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AN EARLY POLYCOTYLID PLESIOSAUR (REPTILIA: SAUROPTERYGIA) FROM THE CRETACEOUS OF HOKKAIDO, JAPAN

TAMAKI SATO[1] AND GLENN W. STORRS

Department of Geology, University of Cincinnati, PO Box 210013, Cincinnati, Ohio 45221-0013, and
Cincinnati Museum Center, Geier Collections and Research Center, 1720 Gilbert Avenue, Cincinnati, Ohio 45202, USA

ABSTRACT—A partial skeleton of a short-necked plesiosaur excavated from the Upper Cenomanian of the Middle Yezo Group of Hokkaido, Japan, includes disarticulated vertebrae, the right half of the pectoral girdle, fragments of the pelvic girdle, ribs, gastralia, and gastroliths. Gastroliths are unusual in short-necked plesiosaurs. Skeletal characters indicate that the specimen belongs to the Family Polycotylidae, well known from North America, the former Soviet Republics, and possibly from New Zealand. They are rare in East Asia and hitherto unknown from Japan. Extensive ossification indicates that this specimen is an adult individual, yet it is smaller than the adult specimens of other known polycotylids. The elongated epipodial bones are a unique character of the specimen but are probably plesiomorphic. The fossil is evidence of biogeographical diversification of the family at the beginning of the Late Cretaceous.

INTRODUCTION

THE PLESIOSAURIA is a clade of Mesozoic marine reptiles known from the Late Triassic to the very end of the Cretaceous. In spite of their widespread occurrence, however, plesiosaurian phylogeny, especially that of Cretaceous forms, is still under debate. The Family Polycotylidae is a group of short-necked plesiosaurs mainly known from the Cretaceous (Figs. 1, 2). Their remains have been found in the Upper Cretaceous of North America (Adams, 1997; Carpenter, 1996; Cope, 1875; Cragin, 1888, 1889; Riggs, 1944; Russell, 1935; Storrs, 1981, 1999; Thurmond, 1968; Welles, 1962; Williston, 1903, 1906, 1908), and to lesser extent in the former Soviet Republics (Otschev, 1976, 1977; Storrs et al., in press) and Australia (Persson, 1960). Wiffen and Moisley (1986) described material from the Upper Cretaceous of New Zealand as ‘‘Pliosauridae genus and species indeterminate’’ under the classification scheme of Brown (1981), including those that show polycotylid affinity but were not confirmed (NZGS, CD459, 461 to 465). Remains of short-necked plesiosaurs from the Maastrichtian of Chile were identified as Dolichorhynchopidae (= Polycotylidae) by Welles (1962). Gasparini and Goni (1985) reported the occurrence of a polycotylid plesiosaur from Argentina, but this later turned out to be an elasmosaurid (Gasparini, personal commun.). Until recently, none were known from East Asia.

The oldest occurrence of the Family Polycotylidae is a partial skeleton of *Dolichorhynchops?* sp. from the Aptian of Australia (Persson, 1960). This is then followed by a series of vertebrae of *Trinacromerum* sp. from the Albian of Texas (Storrs, 1981). The specimen described here, UMUT MV 19965, is from the Cenomanian, just before the appearance of various polycotylid species in the Late Cretaceous. Latest records of the family from North America are from the Campanian (Adams, 1997; Sato, 1999). Although elasmosaurid plesiosaurs are known from the Maastrichtian of the Pacific and Gulf coasts (Storrs, 1981; Welles, 1962), no polycotylid plesiosaurs have been reported from this stage in North America. Stratigraphic refinement of the polycotylid specimens from New Zealand and former Soviet Republics is required for detailed discussion.

In the summer of 1990 and 1991, a partial polycotylid skeleton was excavated from a riverside cliff along the Obirashibe River, Obira area, Hokkaido, Japan (Fig. 3). The present specimen consists of the right half of the trunk, a forelimb, and disarticulated vertebrae (Fig. 4). Most of the fossil occurred in extremely hard calcareous concretions. Preliminary reports of the specimen were given by Sato (1997a,b). Sato and Tanabe (1998) discussed the stomach contents of the specimen.

Accompanying fossils show that this specimen is from the *Biostrina nipponica* Zone of the Middle Yezo Group of late Cenomanian to early Turonian age (e.g., Igi et al., 1958; Takayanagi and Okamura, 1977; Taketani, 1982; Tanabe et al., 1977). A geological survey in 1994 collected *Desmoceras* sp. and *Inoceramus costatus* that are characteristic of the late Cenomanian (Tanabe et al., 1977). This locality is relatively poor in megafossils compared with other parts of the Middle Yezo Group. The outcrops are mainly composed of monotonous siltstone, suggesting a constant supply of fine sediments in a low energy, offshore environment. The strata at the locality dip about 50 degrees west, and are almost perpendicular to the outcrop surface, suggesting that missing parts of the fossil had been eroded away before excavation. The occurrence of the Japanese plesiosaur indicates a wide biogeographic and morphological diversification of the Family Polycotylidae at the beginning of the Late Cretaceous.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York; FHSM, Fort Hays Sternberg Museum, Kansas; KUVP, Natural History Museum, University of Kansas; MCZ, Museum of Comparative Zoology, Massachusetts; MM, Manitoba Museum, Winnipeg, CANADA; SMP-SMU: Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas; TMM: Texas Memorial Museum, University of Texas at Austin; UMUT: University Museum, University of Tokyo, JAPAN; USNM: United States National Museum, Washington, DC; YPM: Yale Peabody Museum, Yale University, Connecticut.

