OSTEOLOGY OF A NEW PLESIOSAUR FROM THE LOWER CRETACEOUS (ALBIAN) THERMOPOLIS SHALE OF MONTANA

PAT S. DRUCKENMILLER¹

Museum of the Rockies, Montana State University, Bozeman, Montana 59717-2730

ABSTRACT—A new taxon of Cretaceous short-necked plesiosaur, *Edgarosaurus muddi*, gen. et sp. nov., is described. The specimen consists of a complete skull, 34 vertebrae including the entire series of 26 cervicals, and a nearly complete forelimb. The new taxon occurs in marine sediments of the Thermopolis Shale (late Albian), deposited during an early transgression of the Western Interior Seaway. The skull of *Edgarosaurus* is the oldest, and one of the best preserved plesiosaur specimens from the Cretaceous Western Interior of North America described to date. *Edgarosarus* differs from the morphologically and stratigraphically close short-necked taxon *Plesiopleurodon wellesi* in a number of cranial characters. In the absence of an established phylogenetic framework, the new plesiosaur is placed in the Polycotylidae, as recently defined by Carpenter in 1996. It is plesiomorphic with respect to other polycotylids in that it possesses a relatively robust and moderately elongated rostrum, a pineal foramen, caniniform teeth, a shorter mandibular symphysis, and a relatively high number of cervical vertebrae.

INTRODUCTION

Plesiosaurs (Diapsida: Sauropterygia) represent a monophyletic clade of Mesozoic marine reptiles (Sues, 1987; Tschanz, 1989; Storrs, 1991). The group existed throughout most of the Mesozoic, from the Late Triassic to the end of the Cretaceous, and enjoyed a wide geographic distribution, occurring in marine and near shore deposits worldwide (Rieppel, 1997). In spite of this wide temporal and spatial distribution, the vast majority of material from which we can interpret their evolutionary history comes from restricted windows of time, notably the Early and Late Jurassic of Europe, and the Late Cretaceous of North America (Tarlo, 1960; Welles, 1962; Brown, 1981). Material from the Early Cretaceous of North America, especially during the initial phases of the expanding Western Interior Seaway, is extremely fragmentary. To date, the earliest described Cretaceous plesiosaur material from the Western Interior is a handful of generically indeterminate plesiosaur vertebrae from the Albian (?) of Clark and Kiowa counties, Kansas (Welles, 1962), a series of Trinacromerum sp. vertebrae from the Albian of Texas (Storrs, 1981), and the skull and partial skeleton of a recently described short-necked taxon *Plesiopleurodon wellesi*. from the lower Cenomanian of Wyoming (Carpenter, 1996). The discovery of a new short-necked taxon from the Albian of south-central Montana helps to expand our knowledge of plesiosaur distribution and diversity during the early expansion of the Western Interior Seaway.

In the spring of 1993 a partial plesiosaur, consisting of a complete skull, the entire series of cervical and pectoral vertebrae, and a nearly complete forelimb, was discovered in the upper member of the Thermopolis Shale (upper Albian) in Carbon County, Montana (Druckenmiller, 1998) (Fig. 1). The well preserved specimen, MOR 751 (abbreviations listed below), represents a new plesiosaur taxon, and represents the oldest and most complete specimen of a plesiosaur described from the Western Interior Basin.

Institutional Abbreviations: BMNH, Natural History Museum, London (specimen numbers prefixed by R); CM, Carnegie Museum, Pittsburgh, Pennsylvania; **KUVP**, University of Kansas Natural History Museum, Lawrence; **MOR**, Museum of the Rockies, Bozeman, Montana.

STRATIGRAPHY

The specimen, MOR 751, occurs in the upper Thermopolis Shale, late Albian marine deposits of the Cretaceous Western Interior Seaway (Fig. 2). At the type locality, these marine shales are underlain by near-shore marine sandstones of the Fall River (Dakota) Sandstone, which record the start of marine transgression over the terrestrial redbed deposits of the Lower Cretaceous Kootenai (Cloverly) Formation. A sequence boundary unconformity separates the Kootenai and Fall River Formations; a transgressive unconformity separates the Fall River Formation and overlying Thermopolis Shale (K. Porter, pers. comm.). Marine shales and siltstones of the Mowry Shale conformably overlie the Thermopolis.

The Thermopolis Shale consists of three units: a lower shale unit, the Skull Creek Member; a middle sandy unit, the Muddy/ Newcastle Sandstone Member; and an upper shale unit, the Shell Creek Member. This paper uses the term "Thermopolis Shale" to refer to all three units, in contrast to some studies which restrict the term to only the lower shale (Eicher, 1960). The Skull Creek Member records the initial transgression of a northern, boreal arm of the seaway into the Western Interior Basin (Vuke, 1984). Deposition of the uppermost Skull Creek shales occurred as the northern and southern arms of the seaway joined and spread the entire length of the North American continent for the first and only time in the Early Cretaceous (Eicher, 1960). The Muddy/Newcastle sandstone (Dyman et al., 1995) represents deposition associated with separation of the northern and southern arms of the seaway during the late Albian regression and subsequent transgression (Vuke, 1984; Porter et al., 1997). An unconformity placed at the base of this sandstone is interpreted as a lowstand surface of erosion, or sequence boundary (Dolson et al., 1991; SB2 of Porter et al., 1997). This sequence boundary corresponds to a basin-wide, eustatically controlled drop in sea level dated at 98.5 Ma, or older (Obradovich, 1993). Deposition of the Shell Creek occurred during the second major Albian transgression, although the northern and southern arms of the Western Interior Seaway did not join until

¹ Present Address: Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada, and Royal Tyrrell Museum of Palaeontology, P.O. Box 7500, Drumheller, Alberta, TOJ 0Y0, Canada; email: pdrucken@ucalgary.ca



FIGURE 1. Locality map of *Edgarosaurus muddi* in south-central Montana.

early Cenomanian time, during deposition of the Mowry Shale (Vuke, 1984).

The new plesiosaur occurs in the Shell Creek Member, approximately 30 m above the top of the Muddy/Newcastle Sandstone Member. Ammonites (MOR-IV 336), identified as *Neogastroplites haasi* (W. Cobban, pers. comm.) were collected at the Bridger Ridge locality, approximately 90 m above the plesiosaur horizon. Radiometric ages of bentonites, recently dated with the 40Ar/39Ar laser fusion method, fall within the biostratigraphic range of *N. haasi*, between 98.54 \pm 0.70 Ma and 98.74 \pm 0.59 Ma (Kauffman et al., 1993; Obradovich, 1993). Thus, the approximate stratigraphic occurrence of the new plesiosaur is constrained by the 98.5 Ma age of the underlying sequence boundary, SB2, and the overlying 98.5–99.0 Ma age of the overlying ammonite (uppermost Albian).

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903 SAUROPTERYGIA Owen, 1860 EUSAUROPTERYGIA Tschanz, 1989 PLESIOSAURIA de Blainville, 1835 POLYCOTYLIDAE Cope, 1869 *EDGAROSAURUS*, gen. nov.

Type and Only Species—*Edgarosaurus muddi*, sp. nov. **Type Locality**—T5S, R24E, Sec. 28 (108° 46' W, 45° 24' N); 5 mi southeast of Edgar, Carbon County, Montana.

Range—Lower Cretaceous (upper Albian), within, or just below the *Neogastroplites haasi* zone, upper Thermopolis Shale.

Etymology—The genus is named after the community of Edgar, Montana, located near the type locality.

