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## OSTEOLOGY AND RELATIONSHIPS OF *COLYMBOSAURUS* SEELEY, 1874, BASED ON NEW MATERIAL OF *C. SVALBARDENSIS* FROM THE SLOTTSMØYA MEMBER, AGARDHFJELLET FORMATION OF CENTRAL SPITSBERGEN

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**ABSTRACT**—*Colymbosaurus* is a genus of long-necked plesiosaurian represented by two valid species: *C. megadeirus* from the Upper Kimmeridge Clay Formation (Kimmeridgian–Tithonian) of the United Kingdom and *C. svalbardensis* from the Slottsmøya Member of the Agardhfjellet Formation (Tithonian–Berriasian) of Svalbard, Norway. Due to the lack of complete and articulated skeletons and a near absence of cranial material, *Colymbosaurus* has been problematic to characterize morphologically. Here, we describe and conduct a phylogenetic analysis on an informative new specimen referable to *C. svalbardensis* from the Slottsmøya Member, preserving a large portion of the axial and appendicular skeleton. The new material contributes important new osteological data for the species and together with an extensive examination of congeners in British museums, clarifies the diagnostic characters of the genus. We provide two new diagnostic characters of the epipodials for the genus and reevaluate the utility of an anteroposteriorly oriented bisecting ridge on the distal end of the propodials. We also present two new diagnostic features for *C. svalbardensis* regarding the neural canal and femoral morphology. A phylogenetic analysis recovers a monophyletic and well-supported *Colymbosaurus*. The new specimen of *C. svalbardensis* confirms that this species is not synonymous with other described Slottsmøya Member plesiosauroids, demonstrating considerable diversity of the clade at high latitudes close to the Jurassic–Cretaceous boundary.

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

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### INTRODUCTION

Plesiosauria is a clade of secondarily aquatic reptiles that inhabited the Mesozoic seas (Taylor and Cruickshank, 1993). Their earliest remains are known from the Late Triassic (Norian; Sennikov and Arkhangelsky, 2010), and by the Early Jurassic plesiosaurians had a worldwide distribution and were diversified into several clades exhibiting a wide range of morphotypes (Benson et al., 2012; Bardet et al., 2014). In the wake of recent broad-scale phylogenetic studies (O’Keefe, 2001; Druckenmiller and Russell, 2008; Ketchum and Benson, 2010; Benson and Druckenmiller, 2014), there is increasing consensus regarding the taxonomic relationships among major plesiosaurian clades. However, relationships within these clades remain problematic. One major small-

skulled, long-necked plesiosauroid clade is Cryptoclididae, known from the Callovian (Middle Jurassic) to the latest Hauterivian (Early Cretaceous) (Benson and Druckenmiller, 2014). Cryptoclidids are predominantly distributed in the northern hemisphere, with the majority of specimens found in the Oxford and Kimmeridge Clay formations of the United Kingdom (Gasparini et al., 2002). Recognizing synapomorphies for Cryptoclididae has proven challenging, because many of the described taxa either lack overlapping material or are known from juvenile specimens (Brown, 1981; O’Keefe et al., 2011; Knutsen et al., 2012a, 2012b, 2012c; Benson and Bowdler, 2014). Following Benson and Druckenmiller (2014), cryptoclidid synapomorphies include large orbits and external nares, a small vertical jugal, the lack of a prefrontal, a strongly emarginated cheek, and reduced tooth ornamentation. Ten cryptoclidid genera are currently recognized (Benson and Druckenmiller, 2014): *Abyssosaurus* (Berezin, 2011), *Colymbosaurus* (Seeley, 1874), *Cryptoclidus* (Phillips, 1871), *Djupedalid* (Knutsen et al., 2012c), *Kimmerosaurus* (Brown, 1981), *Muraenosaurus* (Seeley, 1874), *Pantosaurus* (Marsh, 1893), *Spitrasaurus* (Knutsen et al., 2012b), *Tatenectes* (Knight, 1900), and *Tricleidus* (Andrews, 1909). Other provisionally valid cryptoclidids also included in the Benson and Druckenmiller (2014) analysis include *Picrocleidus beloclis* (Andrews, 1910) and ‘*Plesiosaurus*’ *manselii* (Hulke, 1870).