SYSTEMATIC PALEONTOLOGY

Order PLESIOSAURIA de Blainville, 1835
Family POLYCOTYLIDAE Cope, 1869

Discussion.—Validity of polycotylid taxa.—There are three problems that have caused confusion in the classification of short-necked plesiosaurs; validity of the Family Polycotylidae, phylogenetic relationship of this family to other plesiosaur families, and distinction of the genera *Trinacromerum* and *Dolichorhynchops*. First of all, monophyly of the family is yet to be confirmed. Most classifications recognize the Family Polycotylidae (Carpenter, 1996; Persson, 1963; Storrs, 1999; White, 1940; Williston, 1925), although the genera included in the family vary

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[1] Present address: Department of Geology and Geophysics, University of Calgary, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada, and Royal Tyrrell Museum of Paleontology, P.O. Box 7500, Drumheller, AB, T0J 0Y0, Canada.

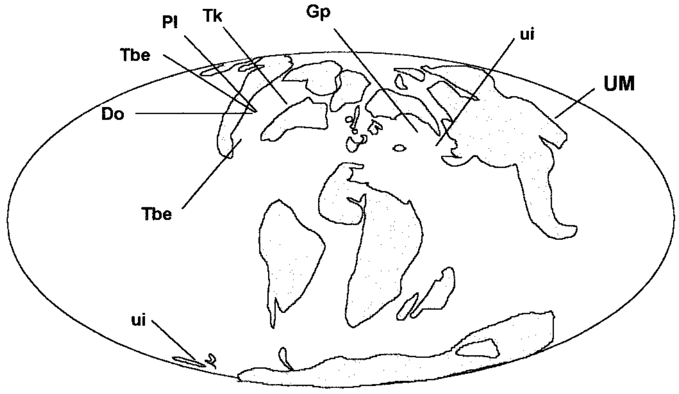

FIGURE 1—Late Cretaceous (Coniacian) paleocoastline and distribution of Upper Cretaceous polycotylid fossils. Abbreviations: Do, *Dolichorhynchops osborni*; Gp, *Georgiasaurus penzensis*; Pl, *Polycotylus latipinnis*; Tbe, *Trinacromerum bentonianum*; Tbo, *T. bonneri*; Tk, *T. kirki*; ui, unidentified polycotylids; UM, UMUT MV 19965. Coastline after Smith et al. (1994).

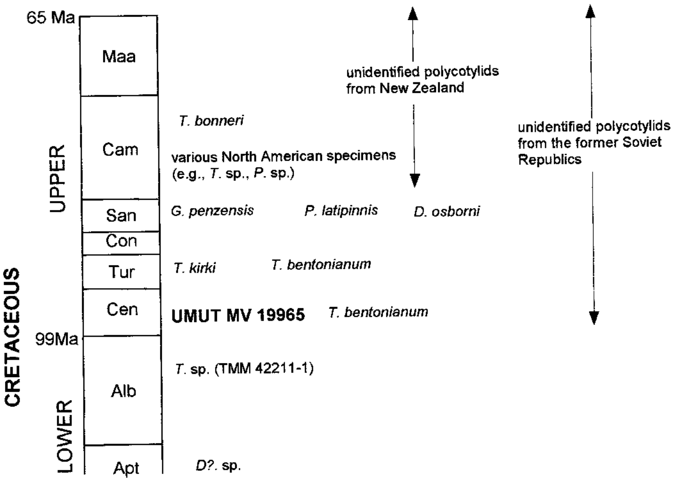

FIGURE 2—Stratigraphic distribution of members of the Family Polycotylidae. See Figure 1 for abbreviations. Data from various sources cited in text.

depending on the classification. Welles (1962) changed the family name to Dolichorhynchopidae, but Thurmond (1968) replaced it with the original Polycotylidae. Otschev (1976) used Trinacromeridae as the family name in his description of a Russian short-necked plesiosaur. The classification scheme proposed by Brown (1981) does not recognize this family, and species within the family have been placed in the Family Pliosauridae together with other short-necked plesiosaurs.

Phylogenetic relationships within the Plesiosauria, especially that of Cretaceous species are yet to be established. Bakker (1993) challenged a long-held assumption that the length of the neck represents two lineages, i.e, long-necked Plesiosauroidea and short-necked Pliosauroidea. Bakker (1993) regarded the Polycotylidae and a group of long-necked plesiosaurs (Elasmosauridae) as descendants of the Jurassic short-necked pliosaurs, while Carpenter (1997) regarded those families as sister groups within the Superfamily Plesiosauroidea. O'Keefe (1999) placed the Family Polycotylidae within a new clade Euplesiosauria with Elasmosauridae and Cryptoclididae. Neither a data matrix nor a cladogram, however, are available for these works. Phylogenetic analyses in Brown and Cruickshank (1994), Bardet et al. (1999), and Carpenter (1999) did not include members of the Family Polycotylidae.

The synonymy problem of *Trinacromerum* and *Dolichorhynchops* started soon after the description of the type specimen of *Dolichorhynchops* by Williston (1903). Welles (1962) abandoned the generic name of *Trinacromerum,* while Storrs (1981) and Adams (1997) held *Trinacromerum* and invalidated *Dolichorhynchops* as a junior sysnonym. On the other hand, Carpenter (1996) recognized both genera as distinct taxa, and Storrs (1999) accepted this solution.