Diagnosis—Moderately sized (approximately 3.5 m in length), short-necked plesiosaur possessing the following suite of characters: pineal foramen present (absent in *Dolichorhynchops* and *Trinacromerum*); fenestra ovalis present (absent in *Dolichorhynchops*); suspensorium vertically oriented (angled posteriorly in *Plesiopleurodon* and *Dolichorhynchops*); six to seven premaxillary teeth (commonly five to six in *Dolichorhynchops*, five in *Trinacromerum bonneri*); caniniform teeth



FIGURE 2. Generalized stratigraphic section of the study area, northern Bighorn Basin, south-central Montana.

present (absent in *Dolichorhynchops* and *Trinacromerum*); relatively short mandibular symphysis bearing six pairs of dentary teeth (eight in *Plesiopleurodon*, 18–20 in *Dolichorhynchops*); 26 cervical vertebrae (19 in *Dolichorhynchops*, 20 in *Trinacromerum*); forelimb phalangeal formula 7-11-10-9-9.

> EDGAROSAURUS MUDDI, sp. nov. (Figs. 3-16)

Holotype and Only Known Specimen—MOR 751, possessing a complete skull, 26 cervical, three pectoral, and five anterior dorsal vertebrae, and a nearly complete forelimb.

Etymology—"Mudd," named in memory of Kevin Mudd (deceased) of Bridger, Montana.

Diagnosis—As for genus.

DESCRIPTION

General Comments

The skull (Figs. 3–8; Table 1) was found articulated to 25 cervical vertebrae, while nine other vertebrae, found in the outwash, easily fit together to form a continuation of the vertebral column. Three dorsal vertebrae, however, could not be rearticulated confidently to the series. The paddle, found within a meter of the posterior end of the vertebral column presumably articulated with the rest of the skeleton before becoming isolated by erosion. The articulated and well preserved state of the specimen, its occurrence in a black, fissile mudstone, and physical location with respect to paleogeographic reconstructions



FIGURE 3. Skull of Edgarosaurus muddi, MOR 751, from the upper Thermopolis Shale of south-central Montana, in left lateral aspect.

(Vuke, 1984) indicates burial in an offshore marine environment.

Prior to mechanical preparation, the skull and articulated atlas, axis, and third cervical vertebra were scanned on a General Electric 9800 Computerized Tomography (CT) scanner. A series of 1 mm digital slices, with 0.5 mm of overlap between slices, was created and saved on 8 mm digital tape. Processed on CEMAX medical hardware, the images yielded a three dimensional computer reconstruction for viewing internal structures of the skull.

An examination of cervical vertebrae and ribs, as well as the proximal propodial fragment suggest that the individual was a



FIGURE 4. Interpretation of *Edgarosaurus muddi*, MOR 751, from the upper Thermopolis Shale of south-central Montana, in left lateral aspect. **Abbreviations: a**, angular; **aiv**, anterior interpretygoid vacuity; **ar**, articular; **bs**, basisphenoid; **cp**, coronoid process; **d**, dentary; **drsq**, dorsal ramus of squamosal; **en**, external nares; **eo**, exoccipital–opisthotic; **ep**, epipterygoid; **f**, frontal; **j**, jugal; **mx**, maxilla; **oc**, occipital condyle; **or**, orbit; **p**, parietal; **pfo**, pineal foramen; **pmx**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pof**, postfrontal crest; **pr**, prootic; **prf?**, prefrontal?; **pt**, pterygoid; **q**, quadrate; **sa**, surangular; **scl**, sclerotic ring; **sq**, squamosal; **stf**, supratemporal fenestra.



FIGURE 5. Skull of Edgarosaurus muddi, MOR 751, from the upper Thermopolis Shale of south-central Montana, in right lateral aspect.

young adult. The neural arches are fused to the vertebral centra, but the sutures remain visible. Similarly, fusion of the cervical ribs with the centrum is nearly complete in all but the anteriormost cervical vertebrae. On the proximal humerus, only a narrow isthmus connects the capitulum to the tuberosity, indicating an adult state (Brown, 1981).

Total body length approximation of *Edgarosaurus* is based on comparisons of the skull plus neck length to total body length ratios from published reconstructions of two nearly complete short-necked plesiosaurs, *Dolichorhynchops osborni*, KUVP 1300 (19 cervical vertebrae) (Williston, 1902) and *Peloneustes philarchus*, BMNH R. 3318 (21–22 cervical verte-



FIGURE 6. Interpretation of *Edgarosaurus muddi*, MOR 751, from the upper Thermopolis Shale of south-central Montana, in right lateral aspect. **Abbreviations: a**, angular; **alv**, alveolus; **ar**, articular; **c**, coronoid; **cp**, coronoid process; **d**, dentary; **ect**, ectopterygoid; **f**, frontal; **j**, jugal; **mx**, maxilla; **pmx**, premaxilla; **po**, postorbital; **pt**, pterygoid; **ptf**, pterygoid flange; **ptrq**, pterygoid ramus of the quadrate; **q**, quadrate; **qrpt**, quadrate ramus of pterygoid; **sa**, surangular; **sp**, splenial; **sq**, squamosal.



FIGURE 7. Reconstruction of skull of *Edgarosaurus muddi*, MOR 751, from the upper Thermopolis Shale of south-central Montana in left lateral aspect. **Abbreviations: a**, angular; **ar**, articular; **d**, dentary; **drsq**, dorsal ramus of squamosal; **en**, external nares; **f**, frontal; **for**, foramen; **g**, glenoid fossa; **j**, jugal; **mx**, maxilla; **or**, orbit; **p**, parietal; **pfo**, pineal foramen; **pmx**, premaxilla; **po**, postorbital; **pof**, postfrontal; **prf**, prefrontal; **q**, quadrate; **sa**, surangular; **scl**, sclerotic ring; **sq**, squamosal; **stf**, supratemporal fenestra.

brae) (Andrews, 1910). For both taxa, skull and neck lengths represent 35–40 percent total body lengths. *Edgarosaurus*, with 26 cervical vertebrae, is assumed to have a proportionately longer pre-trunk length estimated at 40–45 percent body total, resulting in an estimated overall length of 3.2–3.7 m.

Dorsal Elements of the Skull

The paired premaxillae form much of the anterior half of the preorbital region of the skull (Figs. 7–8). There are six to seven alveoli on the left premaxilla, and at least six on the right premaxilla that bear large, procumbent, slightly recurved, caniniform teeth. The premaxilla bulges outward around the third and fourth alveoli. On the left side of the skull, the digitate premaxilla-maxilla suture runs posteromedially from the tooth row margin just posterior to alveolus six. Slender dorsal processes of the premaxillae extend caudad along the skull midline. Unlike *Plesiopleurodon wellesi* (Carpenter, 1996), they do not form the dorsal margin of the external nares but separate the frontals and taper to a point just anterior to the frontal-parietal suture (Fig. 8). The anterior portion of the premaxilla is pitted and several nutrient foramina are present dorsal to the premaxillary and maxillary tooth rows.

The maxilla contacts the premaxilla along a straight suture extending to the region of the external nares. The right naris is crushed nearly shut, while the left is largely undistorted. Here, the maxilla forms at least the anterolateral corner of the naris. The region between the external nares and the orbits is poorly preserved and the presence of a prefrontal is uncertain. Likewise, it is not possible to detect the lachrymal, which may be lacking in sauropterygians altogether (Storrs, 1991). The maxilla appears to form the poorly preserved ventral rim of the orbit, but no sutures are visible. It continues caudad into a long, slender posterior ramus that extends to the midpoint of the ventral surface of the temporal bar. The left maxilla bears 26 alveoli that diminish in size caudad. Crushing of the right maxilla prevents an accurate tooth count.