Colymbosaurinae (Benson and Bowdler, 2014) is a cryptoclidid subclade diagnosed solely on postcranial features due to the

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paucity of cranial material for this group (Benson and Bowdler, 2014). Seven species are referred to this subclade, including British (*Colymbosaurus megadeirus*; Seeley, 1869), North American (*Pantosauros striatus*; Marsh, 1893; O'Keefe and Wahl, 2003), and Russian (*Abyssosaurus nataliae*; Berezin, 2011) taxa. Notably, all four of the plesiosauroids currently described from the Upper Jurassic Slottsmøya Member Lagerstätten of Spitsbergen (*Colymbosaurus svalbardensis*, *Djupedalid engeri*, *Spitrasaurus larseni*, and *S. wensaasi*; Knutsen et al., 2012a, 2012b, 2012c) are also members of this clade.

The high Arctic island of Spitsbergen, part of the Norwegian Svalbard archipelago, has yielded many important remains of marine reptiles from the Upper Jurassic Slottsmøya Member of the Agardhfjellet Formation. At present, a total of three new monospecific genera of ichthyosaurs and two new genera and four species of plesiosauroids have been described, all of which are endemic to this region (Hurum et al., 2012; Delsett et al., 2016). The first cryptoclidid described from the Slottsmøya Member Lagerstätten was '*Tricleidus*' *svalbardensis* (Persson, 1962). An additional 23 cryptoclidid skeletons were excavated from the Slottsmøya Member between 2004 and 2012. Based on new morphological data derived from some of this material, Knutsen et al. (2012a) referred the holotype specimen of '*Tricleidus*' *svalbardensis* (PMO A27745) to the British Kimmeridgian genus *Colymbosaurus*, along with two other partial postcranial skeletons (PMO 216.838, PMO 218.377).

Despite being known from numerous specimens in the Kimmeridge Clay Formation and now the Slottsmøya Member of Spitsbergen, *Colymbosaurus* has proven difficult to diagnose, in part due to the near absence of cranial remains and a scarcity of associated material. This problem was further compounded by the suggestion that *Colymbosaurus* is synonymous with *Kimmerosaurus langhami* (Brown, 1981; Brown et al., 1986), also from the Kimmeridge Clay Formation, an idea that is now discounted (Benson and Bowdler, 2014). Recently, Benson and Bowdler (2014) reexamined and rediagnosed this taxon on the basis of three diagnostic characters: (1) a postaxial flange bearing a single large postaxial ossicle facet of subequal size to the other epipodial facets; (2) an anteroposteriorly oriented ridge bisecting the distal facets on the propodials; and (3) cervical vertebrae that are slightly anteroposteriorly shorter than dorsoventrally high and lack a lateral ridge. Here, we describe the most complete Slottsmøya Member specimen referable to *Colymbosaurus svalbardensis*, PMO 222.663. The new material from the Slottsmøya Member and a reexamination of additional material from the Kimmeridge Clay Formation permit a reevaluation of diagnostic characters for both the genus and *C. svalbardensis*.

**Institutional Abbreviations**—**CAMSM**, Sedgwick Museum of Earth Science, Cambridge University, Cambridge, U.K.; **GLAHM**, The Hunterian Museum, University of Glasgow, Glasgow, U.K.; **LEICS**, Leicester New Walk Museum, Leicester, U.K.; **MANCH**, The Manchester Museum, Manchester, U.K.; **NHMUK**, Natural History Museum, London, U.K.; **NOTNH**, Wollaton Hall, Nottingham, U.K.; **OUM**, Oxford University Museum of Natural History, Oxford, U.K.; **PETRM**, Peterborough Museum, Peterborough, U.K.; **PMO**, Paleontological Museum Oslo, University of Oslo, Oslo, Norway; **PMU**, Paleontological Collections, Museum of Evolution, Uppsala University, Uppsala, Sweden; **SVB**, Svalbard Museum, Longyearbyen, Norway; **YORKM**, York Museum and Art Gallery, York, U.K.

### Geological Setting

The Slottsmøya Member is the uppermost of four members of the Agardhfjellet Formation that spans a Middle Jurassic to Lower Cretaceous marine succession on Spitsbergen. The Agardhfjellet Formation is separated from the overlying Lower Cretaceous Rurikfjellet Formation by a regionally recognizable

layer known as the Myklegardfjellet Bed (Dypvik et al., 1991) (Fig. 1). The Slottsmøya Member consists of 55–70 m of dark gray to black silty mudstone, which is often weathered into paper shale. There are discontinuous silty beds with associated siderite and dolomite interbeds and siderite nodules, some of which are interpreted as storm deposits (Rousseau and Nakrem, 2012).