Evaluation of the above three problems is beyond the scope of this study. In this paper, we basically follow the classification scheme proposed by Carpenter (1996) in which *Trinacromerum* and *Dolichorhynchops* are recognized as distinct genera of the Family Polycotylidae. In addition, *Trinacromerum bonneri* Adams, 1997 is recognized; its description appeared later than the work of Carpenter (1996).

Genus and species indeterminate
Figures 4–7

Material Examined.—University Museum, University of Tokyo UMUT MV 19965, consisting of two cervicals, one dorsal, two sacrals, four caudals, three vertebrae of unknown position, right half of the pectoral girdle, ribs, right forelimb, fragmentary pectoral girdle, and stomach contents.

Occurrence.—Upper Cenomanian of the Middle Yezo Group, *Biostrina nipponica* Zone. A riverside cliff of Obirashibe River, Obira Area, Hokkaido, Japan (142′01″E, 44′06″N)

Description.—There are twelve disarticulated amphicoelous to amphiplatyan vertebrae. Serial position of each vertebra was identified based on the position of the rib facets on the centrum in the cervicals and on the transverse process in the dorsal (Brown, 1981), and on the presence of chevron facets in the caudals. Except for a dorsal, the vertebrae are uncrushed, but all are more or less damaged, having lost their neural spines and transverse processes. None of the vertebrae has sutures between centrum and neural arch, suggesting that this is a well-ossified individual. Measurements of the vertebrae are given in the Appendix. Letter designations have been arbitrarily assigned to the vertebrae based upon presumed sequence during life.

Cervical A (Fig. 5.1, 5.2) has a clearly defined lip on the concave posterior face with a pair of depressions, each with a

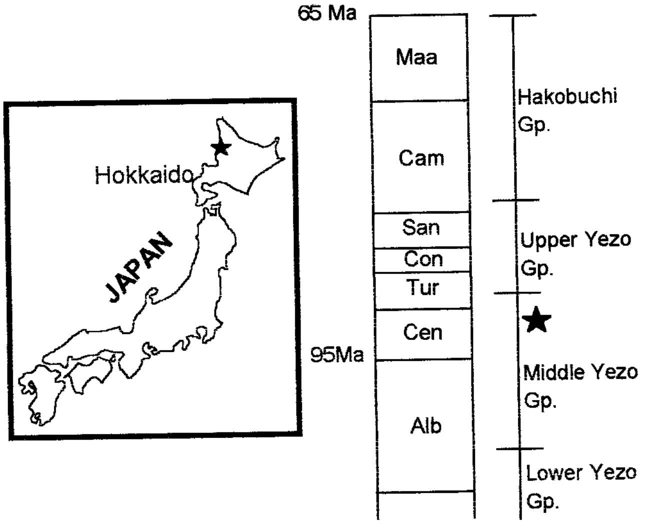

FIGURE 3—Locality map and stratigraphic position of UMUT MV 19965.

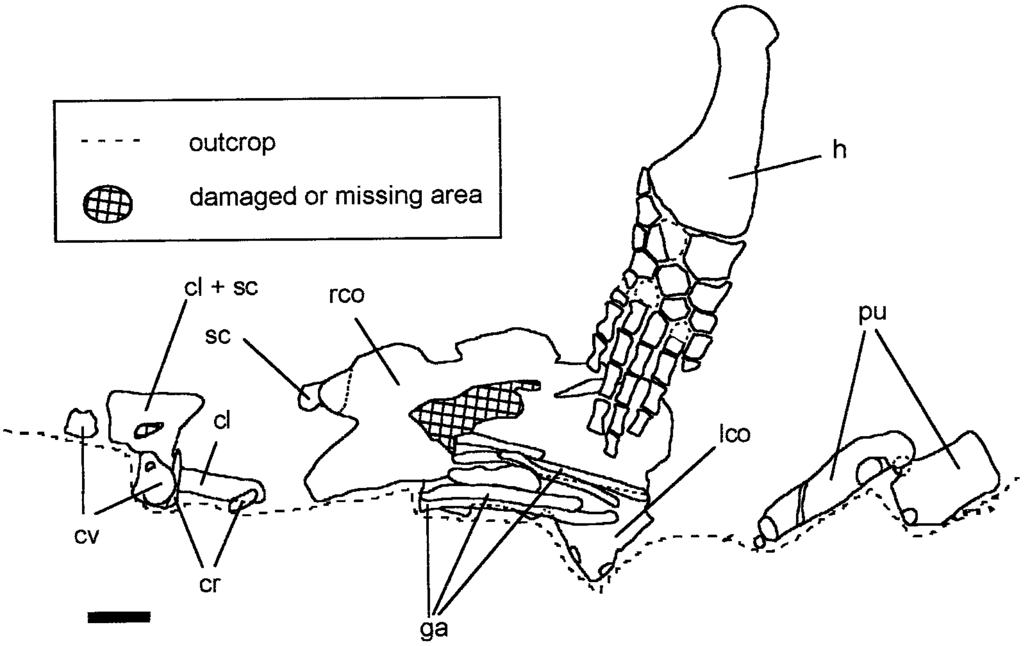

FIGURE 4—Distribution of the skeletal elements of UMUT MV 19965 and some of the associated fossils in the bedding plane. Scale bar = 10 cm. Abbreviations: lco, left coracoid; rco, right coracoid; cr, cervical rib; cv, cervical vertebrae; cl + sc, clavicle + scapula; ga, gastralia; h, humerus; pu, pubis. See Figure 5 for forelimb elements.