The frontals are separated along the dorsal midline by the dorsal processes of the premaxilla. The anterior margin of the

frontal cannot be discerned. It is also unclear whether the frontals form the dorsal rim of the orbit or if this border is shared by the prefrontals. A deeply digitate suture, positioned in line with the posterior margin of the orbits, marks the frontal-parietal contact (Fig. 8). Thin, blade-like processes of the frontals extend and meet ventrally, forming a bony septum between the orbits. The lateral walls of the olfactory sulcus, present as a medial groove or foramen, are housed in these ventral processes (Carpenter, 1997).

In the postorbital region, the right side is crushed. In contrast, the left side remains largely intact but is partially obscured by matrix. Ventrally, the postorbital contacts the jugal near the base of the postorbital bar along an oblique, straight suture running anterodorsally to posteroventrally. A thin flange extends along the medial surface of the postorbital bar forming a partial internal wall between the orbit and the supratemporal fenestra.

The exact size and shape of the postfrontal are uncertain. Its inferred position lies at the dorsolateral corner of the orbits, bounded by the postorbital laterally and ventrally, the supratemporal fenestra posteriorly, the parietal medially, and the frontal anteriorly. A low crest (pofc, Fig. 4) runs on each side of, and roughly parallel to the longitudinal midline of the skull in this region. Similar crests have been described on the postfrontal in *Pliosaurus brachyspondylus* (Taylor and Cruickshank, 1993) and in *Rhomaleosaurus zetlandicus* (Taylor, 1992).

The left jugal is well preserved and intact, while the right is incomplete and partially displaced. The jugal forms the posterolateral margin of the orbit and the anterolateral margin of the supratemporal fenestra. The maxilla underlies the jugal. Posteriorly, the contact with the squamosal remains unclear although the jugal appears to form at least the anterior half of the rim of the lower temporal bar. Two conspicuous foramina at the base of the postorbital bar perforate each jugal.

The parietals form the roof of the braincase and, along the ventral midpoint, contact the supraoccipital. A conspicuous pineal foramen is situated just posterior to the frontal-parietal sutures, in line with the anterior margin of the supratemporal fenestra (Figs. 4, 8). CT imaging shows that the pineal foramen



FIGURE 8. Reconstruction of skull of *Edgarosaurus muddi*, MOR 751, from the upper Thermopolis Shale of south-central Montana, in dorsal aspect. **Abbreviations: drsq**, dorsal ramus of squamosal; **en**, external nares; **f**, frontal; **j**, jugal; **mx**, maxilla; **or**, orbit; **p**, parietal; **pf**, pineal foramen; **pmx**, premaxilla; **po**, postorbital; **pof**, postfrontal; **prf**, prefrontal; **sq**, squamosal; **stf**, supratemporal fenestra.

perforates the parietal and slopes ventrally and posteriorly from its dorsal opening. Dorsally, the parietals meet along the midline to form a distinct sagittal crest. A thickened flange on the anteroventral corner of the parietal may have allowed for a contact with the epipterygoid reinforced by ligaments. This contact, however, is now lost due to crushing.

The parietal-squamosal suture extends from a point along the apex of the posterior third of the sagittal crest and runs ventrolaterally along the medial wall of the supratemporal fenestra (Figs. 7–8). A distinct change in bone fiber orientation also occurs between the posterior margin of the parietal and the anterior edge of the dorsal ramus of the squamosal, similar to that described by Taylor (1992) for *Rhomaleosaurus zetlandicus*. The squamosals overlap the parietals dorsally along this contact. This overlapping contact is also apparent in CT images.

Each suspensorium of *Edgarosaurus muddi*, composed of the squamosal and quadrate, is oriented along the vertical axis, not inclined posteriorly as in *Trinacromerum bentonianum* and *Plesiopleurodon wellesi* (Carpenter, 1996). The squamosals form the posterior wall and part of the lateral wall of the supratemporal fenestra. The dorsal ramus of each squamosal meets its opposite at a digitate suture along the dorsal midline. Together, the posterior portions of the parietals and the dorsal ramus of the squamosal form a shelf that overhangs the back of the skull. This shelf extends posteriorly, beyond the occipital condyle,

TABLE 1. Selected skull and paddle dimensions of *Edgarosaurus muddi*.

Measurement	Dimensions (in mm)
Skull length (rostrum to quadrate)	475
Rostrum length (rostrum to anterior orbit margin)	255
Supratemporal fenestra length (on dorsal midline)	115
Subtemporal fenestra length	105
Orbit length	87
Estimated skull width	150(?)
Pineal foramen length	10
Left maxillary tooth row length	245
Left premaxillary tooth row length	115
Maximum maxillary tooth crown height	49
Anterior interpterygoid vacuity length	68
Posterior interpterygoid vacuity length	61
Mandibular symphysis length (ventral surface)	145
Mandible length	520
Retroarticular process length	40
Dentary tooth row length	360
Radius width	85
Radius length	48
Ulna width	68
Ulna length	48

nearly to the third cervical vertebra. The ventral ramus of the squamosal forms part of the posterior portion of the lateral temporal bar, extending anteriorly to contact the jugal.

The quadrate constitutes the remainder of the suspensorium. Medial and lateral condyles are visible on the left quadrate, but are fractured and distorted. The pterygoid ramus of the quadrate unites with the quadrate ramus of the pterygoid along a squamous contact, with the pterygoid lying medial to the quadrate.

Four or five elements of the sclerotic ring (scl, Fig. 4) remain within the left orbit. Crushed inwards, they now rest along the left lateral surface of the ventral process of the frontal. Two well preserved plates measure approximately 15 mm along each edge and vary between 0.5 and 1.5 mm in thickness. On each, the bone fiber radiates laterally from a central point, akin to spokes on a wheel. Adjacent plates contact end to end, with no apparent overlap along their lateral margins. Sclerotic plates are infrequently reported in plesiosaurs, but are described in the North American Cretaceous forms *Styxosaurus* (*Cimoliosaurus*) *snowii* (Williston, 1890:175), *Dolichorhynchops osborni* (Williston, 1903:18–19), and *Trinacromerum bentonianum* (*willistoni*) (Riggs, 1944:78), as well as several European genera (see Andrews, 1910:9; Linder, 1913:345–346; Storrs and Taylor, 1996:416; Storrs, 1997:155, and others).

Braincase

The right exoccipital–opisthotic is well preserved and largely uncrushed. Three foramina allow for passage of cranial nerves and blood vessels, piercing the right exoccipital–opisthotic near the base of the paraoccipital process. Two closely associated foramina, placed posteriorly on the exoccipital–opisthotic, are interpreted as exits for cranial nerve XII. A single large foramen, anterior to the opening for XII, may represent exits for IX, X, and XI, as well as the jugular vein. The ventral portion of the posterior vertical semicircular canal as well as the posterior portion of the horizontal semicircular canal appear within the left exoccipital–opisthotic. The paraoccipital process extends posterolaterally from the lateral surface of the exoccipital–opisthotic to a distal facet for reception with the squamosal.

