen in *P. latipinnus* and *T. kirki*).
27. Medial coracoid foramina: 0) absent, 1) present (O'Keefe, 2004, char. 78, and Schumacher, unpublished manuscript, char. 27).
28. Ilium morphology: 0) blunt proximal end, 1) tapered proximal end.
29. Ilium morphology: 0) straight, 1) curved (Storrs, 1997).
30. Relative length of pubis/ischium: 0) pubis longer than ischium, 1) pubis shorter than ischium (modified from O'Keefe, 2001, char. 3).
31. Ischium length relative to width: 0) short, 1) long, 2) very long (modified from Schumacher, unpublished manuscript, char. 29).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis of polycotylids discussed in text. Question marks indicate absence of applicable information for that taxon. *Plesiosaurus* and *Tricleidus* comprise outgroup.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Plesiosaurus	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Tricleidus	0	?	0	0	0	0	0	0	0	?	0	0	0	0	0	?	?
Edgarosaurus	1	1	1	3	1	0	1	0	2	1	2	1	2	0	?	?	0
Palmula quadratus	0	?	0	?	0	?	2	1	?	1	?	1	?	0	1	2	0
UMUT MV 19965	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	1	0
Thililua	0	1	0	2	0	1	2	1	2	?	2	1	0	0	1	?	?
Eopolycotylus rankini	0	?	0	?	1	?	2	1	1	1	?	1	?	0	1	?	1
Polycotylus latipinnus	0	2	0	3	1	1	2	1	2	?	3	1	2	0	2	0	0
Dolichorhynchops	1	1	0	2	0	1	2	1	2	1	3	1	2	0	1	1	0
Trinacromerum	0	2	0	3	0	1	2	1	2	1	3	1	2	1	1	0	0

Taxon	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Plesiosaurus	2	0	0	0	0	0	1	0	0	0	0	0	0	0
Tricleidus	0	1	0	1	?	0	0	0	0	0	0	?	?	?
Edgarosaurus	?	1	?	1	1	0	?	?	?	?	?	?	?	?
Palmula quadratus	0	1	1	2	1	0	?	?	0	?	0	1	1	1
UMUT MV 19965	?	1	1	2	1	?	?	2	?	1	?	?	1	?
Thililua	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eopolycotylus rankini	1	1	1	1	1	1	0	2	0	1	1	1	1	1
Polycotylus latipinnus	2	1	1	1	1	1	0	2	1	1	1	1	1	2
Dolichorhynchops	1	0	1	1	1	1	0	2	0	1	0	0	1	1
Trinacromerum	1	1	1	1	1	1	0	2	0	1	0	0	1	1