foramen on the ventral surface of the centrum. On the lower left side of the centrum, a fragmentary single-headed cervical rib is attached. Cervical B (Fig. 5.3) retains an incomplete neural spine with prezygapophysis. No foramina are seen on the lateral or ventral surface of the dorsal vertebra. Two sacrals retain the base of the neural spine, and there are depressions on the lateral sides. The ventral foramina of the sacrals are not set in paired depressions as are those of cervical A. A pair of foramina are present on the hourglass-shaped floor of the neural canal. Caudal A has two chevron facets, a distinct one on the left part of the posterior ventral edge and a slight depression on the anterior edge of the centrum. There are no foramina on the ventral and lateral surfaces of the centrum of caudal B, but a pair of pits is located in the middle of the floor of the neural canal. Caudal C (Fig. 5.4) has two foramina on its ventral surface and a pair of chevron facets on the posterior end but none on the anterior end, at least on the prepared left side. The centra of the posterior caudals are nearly cylindrical and almost platycoelous, and there are no chevron facets.

A considerable part of the right half of the pectoral girdle is present (Fig. 4 and 6). Remains of the clavicle, scapula, and coracoid show their original spatial relationships but not their exact shape. There is an elongated platy bone fragment lying across the pectoral fenestra. It is probably a displaced portion of the clavicular arch or coracoid, but is too fragmentary for positive identification.

The posterior half of the right clavicle retains its natural edge only where it contacts the scapula and at the edge of the pectoral fenestra. Much of the anterior edge of the pectoral fenestra as preserved is formed by the posterior margin of the clavicle. The clavicle should overlie the dorsal side of the scapula, but the two bones are so fused that the suture is not visible. On the medial portion of the clavicle is an anterior fragment of the coracoid, which is detached from the main part. The clavicle is elongated caudad, but the end is not preserved.

Most of the dorsal blade and ventral ramus of the right scapula is not preserved. The posterior portion of the scapula is broken off and displaced caudad, lying under the articular facet of the coracoid. Much of the ventral ramus is missing, but the remains suggest it underlay the clavicle.

The right coracoid is relatively well-preserved, but only a small portion along the median line is preserved of the left. The anterior tip of the median process is broken off and preserved on the ventral side of the clavicle. A thick transverse bar is present posterior to the pectoral fenestra and is thickest at the glenoid facet (about 6 cm thick) while the median end, at the base of the anterior process, is about 3 cm thick. There are a few pits posterior to the transverse bar along the median edge, as in other polycotylid plesiosaurs such as *Dolichorhynchops* (Williston, 1903).

An almost complete right forelimb is preserved (Fig. 7). Most of the distal half of the ulna, a few carpals and metacarpals, and several phalanges are missing, but the other bones are well preserved in articulation. The humerus has a spheroid proximal head, slender shaft, and expanded and dorsoventrally flattened distal end. Morphological features around the proximal end are not very clear due to its breakage during excavation. The humerus is constricted below the head, and the unbroken part of the neck has a rough surface. The posterior edge of the humerus is a smooth convex curve from the neck to the wide and flattened distal end, while the anterior edge is approximately straight. The two articular facets for the radius and ulna are concave and clearly defined. In addition, there are two facets for supernumeraries that are flat or even rather slightly convex. The distal end of the humerus is dorsoventrally thickest (40 mm) at the facet for the radius.

The epipodials and carpals are polygonal. The radius is pentagonal with a small but obvious process at the lateroproximal corner that may be of taxonomic value as well as a sign of age. The proximal end of the radius is convex to fit the concave end of the humerus. The ulna is damaged but from the space between other bones, it is assumed to have been an irregular hexagon articulating with humerus, radius, intermedium, ulnare and two supernumeraries. All three proximal carpals are preserved. The

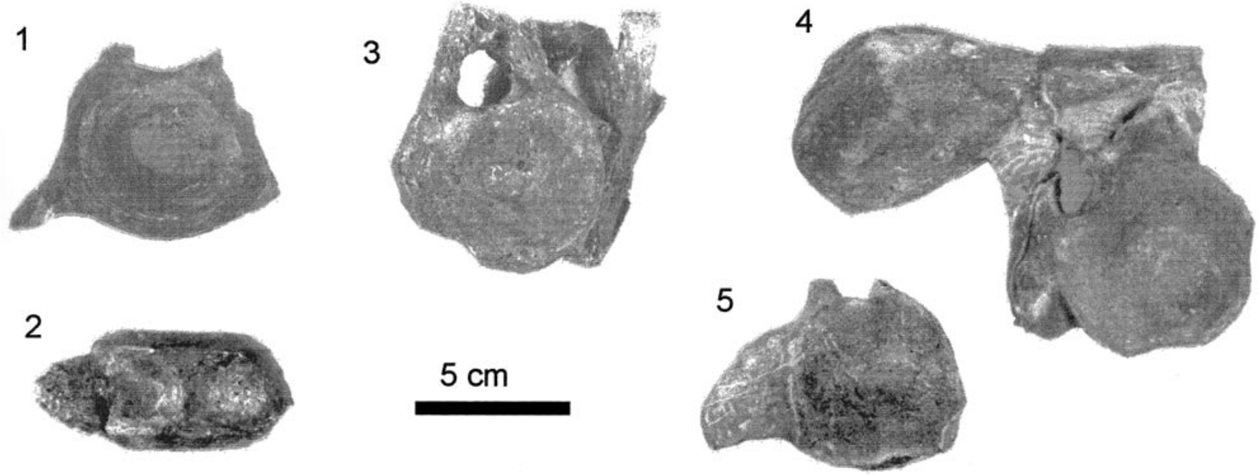

FIGURE 5—UMUT MV 19965. *1,* Cervical A in posterior view; *2,* same in ventral view; *3,* cervical B; *4,* caudal A and the distal end of ilium; *5,* caudal C. Scale bar = 10 cm.