The supraoccipital forms the dorsal margin of the foramen magnum. A ventral facet for reception of both the exoccipital– opisthotic and prootic is visible on the left side of the supraoccipital. This facet is perforated by the dorsal continuation of both the anterior and posterior vertical semicircular canals. Dor-



FIGURE 9. Interpretation of ventral surface of braincase of *Edgaro-saurus muddi*, MOR 751, from the upper Thermopolis Shale of southcentral Montana, in dorsal aspect. **Abbreviations: aiv**, anterior interpterygoid vacuity; **bo**, basioccipital; **bs**, basisphenoid; **ds**, dorsum sellae; **eof**, exoccipital–opisthotic facet; **ep**, epipterygoid; **fo**, fenestra ovalis; **for**, foramen; **fos**, fossa; **icf**, internal carotid foramen; **lcp**, lower cylindrical process; **oc**, occipital condyle; **piv**, posterior interpterygoid vaccuity; **pr**, prootic; **ps**, parasphenoid; **psd**, parasphenoid dish; **pt**, pterygoid; **ptw**, pterygoid wing; **st**, sella turcica; **ucp**, upper cylindrical process; **VI**, abducens foramen.

sally, the supraoccipital contacts the ventral surface of the parietals. The prootic structure is best observed on the left side of the skull. The facet for the supraoccipital faces posterodorsally and is pierced by an opening for the anterior vertical semicircular canal. The contact with the exoccipital-opisthotic is obscured from view, but the distinct horizontal semicircular canal, visible on the anterior facet of the exoccipital-opisthotic, presumably continued into the prootic. The utriculus is represented by a recess on the dorsomedial surface of the prootic. The anteroventral portion of the prootic is a pillar of bone that forms the anterior margin of the fenestra ovalis. A small foramen at the base of this pillar may represent the exit for cranial nerve VII. The fenestra ovalis forms a distinct opening in the lateral wall of the braincase. Roughly circular in outline, its margin is composed almost equally in thirds by the prootic anteriorly, the exoccipital-opisthotic posteriorly, and the basioccipital ventrally. No evidence for an osseous stapes was observed.

Largely undistorted and well preserved, the basicccipital forms the posterior portion of the basicranium (Fig. 9). The occipital condyle, slightly heart shaped in posterior view, lacks a notochordal pit. A shallow constriction rings the occipital condyle, setting it off from the rest of the basioccipital. The exoccipital-opisthotic does not participate in the occipital condyle. Prominent basipterygoid processes are borne solely on the basioccipital and are not shared with the basisphenoid. The roughened articular facet for reception of the pterygoid is angled and faces both anterolaterally and ventrolaterally. The ptervgoids underlie and fuse with the ventral surface of the basioccipital, forming a distinct shelf of bone that projects 10 mm caudad, ventral to the occipital condyle. The basioccipital bears large, roughened exoccipital-opisthotic facets, which lie immediately lateral to the posterior floor of the braincase. A longitudinally oriented elliptical fossa occurs on the floor of the braincase near the anterior end of the basioccipital. A similar ovoid fossa on the floor of the foramen magnum is known in the elasmosaur Libonectes (Carpenter, 1997).

The basisphenoid is very well preserved. The basiccipitalbasisphenoid suture apparently remains unfused. The prootic attaches to the dorsolateral surface of the basisphenoid just posterior to the upper cylindrical processes.

The floor of the braincase is formed of two steps (Fig. 9). The lower, anteriormost step, formed by the floor of the sella turcica, once housed the pituitary. It is bounded laterally by the wing-like projections of the lower cylindrical processes. Two paired, conspicuous foramina, for passage of the internal carotids, perforate the sella turcica along its posteroventral surface. The second step, the dorsum sellae, lies posterior to, and partially overhangs the sella turcica. The upper cylindrical processes extend anterolaterally from this surface. Each upper cylindrical process is pierced at its base by a foramen for cranial nerve VI that runs from its posterodorsal to anteroventral surface. A single foramen (fo, Fig. 9) pierces the floor of the dorsum sellae near the longitudinal midline.

The parasphenoid fuses to the ventral surface of the basisphenoid where it forms a narrow median keel that both divides the posterior interpterygoid vacuity and forms its anteriormost margin (Fig. 10). At its anterior end, the parasphenoid forms a wedge of bone that participates in the floor of the palate and separates the posterior interpterygoid vacuity from the anterior interpterygoid vacuity. Here, an elongate, dish-shaped structure lies on the dorsal surface of the parasphenoid. The pterygoids, immediately lateral to this structure, contact the parasphenoid along a digitate suture. At its posterior end, the parasphenoid abuts the posterior margin of the posterior interpterygoid vacuity and delimits the anteriormost extent of the fused suture between the left and right pterygoids.

Palate

The vomers fuse together along the midline in the anterior half of the skull. Dorsal to the vomers, the anterior rostrum houses the large maxillary secondary dental alveoli, clearly visible in longitudinal CT images (Fig. 11). A narrow longitudinal ridge of bone extends along the ventral midline of the palate from the anterior union of the premaxillae, to the region of alveoli six or seven where the palate flattens between the maxillae. At this point the vomers clearly separate the maxillae but, anteriorly, the extent to which the vomers contact or split the premaxillae is uncertain. Primary dental alveoli for the early replacement teeth are present within grooves that parallel the ridge on each side. The vomeronasal fenestra, typically occurring at the anterior end of the vomer (Carpenter, 1997), is absent in Edgarosaurus muddi. Posteriorly, contacts with the palatines and pterygoids are not visible. Internal nares could not be identified with certainty on the palate.

The lateral contact between the palatine and maxilla is not clear. The presence of suborbital fenestra is equivocal. The palatine butts against the pterygoid medially along a straight con-



FIGURE 10. Reconstruction of palate of *Edgarosaurus muddi*, MOR 751, from the upper Thermopolis Shale of south-central Montana, in palatal aspect. **Abbreviations: aiv**, anterior interpterygoid vacuity; **alv**, alveolus; **ect**, ectopterygoid; **j**, jugal; **mx**, maxilla; **oc**, occipital condyle; **pal**, palatine; **palv**, primary alveolus; **piv**, posterior interpterygoid vacuity; **pmx**, premaxilla; **ps**, parasphenoid; **pt**, pterygoid; flange; **ptrq**, pterygoid ramus of the quadrate; **q**, quadrate; **qrpt**, quadrate; **v**, vomer.

tact. This contact terminates posteriorly at a small palatal fenestra approximately 10 mm wide by 20 mm long (Fig. 10). The anterior and lateral margins of the fenestra are formed by the palatine, while the pterygoid and/or ectopterygoid forms the medial and posterior margins of the fenestra. Posterolaterally, the palatine contacts the ectopterygoid.

The ectopterygoids form the anterior margins of the subtemporal fenestrae and, together with the lateral rami of the pterygoids, create braces to transfer loadings between the palate and the lateral wall of the skull roof. The left ectopterygoid is best preserved. Laterally, the ectopterygoid fuses to the medial wall of the jugal. It contacts and lies ventral to the lateral ramus of the pterygoid, uniting to form a distinct pterygoid flange (ptf, Fig. 10) that bears a boss on its ventral surface.

The two anterior rami of the well-preserved pterygoids are separated by an anterior interpterygoid vacuity, 8 mm wide and 80 mm long. A small wing of bone (ptw, Fig. 9), just anterior to the basal articulation, projects medially from the lateral ramus and partly extends over the fenestra that communicates between the dorsal surface of the palate and the posterior interpterygoid vacuity. The anteromedial portion of the posterior ramus of the pterygoid contacts the anterolateral corner of the basisphenoid forming the basal articulation. Ventral to the basal articulation, the paired pterygoids are split by the anterior end of the posterior interpterygoid vacuity. The pterygoids resume contact with the basicranium at the basipterygoid articulations. Here, the left and right pterygoids appear to expand medially and meet their opposite along the midline, forming a shelf of bone that forms the posterior margin of the posterior interpterygoid vacuity (Fig. 10). The pterygoids also appear to expand dorsally, infilling the area ventral and medial to the basipterygoid processes. This slightly differs from, and may be a modification of, the pterygoid structure described by Carpenter (1997) for the Cretaceous elasmosaur *Libonectes* and the polycotylid *Dolichorhynchops* where the pterygoids form simple flat plates ventral to the basicranium.