The Slottsmøya Member represents approximately 12 million years of deposition spanning the upper Tithonian to the lower Berriasian (Hammer et al., 2012). As summarized in Delsett et al. (2016), detailed stratigraphic and isotopic work has divided the member into lower (–22–0 m), middle (0–27 m), and upper (27–52 m) units (Fig. 2), using a distinctive echinoderm bed ('yellow layer') as a lower marker bed (0 m; Rousseau and Nakrem, 2012) and the *Dorsoplanites* layer as a second, stratigraphically higher marker bed (27 m; Nagy and Basov, 1998; Collignon and Hammer, 2012; Hammer et al., 2012; Hjalmarsson et al., 2012). The specimen described here (PMO 222.663) is from the middle unit (Fig. 2), a particularly fossiliferous stratigraphic interval (~14 m) from which six ichthyosaur and six plesiosaur specimens have been excavated (Delsett et al., 2016). Specimen PMO 216.838, the recently referred specimen of *Colymbosaurus svalbardensis* (Knutsen et al., 2012a), was also found in this same interval. However, the exact stratigraphic position of the holotype specimen (PMO A27745) is unknown.

### MATERIALS AND METHODS

Specimen PMO 222.663 was excavated on the mountain of Janusfjellet over two field seasons (2010–2011). The specimen was mechanically prepared using air scribes, air abrasion, and small manual tools. In addition to this new specimen, the holotype of *Colymbosaurus svalbardensis* (PMO A27745) and the two previously referred specimens (PMO 216.838 and PMO 218.377; Knutsen et al., 2012a) were reexamined in the course of this study. In addition to the *C. svalbardensis* material, Kimmeridge Clay Formation specimens were also examined in several U.K. museums. Two of these specimens, NHMUK R10062 and OUM J.3300, are reasonably complete and can be referred to *Colymbosaurus*. To add to the diagnostic features defined by Benson and Bowdler (2014), 22 propodials referred to or with similar morphology to *Colymbosaurus* were examined and measured (Supplementary Data 1, Table S1). The majority of these are from the Kimmeridge Clay Formation held in U.K. museums, save PMO 222.663 and the holotype of *C. svalbardensis* (PMO A27745) from Spitsbergen (Knutsen et al., 2012a). All specimens that were included in this study, with the exception of CAMSM J68344, are from a mature ontogenetic stage. Some specimens include several propodials (OUM J.3300, PMO 222.663, and MANCH LL.5513/MANCH LL.5514) and were examined to assess variation in humeri and femora. More propodial material resembling *Colymbosaurus* is available in private collections and in unregistered material at other museums; these were examined but not included in this study. Whenever possible, the presence or absence of the distal anteroposteriorly oriented ridge, used as one of the diagnostic features by Benson and Bowdler (2014), was recorded and defined by a distinct ridge extending on both epipodial facets.

### SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860  
PLESIOSAURIA de Blainville, 1835  
PLESIOSAUROIDEA Gray, 1825  
CRYPTOCLIDIDAE Williston, 1925  
COLYMBOSAURINAE Benson and Bowdler, 2014  
*COLYMBOSAURUS* Seeley, 1874