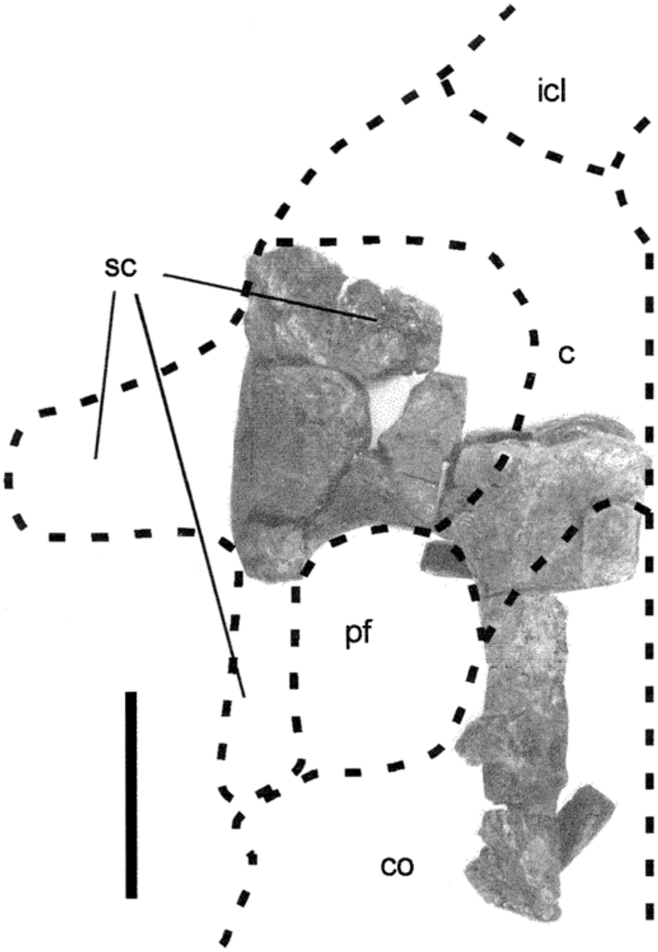

FIGURE 6—Anterior portion of the pectoral girdle of UMUT MV 19965. Abbreviations: cl, clavicle; sc, scapula, co, coracoid, pf, pectoral fenestra. Dashed lines suggest a reconstruction based on *Dolichorhynchops osborni* (Williston, 1903). Scale bar = 10 cm.

radiale has a marked process at its lateroproximal edge like the radius. Three supernumeraries lie along the posterior side of the forelimb; one is next to the broken ulna and proximal to the ulnare, two are directly articulated to the humerus, lateral to the ulna. Distal carpals I and II are in place, but distal carpal III is missing, perhaps lost during excavation.

The fifth digit is posteriorly offset at the metacarpal, and metacarpal V is not in line with the other metacarpals, a condition seen in Late Jurassic and Cretaceous plesiosarus. In general, the phalanges are stout at the proximal end, and become slender and more cylindrical in shape toward the distal end. There are several disarticulated distal phalanges whose precise position cannot be reconstructed.

There are fragments of ribs on the anterior pectoral girdle, and at least five gastralia are arranged on the coracoids in parallel with the medial line. Three are almost straight, and two have a significant upward curvature. None of them has a complete end.

The ventral half of the right ilium is preserved. The ventral articular facets are flat and are subtriangular in shape. The boundary between ischial and acetabular facets is not clearly defined, but the former is about twice as large as the latter. The margins of the facets are slightly raised.

Only a small portion of the right pubis is preserved. The preserved portion of the pubis is slightly convex dorsally near the acetabular face, but nearly flat toward the midline, except for the area locally distorted by an overlying centrum. It is thickest at the acetabulum and thinnest at the center, and gradually increases its thickness toward the missing medial symphysis.

Two pebble-sized clasts were found on the posterior end of the right coracoid. In addition to their occurrence at the stomach region, their rounded shape and lithology that differs from the sediments surrounding the plesiosaur skeleton suggest that they are gastroliths. There are a number of reports of gastroliths from elasmosaurid plesiosaur skeletons (e.g., Darby and Ojakangas, 1980), but no reliable reports from polycotylid skeleton (Storrs, 1993). A number of cephalopod jaw apparati preserved in the stomach region are regarded as dietary remains (Sato and Tanabe, 1998).