In lateral view, the epipterygoid (ep, Fig. 4) is a triangular blade of bone similar to that described for *Libonectes* but unlike the laterally compressed rod of bone seen in *Dolichorhynchops* (Carpenter, 1997). It projects dorsally from the basal articulation, lies lateral to the sella turcica and contacts the prootic along its posterolateral corner. The dorsal tip of the epipterygoid is somewhat thickened and roughly textured, presumably for a ligamentous attachment to the parietal dorsally. Cranial nerve V would have passed from the braincase through a lateral opening, bounded anteriorly by the epipterygoid and posteriorly by the prootic.

Mandible

Both mandibular rami are preserved. The right mandible is displaced along the lateral surface of the skull. The left ramus remains nearly in the life position but is tightly pressed against the left palate. Anteriorly, the mandibular rami unite medially to form a stout mandibular symphysis that extends posteriorly, and includes the first six pairs of dentary teeth, in contrast to the eight pairs of symphyseal teeth seen in *Plesiopleurodon wellesi* (Carpenter, 1996).

Just anterior to the coronoid eminence, the dentary interdigitates with the surangular dorsally, and the angular ventrally (Fig. 12). Medially, anterior extensions of the coronoid, splenial, and angular cover the dentary, with the exception of its dorsal margin, which is exposed at the base of the tooth row. The external surface of the dentary is roughened and pitted at the anterior end. There are 29-30 secondary alveoli in the left dentary and 31 in the right. The anterior six to seven alveoli bear robust, caniniform teeth that decrease in size caudad. The anterior two teeth are strongly procumbent, inclined at nearly 45 degrees from the vertical, with successive teeth becoming progressively more vertical posteriorly. A groove for the primary dental alveoli is bounded laterally by each tooth row and medially by a small ridge. Well developed anteriorly, the ridge unites with that on the other ramus in the region of the mandibular symphysis forming a large, single median ridge. A weakly developed diastema is present between alveolus three and four.

The coronoid is a slender, laterally compressed bone that runs along the dorsomedial surface of the dentary for most of its length. The posterior margin of the coronoid originates immediately anterior to the coronoid eminence, contacting the surangular laterally and the splenial ventrally. It is uncertain if the coronoid extends into the mandibular symphysis.

The splenials are poorly preserved. A narrow blade of bone, each splenial lies along the ventromedial surface of the mandibular ramus. The anterior margin of the splenial cannot be seen. The splenial appears to butt against or slightly overlap the coronoid along its dorsal margin and considerably overlaps the angular along its ventral margin. The splenial also forms the medial wall of the meckelian canal. The canal has been lost



FIGURE 11. CT image of skull of *Edgarosaurus muddi*, MOR 751, from south-central Montana, in left lateral view. Anterior is at left of image. Abbreviations: d, dentary; dt, dentary tooth; et, erupted tooth; mx, maxilla; or, orbit; pmx, premaxilla; umt, unerupted maxillary tooth; upt, unerupted premaxillary tooth.

to crushing in both rami. The posterior termination of the splenial is uncertain due to poor preservation in that region.

The presence of a prearticular is equivocal. A portion of the right prearticular may be represented as a thin splint of bone that lies in a trough formed in the angular. Its anterior margin cannot be discerned. The inferred posterior margin extends toward the anteromedial corner of the medial condyle of the articular.

The surangular is a thin wedge of bone, which lies hidden at its anterior end between the coronoid medially and the dentary laterally. It is overlapped by the dentary at its anterolateral corner, along a broadly digitate suture. Several foramina perforate the surangular adjacent to this contact. The surangular forms the apex of a very pronounced coronoid eminence. Posterior to the coronoid eminence, the dorsal margin of the surangular descends posteroventrally as a thin, laterally compressed blade of bone to the anterolateral corner of the glenoid fossa. A conspicuous, broad and shallow fossa, interpreted as the posterior margin of the adductor fossa (af, Fig. 12), is bounded laterally by this dorsal blade. Posteriorly, the adductor fossa is bounded by the anterior edge of the lateral condyle of the glenoid fossa and medially by a dorsomedial crest. In cross section through the adductor fossa, the dorsomedial crest appears to represent the contact between the surangular and the angular. This contact slopes ventrolaterally and can be traced to the lateral surface of the mandible. The articular appears to be firmly fused to the surangular along their contact and no vestiges of a suture can be discerned.

Anteriorly the angular is a narrow wedge of bone lying between the dentary and splenial. In ventral view it can be seen



FIGURE 12. Reconstruction of mandible of *Edgarosaurus muddi*, MOR 751, from south-central Montana. **A**, lateral aspect. **B**, medial aspect. **Abbreviations**: **a**, angular; **af**, adductor fossa; **alv**, alveolus; **ar**, articular; **c**, coronoid; **cp**, coronoid process; **d**, dentary; **for**, foramen; **gl**, glenoid fossa; **ms**, mandibular symphysis; **pra**?, prearticular?; **sa**, surangular; **sp**, splenial.

to extend into the mandibular symphysis, join its opposite, and terminate below alveolus five. In lateral view, and at a point roughly ventral to the coronoid eminence, the angular loses contact with the dentary and the surangular forms its dorsolateral border. Medially, a trough for reception of the posterior termination of the splenial, and possibly for the prearticular, forms its dorsomedial border. Caudad, the angular forms the ventral and ventrolateral portion of the retroarticular process. A deep, longitudinal cleft is formed in the angular, immediately anterior to the anteromedial margin of the glenoid fossa. The lateral wall of the cleft is formed entirely in the angular where the angular sends a dorsal flange to participate with the surangular in the dorsomedial crest. The posterior margin of the cleft is partly, if not entirely, formed in the articular while the medial wall is possibly formed by the prearticular. A large foramen pierces the posterior corner of the cleft and appears to extend into the articular. The cleft is interpreted to represent the posterior vestige of the meckelian canal (Taylor, 1992).

The articular fuses along its entire margin with the angular and surangular. Both the glenoid fossa and the dorsomedial portion of the retroarticular process are formed in the articular. The glenoid fossa is of the typical bicondylar arrangement seen in plesiosaurs for reception of the quadrate (Storrs and Taylor, 1996). The posterior margin of the glenoid fossa is deeply indented by a notch that leads ventrally into a large foramen just posterior to the glenoid fossa and into the articular, creating distinct medial and lateral condylar margins. The anterior margins of the glenoid fossa form the posterior end of the adductor fossa laterally and the angular cleft medially. The concave dorsal surface of the retroarticular process slopes medially and is roughened posteriorly for insertion of the *M. depressor mandibulae* (Taylor, 1992).

A complete hyoid, a rod of bone 48 mm long and averaging 4 mm wide, was found pressed against, and parallel to, the ventral keel of the parasphenoid where it divides the posterior interpterygoid vacuity. The poorly preserved remains of a second possible hyoid element were found in close proximity to the first.

Dentition

Nearly all of the teeth have been preserved. A few teeth were displaced, but the vast majority remain in sockets in their original life position. Unfortunately, tooth preservation is poor due to gypsum permineralization and infiltration. Consequently, only small areas of enameled surface are visible. A fairly reliable tooth count can be made, however. A full complement of 31 to 32 alveoli is preserved in the upper left tooth row, six to seven in the premaxilla and 26 in the maxilla. The right premaxilla also bears at least six alveoli, but only 15 alveoli can be counted in the right maxilla due to damage and loss at its posterior end. There are 29 to 30 alveoli (probably 30) in the left dentary and 31 in the right. Several smaller, primary alveoli are visible in a groove or trough, lingual to the secondary alveoli.