**Type Species**—*Colymbosaurus megadeirus* (Seeley, 1869).

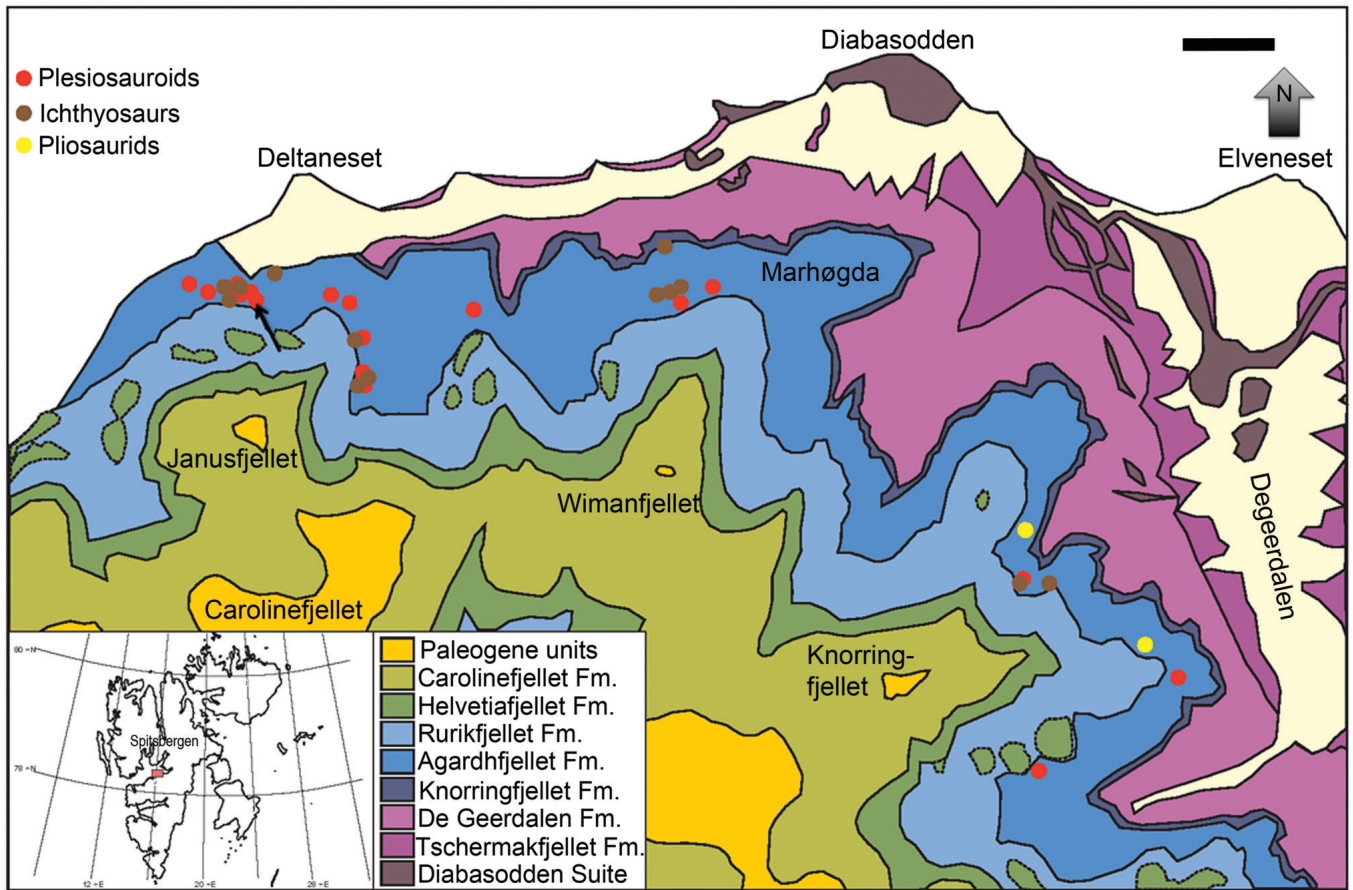


FIGURE 1. Geological map of study area, including the Agardhfjellet Formation and excavation sites. The black arrow indicates the location of PMO 222.663. Modified from Dallmann et al. (2001) and Hurum et al. (2012). Scale bar equals 1 km.

**Valid Referred Species**—*Colymbosaurus svalbardensis* (Persson, 1962).

**Occurrence**—Upper Jurassic; Kimmeridge Clay Formation, Kimmeridgian–early Tithonian, U.K.; Agardhfjellet Formation, Tithonian–early Berriasian, Svalbard, Norway.

**Emended Diagnosis**—A large cryptoclidid with the following features: mid-cervical vertebrae marginally anteroposteriorly shorter than dorsoventrally tall and lacking a longitudinal ridge on the lateral surface (modified from Benson and Bowdler, 2014); middle caudal centra subrectangular due to a flat ventral surface, with widely spaced chevron facets; propodials with a large posterodistal expansion at least twice as large as the preaxial expansion, bearing a single postaxial ossicle facet of subequal size to the epipodial facets (modified from Benson and Bowdler, 2014); ulna conspicuously anteroposteriorly wider than the radius and proximodistally short; fibula symmetrically pentagonal in outline having equally long pre- and postaxial margins and with facets for the fibulare and astragalus subequal in length.