Discussion.—There are no sutures on the vertebrae to suggest immaturity, and this specimen is probably of an adult individual whose ossification is complete. In fact, the fused girdle elements, humerus with clearly defined articular facets, polygon-shaped

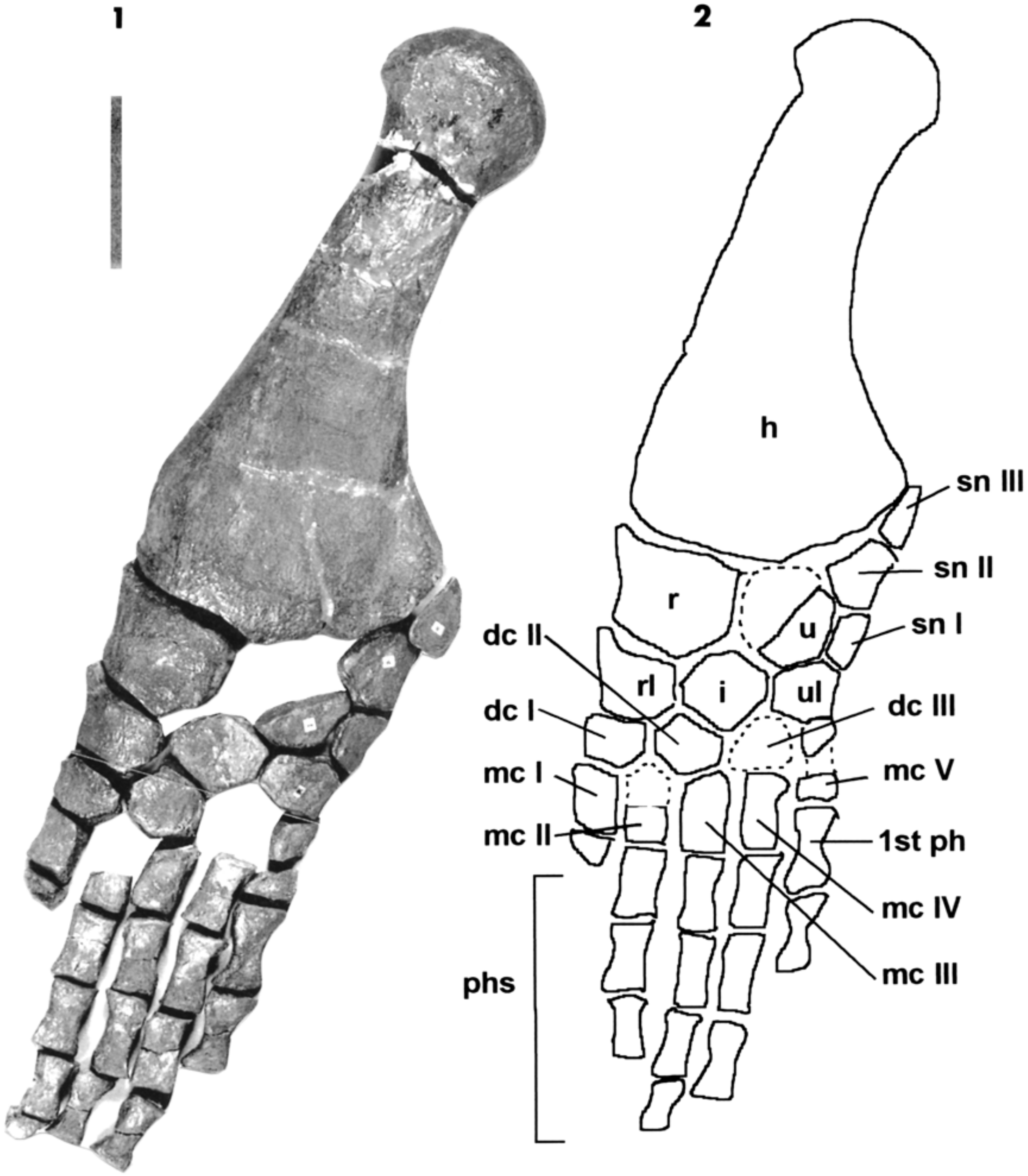

FIGURE 7—Right forelimb of UMUT MV 19965. Abbreviations: dc, distal carpal; h, humerus; I, intermedium; mc, metacarpal; ph, phalanx (phs, phalanges); r, radius; rl, radiale; sn, supernumeraries; u, ulna; ul, ulnare. Scale bar = 10 cm.

paddle elements, anteroproximal processes of some limb bones, and well preserved supernumeraries indicate its complete state of ossification (see the ontogenetic series of *Cryptoclidus* in Andrews, 1910).

Because of the lack of a definition for Polycotylidae within a phylogenetic framework and the incompleteness of the specimen, we had to take a rather phyletic approach in determining its taxonomy. The lack of skull elements in UMUT MV 19965 prevents verification of the diagnostic characters of the skull given by Carpenter (1996). There are only four postcranial characters; short neck, 19–26 cervicals, cervical ribs single-headed, epipodials short and wide. However, those characters are not necessarily unique to this family, and comparison with other families and evaluation of additional characters not employed in the Carpenter's (1996) diagnosis seem to be required.