CT imaging clearly reveals the size and position of replacement teeth within the rostrum. The bulk of the maxilla, anterior to the orbits, houses the large, caniniform replacement teeth. A conspicuous example can be seen in the tooth emerging from position seven in the upper left tooth row (umt, Fig. 11). Externally, only 5 mm of the crown is visible erupting from the alveolus. CT images, however, reveal the 40 mm remainder of a large crown and root within the maxilla. The base of the root begins dorsally, nearly at the maxilla-premaxilla suture and can be traced anteroventrally past a bulbous root with a radiotransparent pulp cavity. The enameled crown is apparent as the conical, radiotranslucent ventral end. Several other teeth are visible in the maxillae, as well as the dentaries. When the upper and lower jaws are occluded, the dorsal and ventral tooth rows deeply interdigitate. This is particularly conspicuous in the mid and anterior regions of the snout where large, curved, caniniform teeth occur. The largest teeth occur in the upper and lower tooth rows between positions 3 through 8. These teeth have crowns that project up to 50 mm beyond the alveolar margin and are 15 mm in diameter at the base of the crown. The two anteriormost teeth in the premaxilla and dentary are inclined anteriorly at nearly 45° from the vertical. Further caudad, the teeth become progressively less procumbent and nearly vertical by upper tooth row positions 8 through 10. The remainder of teeth in the posterior half of the ramus is considerably smaller, averaging 10-15 mm in height. The tooth row terminates beneath the posteroventral corner of the orbits.

The enameled crowns of the teeth, although poorly preserved, all appear to be nearly circular in cross section. The anterior teeth are curved, while the small posterior teeth appear to be simple, straight cones. Numerous wavy, longitudinal and in some cases bifurcating striations are present on the outer enameled surface. Striations are present on all sides of the teeth but it is not possible to discern whether they are more numerous on the lingual or labial surfaces. No evidence of wear facets was observed.

Atlas and Axis

The atlas and axis elements form a single unit that is fused together with the exception of the atlas intercentrum and atlas neural arches. Suture lines between the other elements are still discernible (Fig. 13). The atlantal cup is a deeply concave, circular to heart shaped socket, formed by the intercentrum ventrally, the neural arches dorsolaterally, and the atlas centrum posteriorly. The atlas centrum does not participate in the anterior rim of the atlantal cup. The atlas intercentrum bears articular surfaces for the basioccipital anteriorly, the neural arches dorsolaterally, and both the atlas and axis centra. The ventral surface of the atlas intercentrum is convex ventrally and bears a broad median keel.

The atlas neural arch bears a large medial facet for union with the atlas centrum, in addition to anterior and ventral facets for the basioccipital and atlas intercentrum, respectively. A very small facet contacts the axis neural arch posterodorsally. Both arches bear broken bases for the neural spines. The neural spine has been displaced and crushed into the neural canal but appears largely fused with the axis neural spine. The concave anterior surface of the atlas centrum houses a distinct notochordal pit at its center. Dorsally, the centrum forms most of the floor of the atlas neural canal, and posteriorly, it is bounded by the large axis centrum. In lateral view, only a small elliptically-shaped portion of the atlas centrum (atc, Fig. 13) is visible between the atlas neural arch and the axis centrum.

The axis morphology of Edgarosaurus muddi is more typical of other cervical vertebrae. The axis centrum forms the bulk of the axis complex. The anterior face of the axis centrum is fused to the atlas centrum and little else can be seen. The concave posterior articular facet lacks a notochordal pit. A short, posteriorly projecting cervical rib articulates to the ventrolateral margin of the centrum. The axis intercentrum is a small, dorsoventrally flattened element firmly fused to the ventral surface of the axis centrum and bears a well-defined ventral keel. Nutritive foramina are not present on the axis centrum ventrally. The axis neural arch is fused to the axis centrum and, to a small extent, anteriorly to the atlas neural arch. The neural spine extends strongly caudad, to a point adjacent to the posterior margin of vertebra number three. The posterior portions of the axis neural spine arches entirely over the neural spine of vertebra three and terminates in a pair of postzygapophyses.

Edgarosaurus muddi possesses a complete series of 26 cer-



FIGURE 13. Atlas and axis of *Edgarosaurus muddi*, MOR 751, from south-central Montana, in left lateral aspect, anterior to left. **Abbreviations: atc**, atlas centrum; **atic**, atlas intercentrum; **atna**, atlas neural arch; **atns**, atlas neural spine; **axc**, axis centrum; **axna**, axis neural arch; **axns**, axis neural spine; **cr**, cervical rib; **cv3** cervical vertebra 3; **poz**, postzygapophysis.

vical vertebrae, defined as those vertebrae of the neck region that bear rib facets exclusively on the centrum (Fig. 14A) (Brown, 1981). Three pectoral vertebrae (Fig. 14B), transitional between the cervical and dorsal vertebrae, share the rib facet on both the centrum and neural arch. The rib facets of the five dorsal vertebrae are borne on the neural arch only. Based on the few proximal rib fragments preserved, as well as rib facets, all ribs are single headed (cercidopleurous).

Beginning with the atlas and axis, the vertebrae progressively increase in size caudad, with vertebral width increasing at a faster rate than vertebral length (width defined as maximum centrum diameter measured on the posterior articular face; length measured along the mid-ventral surface of the vertebra). The articular facets of the cervical vertebrae are nearly circular in outline, while those of the posterior three uncrushed pectorals become nearly heart-shaped in outline. The articular facet appears proportionately more deeply concave in anterior cervicals than in pectorals. With the exception of the anterior face of the axis, a notochordal pit is absent. The zygapophyses of the posterior cervical vertebrae are largest both proportionately and in absolute size. The zygapophyses quickly diminish in size through the pectoral series, and are not preserved on the dorsal vertebrae. Ventrally, a distinct longitudinal keel splits a pair of nutrient foramina. The keel diminishes posteriorly through the pectoral vertebrae and is concomitant with the migration of the ventral nutrient foramina dorsally to the lateral surface of the centrum. Beginning at vertebra 28 and continuing caudad, a single or sometimes closely paired nutritive foramen is present ventrally along the midline.

Appendicular Skeleton

The proximal humerus fragment bears a well-developed capitulum and tuberosity (Fig. 15). The articular surface of the capitulum is deeply pitted, while the tuberosity is smooth. The preaxial margin of the distal half of the humerus appears



FIGURE 14. Vertebrae of *Edgarosaurus muddi*, MOR 751, from south-central Montana, in left lateral aspect, anterior to left. **A**, cervical vertebra 10. **B**, pectoral vertebra 28. **Abbreviations: cnt**, centrum; **cr**, cervical rib; **na**, neural arch; **ns**, neural spine; **poz**, postzygapophysis; **pcrf**, pectoral rib facet; **prz**, prezygapophysis.

straight while the postaxial surface appears concave and expands distally. Rugosities, representing the distal extent of muscle insertions are visible along the preaxial, postaxial, and ventral surfaces of the humerus. The distal end of the humerus is expanded, with the radial facet being larger and more pronounced than the ulnar.

Both epipodials are broader than long (Fig. 16). The radius is larger than the ulna and pentagonal in outline. It contacts the intermedium posterolaterally and the radiale distally, in addition to the humerus and ulna. Beginning along the anterior margin of the radius, the leading edge of the paddle becomes angled backwards in a smooth arc that continues to the paddle's distal end. The ulna is notched along its anterior margin for the epipodial foramen. Distally, the ulna contacts both the intermedium and ulnare.

The mesopodials consist of a proximal row of three carpals, the radiale, intermedium, and ulnare as well as a row of three distal carpals. The fifth metacarpal has shifted proximally into



FIGURE 15. Proximal propodial fragment of *Edgarosaurus muddi*, MOR 751, from south-central Montana, in dorsal aspect. **Abbreviations:** cap, capitulum; **i**, isthmus; **t**, tuberosity.