**Referred Material**—NHMUK R10062, a partial skeleton including cervical, dorsal, and caudal vertebrae, dorsal ribs, a coracoid, ischium and pubis, and a right humerus and some associated limb elements; OUM J.3300, an incomplete skeleton including a partial right mandible, cervical, dorsal, and caudal vertebrae, partial pectoral girdle, four propodials, and disarticulated limb elements.

**Remarks**—Specimen NHMUK R10062 has not been previously described in detail but was informally referred to *Colymbosaurus* by Brown (1984), whereas OUM J.3300 is currently undescribed but can be confidently referred here to *Colymbosaurus*.

Specimen NHMUK R10062 is one of the most complete specimens referable to *Colymbosaurus*. The preserved mid-dorsal vertebra exhibits a tall neural canal similar to *Colymbosaurus svalbardensis*. The mid-caudals are pentagonal in anterior view, with widely spaced chevron facets as in *Colymbosaurus*. No anteroposteriorly oriented ridge is visible on the distal articular surface of the humerus, similar to some propodials of *Colymbosaurus megadeirus* (Benson and Bowdler, 2014). For this reason, Benson and Bowdler (2014) referred NHMUK R10062 to Plesiosauroidea incertae sedis. The ilia of NHMUK R10062 are nearly identical to those found in PMO 222.663 in their general morphology. They share a subequal expansion of the dorsal end and are mediolaterally compressed.

Specimen OUM J.3300 is the only *Colymbosaurus* specimen to have cranial material, consisting of a partial right mandible along with several possible cranial fragments and the majority of the postaxial skeleton. It is referred to *Colymbosaurus* on the basis of mid-cervical vertebrae that are marginally anteroposteriorly shorter than dorsoventrally tall and lack a longitudinal ridge on the lateral surface. The specimen shares the morphology of the postaxial expansion of the propodials with *Colymbosaurus*, the ulna is conspicuously anteroposteriorly wider than the radius and proximodistally short, and the fibula is pentagonal with subequally large facets for the astragalus and the fibulare.

*COLYMBOSAURUS SVALBARDENSIS* (Persson, 1962)  
(Figs. 3–11)