The number of the cervicals is not known in the Japanese specimen, but the cervicals have rib facets for single-headed ribs. The centra of the cervicals are proportionally short compared to those of Elasmosauridae, and they lack the lateral ridge of the centrum that is typically observed in the anterior cervicals of long-necked forms (Brown, 1981). The lateral sides of each centrum are concave to flat in the Japanese specimen and if concave, the rims of the articular faces are elevated and expanded at the anterior end. This condition is characteristic among members of the Family Polycotylidae (personal observation; Bardet, personal commun.). Cretaceous ‘‘pliosauroids’’ (*Brachauchenius*, *Plesiopleurodon*, and *Kronosaurus*) have single-headed cervical ribs, but the Japanese specimen differs in the size and morphology of the humerus. Comparison of the vertebral characters with those of the Family Cryptoclididae is complicated, because of the lack of diagnostic characters at family level. *Cryptoclidus* has cervical centra that are proportionally longer than that of the Japanese specimen, while the cervical vetebrae of *Morturneria* (Chatterjee and Small, 1989; Chatterjee and Creisler, 1994) are platycoelous, and have distinct binocular-shaped articular faces. In addition to the substantial difference in size, the anterior cervicals of *Aristonectes* (Cabrera, 1941) are more elongated, while the shortened posterior cervicals differ in the ornamentation of the centrum.

Evaluation of the ''shortness'' of the epipodials depends on the taxa to be compared. In this case, the epipodials are relatively long in comparison with other polycotylid plesiosaurs, longer than or comparable to those of cryptoclidids (Andrews, 1910; Cabrera, 1941), but shorter than those of earlier plesiosaurs such as *Plesiosaurus* (Storrs, 1997) and *Pliosaurus* (Andrews, 1913). This character varies with the members of Family Elasmosauridae; those of the Japanese plesiosaur are longer or comparable to those of many elasmosaurids from the Upper Jurassic and younger strata, but shorter than those of the Lower Jurassic *Microcleidus* (Watson, 1911).

The vertebrae of UMUT MV 19965 are smaller than those of *Polycotylus* and *Trinacromerum* specimens, with the exception of some juvenile specimens (see Tables in Appendix). Concavities on the lateral surface of the centrum are obvious throughout the vertebral column in *P. latipinnis* (YPM 1125) and *D. osborni* (MCZ 1064), shallowly concave in dorsals of *T. kirki* (Russell, 1935 p. 386), and barely seen in presacrals of *T. bentonianum* (USNM 10945). There seems not to be a generalized change in this character in relation to body size at the family level.

There are no ventral foramina in a few of the centra of the Japanese specimen, unlike most of the vertebrae among the described polycotylids, but this is known to be a variable character (Storrs, 1981). At least two of the vertebrae have a pair of foramina on the dorsal surface of the centra, on the floor of the neural canal. Such foramina in *T. bentonianum* (USNM 10945) are located in a pair of depressions in the canal, whereas the foramina in UMUT MV 19965 are simple pits on a plain floor.

Chevron facets on the caudal vertebrae have been used to distinguish *Polycotylus* and *Dolichorhynchops* (Williston, 1906; Carpenter, 1996). In *Polycotylus*, there are two prominent facets on both the anterior and posterior central faces, while in *Dolichorhynchops* and *Trinacromerum*, the facets are not prominent and are restricted mostly to the posterior face. Three of the caudal vertebrae of UMUT MV 1996 have moderately prominent chevron facets similar to *Dolichorhynchops* and *Trinacromerum*, not the prominent facets seen in *Polycotylus.* Two other caudals have no facets and probably came from the distal end of the tail.

There are few polycotylid specimens with measurable propodial bones and reliable specific identification. Several isolated polycotylid propodials have been described as type specimens of polycotylid species (those in quotes in Appendix) that were later invalidated (Welles, 1962). The humerus of UMUT MV 19965 is smaller than that of ''*T. latipinnis*'' (Williston, 1903) and the holotypes of *T. kirki* and *T. bonneri* (KUVP 40002; Adams, 1997), comparable to the type specimens of ''*T. latimanus*'' and ''*T. anonymum*'', and larger than that in ''*T. dolichopus*'' and *D. osborni* specimens. Distinct features of the Japanese specimen are the relatively elongated epipodials and additional ossifications at the lateroposterior corner of the radius and radiale (Fig. 5). Such an additional ossification is likely to be an indication of old age, but the large epipodials may have taxonomic meaning. Compared to other polycotylid specimens of both juveniles and adults, the radius is long proximodistally, and the articular face for the radiale is not as large, relative to the faces for intermedium and radiale. Jurassic plesiosaurs such as *Plesiosaurus* have long epipodials, considered to be plesiomorphic for Plesiosauria (Storrs, 1997). Brown (1981) noted a chronological trend for shortening of the epipodials in Plesiosauria. The long epipodials seen in the Japanese specimen may suggest the retention of the primitive character within the Polycotylidae. This is in line with the relatively early chronological position of the specimen.

As discussed above, UMUT MV 19965 has potentially unique characters in the elongated epipodials, in addition to its notably small size as an adult individual. In spite of the evidence of complete ossification in the vertebrae, fused pectoral girdle, and the elements of the limb, the measurements of the vertebrae and limbs, suggest that its size was comparable to or smaller than adult polycotylid specimens, but larger than the compared *Dolichorhynchops* specimens. These facts suggest that the fossil may represent a new taxon. The skeleton, however, lacks so many parts of the body and the skull, that it would be unwise to designate it the holotype of a new taxon because this would be extremely difficult to diagnose. Its incompleteness also prevents detailed analysis of its phylogenetic relationship to other polycotylids. We must await the discovery of a better-preserved specimen.

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Appendix I

Tables of measurements of UMUT MV 19965 and other polycotylid specimens.

Table *1* Measurements of vertebral centra of UMUT MV 19965 (in mm).