FIGURE 16. Left pectoral paddle of *Edgarosaurus muddi*, MOR 751, from south-central Montana, in ventral aspect. Abbreviations: epf, epipodial foramen; dc1–3, distal carpal 1–3; h, humerus; itm, intermedium; rd, radius; rdl, radiale; ul, ulna; uln, ulnare; I–V, metacarpals I–V.

the distal carpal row and contacts the ulnare, as is typical in all plesiosaurs. The metacarpal row becomes progressively phalangiform posteriorly. The five digits are closely contacted along their lateral margins and effectively form a single, posteriorly curved blade. The digits are well preserved even to their distal ends and display typical plesiosaurian hyperphalangy. The phalangeal count is I-7, II-11, III-10, IV-9 and V-9.

DISCUSSION

In general morphology and stratigraphic range, Edgarosaurus resembles Plesiopleurodon wellesi, a large-skulled pliosaurid taxon from the Belle Fourche Shale (lower Cenomanian) of Wyoming (Carpenter, 1996, 1999). Personal examination of the Plesiopleurodon type specimen, CM 2815, reveals that many important comparative features of the skull, including the braincase, palate, and many sutures, are unfortunately obscured by a hard, dark grey concretionary matrix. However, a number of autapomorphies can be observed in each taxon, when viewed in the context of an assessment of relative ontogenetic states. As in MOR 751, the neural arches are fused to the centra in the cervical vertebrae of CM 2815, and the suture separating the neural arches and centra remains visible. The degree of separation between the humeral tuberosity and head, however, is less pronounced in CM 2815 than in MOR 751, indicating a possibly slightly younger relative stage of development. In spite of this ontogenetic similarity, the skull of CM 2815 is 50 percent longer than MOR 751. The supratemporal fenestra of CM 2815 is also conspicuously larger than the orbit (ratio of orbit length to supratemporal fenestra length) when compared to MOR 751, and the suspensorium angles posteriorly in CM 2815, as opposed to the vertical orientation seen in MOR 751. Relative sizes of the supratemporal fenestrae (length versus width) and suspensorium orientation were the two primary characters employed by Carpenter (1989, 1996) to distinguish the Late Cretaceous polycotylids Trinacromerum and Dolichorhynchops at the generic level. Although Carpenter (1996: 264) describes the premaxillae as forming the dorsal edge of the external nares in Plesiopleurodon, this character is equivocal in CM 2815, as is the presence of a pineal foramen. Differences in the mandible of CM 2815 include the presence of eight symphyseal teeth (six in MOR 751), an irregular tooth row margin (straight in MOR 751), a ventromedial deflection of the dorsal surface retroarticular process (horizontal in MOR 751), and the lesser degree of development of caniniform teeth.

SYSTEMATIC RELATIONSHIPS

The phylogenetic relationships within the Plesiosauria are currently in a state of flux (Brown and Cruickshank, 1994; Storrs, 1997; Carpenter, 1999). Traditional classifications reflect a long-held assumption that the large-skulled, short-necked plesiosaurs in the Superfamily Pliosauroidea, and the smallskulled, long-necked plesiosaurs in the Superfamily Plesiosauroidea represent monophyletic clades within the Plesiosauria (Welles, 1943; Persson, 1963; Brown, 1981). Recently, several workers have questioned the validity of this hypothesis (Bakker, 1993; Carpenter, 1996; O'Keefe, 1999).

Problems with the phylogenetic relationships and classification of the Polycotylidae have recently been discussed by Sato and Storrs (2000). In the absence of an established phylogenetic framework for short-necked plesiosaurs, systematic placement of *Edgarosaurus* is difficult. Published diagnoses for the shortnecked families Pliosauridae (Tarlo, 1960; Persson, 1963; Brown, 1981) and Polycotylidae (Williston, 1903; Welles, 1962; Carpenter, 1996) overlap and vary in many characteristics. Brown (1981) placed all short-necked taxa, including traditional polycotylid genera, into the Pliosauridae, while other workers have separated the two families based primarily on postcranial characters.

In an attempt to rectify this confusion, Carpenter (1996) distinguished the Polycotylidae and Pliosauridae based on differences in palatal structure. Two palatal types were described. The first condition is seen in Jurassic pliosaurids and *Brachauchenius* in which the pterygoids fold beneath the basicranium, in contrast to the more derived condition seen in *Trinacromerum* and *Dolichorhynchops* in which the pterygoids extend as flat plates ventral to the basicranium. Furthermore, Carpenter (1997) proposed a close sister group relationship between polycotylids (*Dolichorhynchops*) and elasmosaurs (*Libonectes*) based on potentially synapomorphic cranial features, including the expansion of the pterygoids ventral to the basicranium, the closure of the pineal foramen, and the presence of a vomeronasal fenestra. This relationship has yet to be demonstrated by a cladistic analysis, however.

Edgarosaurus differs from polycotylids as defined by Carpenter (1996) in that it retains a pineal foramen, lacks a vomeronasal fenestra, and bears caniniform teeth. However, *Edgarosaurus* does appear to share the derived condition of the palate seen in polycotylids. Additionally, the presence of single-headed ribs and short and wide epipodials suggests a closer relationship to polycotylids than pliosaurids. Therefore, until further work on the phylogenetic relationships of short-necked plesiosaurs is completed, *Edgarosaurus* is provisionally placed in the Polycotylidae.

Concomitant with its stratigraphic occurrence, *Edgarosaurus* displays a number of plesiosmorphic characters with respect to polycotylids. These include possession of a relatively robust and moderately elongated rostrum, retention of a pineal foramen, the presence of caniniform teeth, and a relatively short mandibular symphysis bearing six pairs of dentary teeth. It also displays a relatively high number of cervical vertebrae (26), a condition it shares with *Polycotylus latipinnis* (Williston, 1906).

CONCLUSIONS

Worldwide, much of our understanding of Late Cretaceous plesiosaur diversity comes from deposits of the Western Interior Seaway of North America. *Edgarosaurus*, from the late Albian Thermopolis Shale, represents one of the earliest and best preserved North American Cretaceous plesiosaurs described to date. As a forerunner to Late Cretaceous taxa, *Edgarosaurus* helps fill a gap in knowledge of plesiosaur morphology and distribution during the early expansion of the seaway. Pending completion of further work on the phylogenetic relationships of the short-necked plesiosaurs, *Edgarosaurus* is provisionally placed in the Polycotylidae as defined by Carpenter (1996). However, its close similarity to *Plesiopleurodon wellesi*, con-

sidered by Carpenter (1996, 1999) to be a pliosaurid, demonstrates that the relationships of short-necked Cretaceous plesiosaurs are still poorly understood.

ACKNOWLEDGMENTS

The author acknowledges the artistic talent of Frankie Jackson for the illustrations in this paper. I thank the collectors, Doug Tingwall, Buck Damone, and Ken Olson for bringing the specimen to the Museum of the Rockies for preparation and study, and the Desavier, Tilstra, Newton, and Bequette families for access to their land. Thanks to D. Berman and E. Hill of the Carnegie Museum for providing access to specimens. CT images were provided by Glen Daleo of the San Diego Children's Hospital. B. Nicholls, M. Taylor, G. Storrs, K. Porter, M. Lavin, F. Jackson and C. Marshall provided helpful advice and reviews. Thanks also go out to C. Horner, B. Cobban, R. Moore, E. Vyse, P. Leiggi, and J. K. and H. S. Druckenmiller. This study was undertaken as part of work towards a master's degree in the Department of Biology at Montana State University-Bozeman supervised by J. Horner and committee members M. Lavin and C. Kaya. Gail and Roland Johnson, Barbara Lee, J. Horner, and the Department of Biology provided funding.