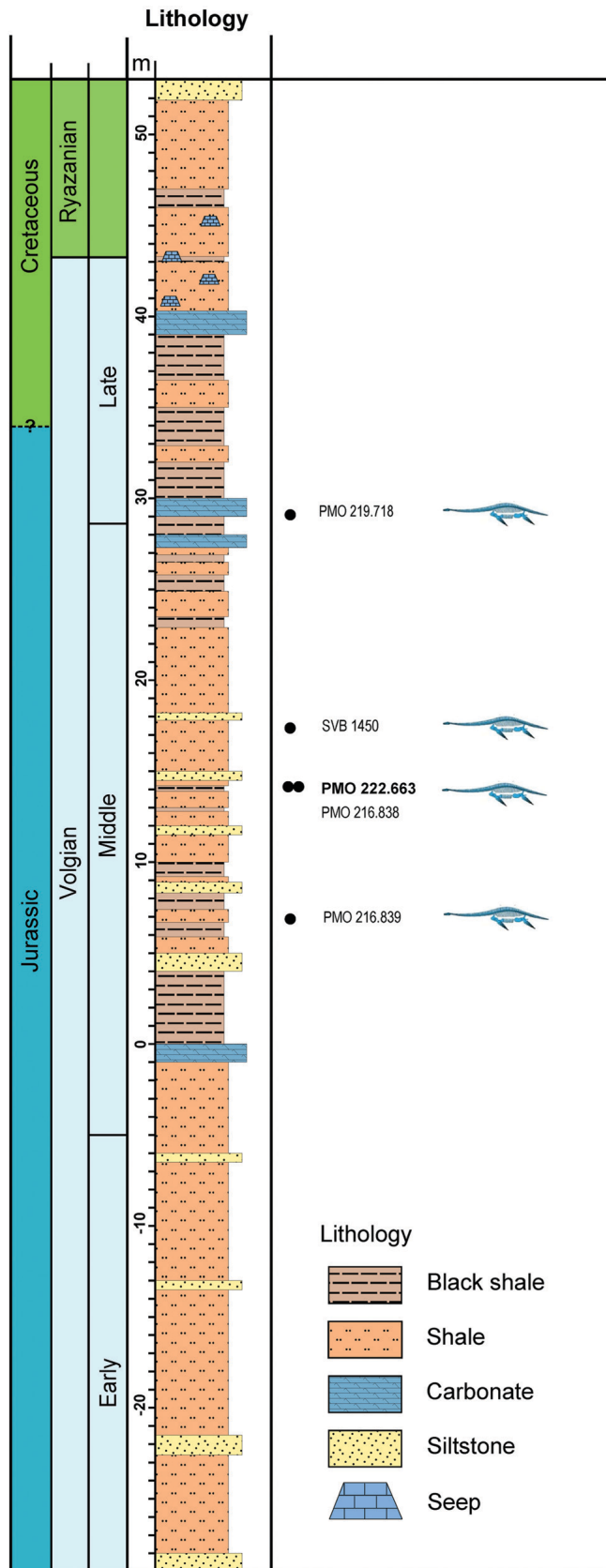


FIGURE 2. The stratigraphic position of PMO 222.663 compared with the referred specimen of *Colymbosaurus svalbardensis* (PMO 216.838) in bold, *Spitrasaurus* (PMO 219.718, SVB 1450), and *Djupeadalia* (PMO 216.839). Modified from Delsett et al. (2016).

#### Holotype—PMO A27745.

**Referred Material**—PMO 222.663 is an incomplete, partially articulated skeleton preserving 14 dorsal and three sacral vertebrae, a nearly complete caudal series, coracoids, partial interclavicle-clavicle complex, both ilia, four propodials, most of the epipodials, and several more distal limb elements. Other referred material includes PMO 216.838 and PMO 218.377 (Knutsen et al., 2012a).

**Emended Diagnosis**—A species of *Colymbosaurus* with four sacral vertebrae (three in *C. megadeirus*). Differs from *Colymbosaurus megadeirus* in having proximodistally shorter epipodials in the hind limb (tibia, fibula length/width ratio) (Knutsen et al., 2012a), a dorsoventrally taller neural canal on the mid-dorsal vertebrae (at least twice as tall as wide), a more gracile femoral shaft (PMO 216.838 is excluded here due to preservation), and a posterior margin of the ischium that is abruptly squared-off and relatively broad (Knutsen et al., 2012a).

**Diagnostic Remarks on PMO 222.663**—This specimen is referred to *Colymbosaurus* on the following basis: (1) the middle caudal centra are subrectangular due to a flat ventral surface, with widely spaced, low chevron facets located ventrolaterally; (2) the propodials possess a large posterodistal expansion at least twice as large as the preaxial expansion and bear a single postaxial ossicle facet of subequal size to the epipodial facets; (3) the ulna is conspicuously anteroposteriorly wider than the radius; and (4) the fibula is symmetrically pentagonal in outline with subequal facets for the fibulare and the intermedium. Specimen PMO 222.663 shares important features with the holotype of *Colymbosaurus svalbardensis* (PMO A27745) and is referred to this taxon on the basis of possessing a neural canal of the middle dorsal vertebrae that is at least twice as tall as wide (maximum internal height/maximum internal width) and relatively short epipodials (tibia length/width ratio).

**Occurrence**—Upper Jurassic Slottsmøya Member of the Agardhfjellet Formation (upper Tithonian–lower Berriasian). The specimen was found 14 m above the ‘yellow layer’ marker bed and 13 m below the *Dorsoplanites* marker bed (Delsett et al., 2016); locality coordinates 33X E518470 N8696400.

#### Taphonomy

Specimen PMO 222.663 consists of a partial axial skeleton with an associated nearly complete appendicular skeleton (Fig. 3). Similar to most of the marine reptile material from the Slottsmøya Member, the specimen has undergone congelifraction (fragmentation due to repeated freeze-thaw cycles) and compaction in certain areas (Delsett et al., 2016). Cranial material, as well as cervical and anterior dorsal vertebrae, is not preserved. In total, 14 partial dorsal vertebrae are preserved, six of which remain in a single articulated series. A total of three compressed sacrae are also present, of which only one preserves an entire neural spine and seven sacral ribs, suggesting the presence of a fourth sacral vertebra. In addition, there are 24 caudal vertebrae, 10 of which are articulated. The majority of these vertebrae are eroded and lack part, if not all, of the neural spine and transverse process. The left pectoral girdle is displaced and lying partially below the right, and is preserved in a more sideritic shale compared with the remainder of the skeleton, resulting in differential compaction of the skeleton in this region. Both femora are preserved, although the left femur is crushed at its proximal end and near the postaxial flange. The right femur has been displaced and shifted 180° relative to the rest of the paddle. The distal limb elements are well preserved and partially articulated in the hind limbs.