Vertebrae	Length	Height	Breadth
Cervical A	40	53	64
Cervical B	40	55	65
Dorsal A	40	56	64
Sacral A	39	55	61
Sacral B	38	57	60
Caudal A	40	57	62
Caudal B	37	51	57
Caudal C	34	52	53
Caudal D	25	32	34

TABLE *2*—Length/height/breadth of the smallest and largest dimensions of vertebral centra of polycotylid plesiosaurs (in mm). Marks and abbreviations: *, juvenile or young individuals; Italic figures, estimation; Number in parenthesis, sequencial number of the vertebra in the vertebral column; Lg/Sm, largest/smallest vertebra of unknown sequential number in the region of the column (i.e. cervical, dorsal etc.); n.a, data not available.

Specimen	Cervical vertebrae
UMUTMV 19965	40/53/64 (A), 40/55/65 (B)
Polycotylus latipinnis (YPM 1125)	38/54/64 (4), 41/80/93 (25)
Trinacromerum bentonianum (USNM 10945)	52/60/68 (Sm), 53/76/82 (Lg)
T. kirki (MM v216)	n.a.
T. ''willistoni'' (KUVP 5070)	29/n.a./n.a. (Sm), 43/n.a./n.a. (Lg)
T. ''brownorum'' (SMPSMU 3025)	34/44/n.a. (4), 45/*70*/n.a. (20)
*''*T. anonynum*'' (YPM 1129)	23/n.a./n.a. (3), 36/n.a./n.a. (21)
**Dolichorhynchops osborni* (KUVP 1300)	28/30/35 (3), 26/38/45 (16)
**D. osborni* (FHSM VP404)	19/23/30 (3), 32/42/n.a. (20)
**D. osboni* (MCZ 1064)	34/22/n.a. (3), 26/46/48
Specimen	Dorsal vertebrae
UMUTMV 19965	40/56/64 (A)
P. latipinnis (YPM 1125)	45/86/98 (30), 57/79/81 (50)
T. bentonianum (USNM 10945)	62/85/90 (Sm), *68*/93/94(Lg)
T. kirki (MM v216)	64/n.a./96 (Sm), n.a./87/97 (Lg)
T. ''willistoni'' (KUVP 5070)	43/n.a./n.a. (Sm), 53/n.a./n.a. (Lg)
T. ''brownorum'' (SMPSMU 3025)	n.a.
*''*T. anonynum*'' (YPM 1129)	34/n.a./n.a. (24), 48/n.a./n.a. (31)
**D. osborni* (KUVP 1300)	n.a.
**D. osborni* (FHSM VP404)	32/47/n.a. (25), 35/50/n.a. (43)
**D. osboni* (MCZ 1064)	38/n.a./n.a. (22), 45/n.a./n.a. (42)
Specimen	Sacral vertebrae
UMUTMV 19965	39/55/61 (A), 38/57/60 (B)
P. latipinnis (YPM 1125)	58/75/79 (54), 59/76/77 (56)
T. bentonianum (USNM 10945)	68/91/92 (Sm), 65/*99*/93 (Lg)
T. kirki (MM v216)	n.a.
T. ''willistoni'' (KUVP 5070)	n.a.
T. ''brownorum'' (SMPSMU 3025)	n.a.
*''*T. anonynum*'' (YPM 1129)	n.a.
**D. osborni* (KUVP 1300)	n.a.
**D. osborni* (FHSM VP404)	33/n.a./n.a. (47), 37/n.a./n.a. (49)
**D. osboni* (MCZ 1064)	37/n.a./n.a. (43), 36/n.a./n.a. (45)
Specimen	Caudal vertebrae
UMUTMV 19965	40/57/62 (A), 25/32/34 (D)
P. latipinnis (YPM 1125)	37/47/47 (69)
T. bentonianum (USNM 10945)	n.a.
T. kirki (MM v216)	n.a./77/86 (Lg)
T. ''willistoni'' (KUVP 5070)	n.a.
T. ''brownorum'' (SMPSMU 3025)	n.a.
*''*T. anonynum*'' (YPM 1129)	38/n.a./n.a. (54), 34/n.a./n.a. (57)
**D. osborni* (KUVP 1300)	25/n.a./40 (n.a), 12/n.a./12 (n.a)
**D. osborni* (FHSM VP404)	35/n.a./n.a. (50), 28/52/n.a. (55)
**D. osboni* (MCZ 1064)	37/n.a./n.a. (46), 30/n.a./n.a. (60)

TABLE *3*—Comparison of the dimensions of propodial bones of UMUT MV 19965 and other polycotylid plesiosaurs (in mm). Marks and abbreviations: *, juvenile or young individuals; **, data recalculated from published figures; L, left; R, right; n.a., data not available.

	Humerus		Femur	
Specimen	Length	Widest breadth	Length	Widest breadth
UMUT MV 19965	R357	R157	n.a.	n.a.
**''*Polycotylus latipinnis*'' (Williston, 1902)	R492	R256	n.a.	n.a.
Trinacromerum kirki (MM v216)	R455	R222+	R473	R236
T. bonneri (KUVP 40002)	R526, L546	R320, L325	R515, L530	R300, L280
**''*T. anonynum*''(YPM 1129)	L340	L167	L380	L170
''*T. latimanus*'' (Williston, 1908)	L351	L250	n.a.	n.a.
*,***Dolichorhynchops osborni* (KUVP 1300)	R260	R140	R380	R170
**D. osborni* (FHSM VP404)	R330	R165	R335	R190