LITERATURE CITED

- Andrews, C. 1910. A descriptive catalogue of the marine reptiles of the Oxford Clay. Part II. British Museum (Natural History), London, 205 pp.
- Bakker, R. T. 1993. Plesiosaur extinction cycles—events that mark the beginning, middle and end of the Cretaceous; pp. 641–664 *in* W. G. E. Caldwell and E. G. Kauffman (eds.), Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.
- Blainville, H. D. de. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système general d'Erpetologie et d'Amphibiologie. Nouvelles annales du Muséum (national) d'Histoire naturelle, Paris 4:233–296.
- Brown, D. S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. Bulletin of the British Museum (Natural History), Geology Series 35:253–347.
- ———, and A. R. I. Cruickshank. 1994. The skull of the Callovian plesiosaur *Cryptoclidus eurymerus*, and the sauropterygian cheek. Palaeontology 37:941–953.
- Carpenter, K. 1989. Dolichorhynchops ≠ Trinacromerum (Reptilia: Plesiosauria). Journal of Vertebrate Paleontology 9(3, suppl.):15A.
- — 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. Neues Jahrbuch f
 ür Geologie und Pal
 äontologie Abhandlungen 201:259–287.
- — 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs (Reptilia: Sauropterygia); pp. 191–216 *in* J.
 M. Callaway and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic Press, San Diego.
- — 1999. Revision of North American elasmosaurs from the Cretaceous of the Western Interior. Paludicola 2:148–173.
- Cope, E. D. 1869. Extinct Batrachia, Reptilia and Aves of North America. Transactions of the American Philisophical Society 14:1–252.
- Dolson, J., D. Muller, M. J. Evetts, and J. A. Stein. 1991. Regional paleotopographic trends and production, Muddy Sandstone (Lower Cretaceous), central and northern Rocky Mountains. Bulletin of the American Association of Petroleum Geologists 75:409–435.
- Druckenmiller, P. S. 1998. Osteology and relationships of a plesiosaur (Sauropterygia) from the Thermopolis Shale (Lower Cretaceous) of Montana. M.S. thesis, Montana State University, Bozeman, 91 pp.
- Dyman, T. S., K. W. Porter, R. G. Tysdal, W. A. Cobban, J. E. Fox, R. H. Hammond, D. J. Nichols, W. J. Perry, D. D. Rice, D. R. Setterholm, G. W. Shurr, J. C. Haley, D. E. Lane, S. B. Anderson, and E. B. Campen. 1995. West–east stratigraphic transect of Cretaceous rocks in the northern Rocky Mountain and Great Plains region, southwest Montana to southwest Minnesota. Geological Society of America Miscellaneous Investigation Series, Map I-2474-A.

Eicher, D. L. 1960. Stratigraphy and micropaleontology of the Ther-

mopolis Shale. Bulletin of the Peabody Museum of Natural History, Yale University 15:1–121.

- Kauffman, E. G., B. B. Sageman, J. I. Kirkland, W. P. Elder, P. J. Harries, and T. Villamil. 1993. Molluscan biostratigraphy of the Cretaceous Western Interior Basin, North America; pp. 397–434 *in* W. G. E. Caldwell and E. G. Kauffman (eds.), Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.
- Linder, H. 1913. Beiträge zur Kenntnis der Plesiosaurier-Gattungen *Peloneustes* und *Pliosaurus*. Nebst Anhang: über die beiden ersten Halswirbel der Plesiosaurier. Geologische und Paläontologische Abhandlungen 11:339–409.
- Obradovich, J. D. 1993. A Cretaceous time scale; pp. 379–396 in W. G. E. Caldwell and E. G. Kauffman (eds.), Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.
- O'Keefe, F. R. 1999. Phylogeny and convergence in the Plesiosauria. Journal of Vertebrate Paleontology 19(3, suppl.):67A.
- Osborn, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. Memoir of the American Museum of Natural History 1:449–507.
- Owen, R. 1860. On the orders of fossil and Recent Reptilia, and their distribution in time. Report of the British Association for the Advancement of Science 29:153–166.
- Persson, P. O. 1963. A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. Lunds Universitets Årsskrift N. F. Avd. 2, 59(1):1– 59.
- Porter, K. W., T. S. Dyman, G. G. Thompson, D. A. Lopez, and W. A. Cobban. 1997. Six outcrop sections of the marine Lower Cretaceous, central Montana, with a section on the palynomorph stratigraphy and age of a late Albian lowstand. Montana Bureau of Mines and Geology Report of Investigation 3, 29 pp.
- Rieppel, O. 1997. Introduction, Part II: Sauropterygia; pp. 107–119 in J. M. Callaway and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic Press, San Diego.
- Riggs, E. S. 1944. A new polycotylid plesiosaur. University of Kansas Science Bulletin, 30(8):77–87.
- Sato, T., and G. W. Storrs. 2000. An early polycotylid plesiosaur (Reptilia: Sauropterygia) from the Cretaceous of Hokkaido, Japan. Journal of Paleontology 74:907–914.
- Storrs, G. W. 1981. A review of occurences of the Plesiosauria (Reptilia: Sauropterygia) in Texas with a description of new material. M.S. thesis, University of Texas, Austin, 226 pp.
- — 1991. Anatomy and relationships of *Corosaurus alcovensis* (Reptilia: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. Bulletin of the Peabody Museum of Natural History 44:1– 151.
- — 1997. Morphological and taxonomic clarification of the genus *Plesiosaurus*; pp. 145–190 in J. M. Callaway and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic Press, San Diego.
- ———, and M. A. Taylor. 1996. Cranial anatomy of a new plesiosaur genus from the lowermost Lias (Rhaetian/Hettangian) of Street, Somerset, England. Journal of Vertebrate Paleontology 16:403– 420.
- Sues, H.-D. 1987. Postcranial skeleton of *Pistosaurus* and interrelationships of the Sauropterygia (Diapsida). Zoological Journal of the Linnean Society 90:109–131.
- Tarlo, L. B. 1960. A review of Upper Jurassic pliosaurs. Bulletin of the British Museum (Natural History), Geology Series 4:145–189.
- Taylor, M. A. 1992. Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. Philosophical Transactions of the Royal Society of London Series B 335:247– 280.
- ---, and A. R. I. Cruickshank. 1993. Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. Philosophical Transactions of the Royal Society of London B 341:399– 418.
- Tschanz, K. 1989. *Lariosaurus buzzii* n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland) with comments on the classification of nothosaurs. Palaeontographica A 208:153–179.
- Vuke, S. M. 1984. Depositional environments of the Early Cretaceous Western Interior Seaway in southwestern Montana and the northern

United States; pp. 127–144 *in* D. F. Stott and D. J. Glass (eds.), The Mesozoic of Middle North America, Canadian Society of Petroleum Geologists Memoir 9.

- Welles, S. P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Memoirs, University of California, Berkeley 13(3):125–215.
- — 1962. A new species of elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. University of California Publications in Geological Sciences 46:1–96.

Williston, S. W. 1890. A new plesiosaur from the Niobrara Cretaceous

of Kansas. Transactions of the Kansas Academy of Science 12: $174{-}178.$

- --- 1902. Restoration of *Dolichorhynchops osborni*, a new Cretaceous plesiosaur. Kansas University Science Bulletin 1(9):241– 244.
- --- 1903. North American plesiosaurs. Part I. Field Columbian Museum Publication 73, Geological Series 2(1):1–77.
- -— 1906. North American plesiosaurs: Elasmosaurus, Cimoliasaurus, and Polycotylus. American Journal of Science 4(21):221–236.

Received 12 April 2000; accepted 17 May 2001.