#### Ontogenetic State

Specimen PMO 222.663 is considered an adult on the basis of fused neurocentral sutures throughout the entire preserved portion of the vertebral column, fused caudal ribs, and distinct and

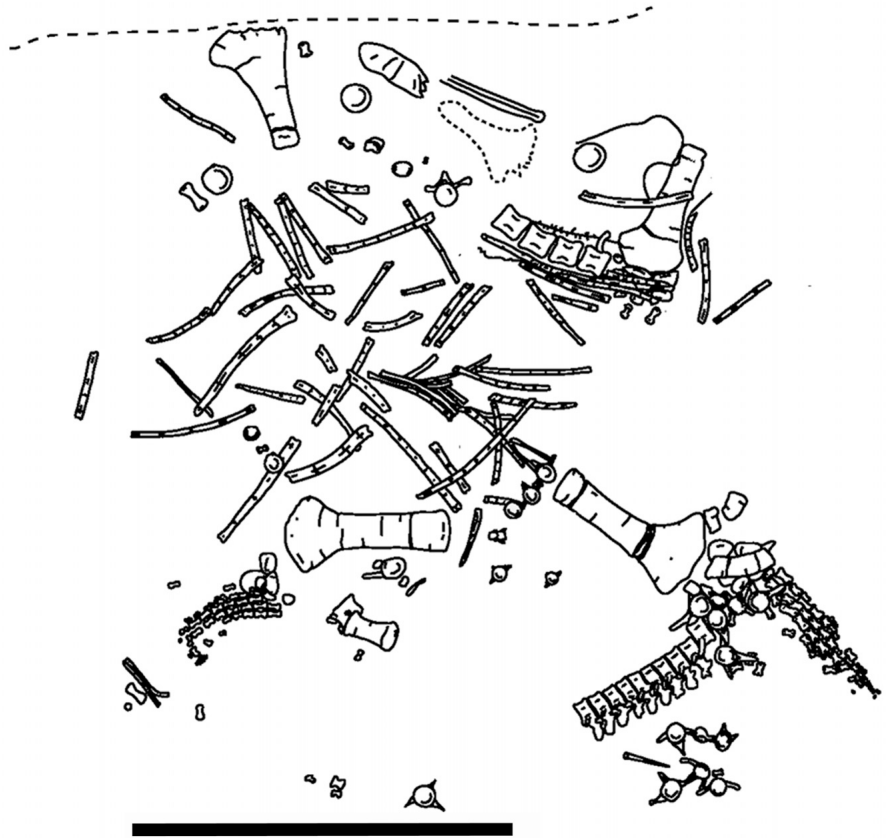


FIGURE 3. Quarry map of PMO 222.663, modified from Delsett et al. (2016). Dashed line indicates erosional slope. Scale bar equals 1 m.

well-formed epipodial facets on the propodials (Brown, 1981). Compared with the syntypes of *Colymbosaurus megadeirus*, PMO 222.663 appears to be slightly smaller based on the size of the vertebrae and propodials (Benson and Bowdler, 2014).

## DESCRIPTION AND COMPARISONS

### Axial Skeleton

**Dorsal Vertebrae**—Due to compression of the dorsal vertebrae in PMO 222.663, only certain aspects of the morphology can be described in detail (Fig. 4A–E). The centra are slightly wider than tall in anterior view, similar to *Tatenectes laramiensis* and NHMUK R10062 (*Colymbosaurus* indet.; Brown, 1984; O’Keefe et al., 2011), whereas the centra in *Muraenosaurus leedsii* are more equidimensional (Andrews, 1910; Brown, 1981).

As in *Colymbosaurus svalbardensis*, the neural canal of PMO 222.663 is significantly taller than wide (Fig. 4D, E), although in PMO 222.663 some of this could be attributed to distortion (Knutsen et al., 2012a). This condition differs from the circular neural canal observed in Kimmeridge Clay Formation cryptoclidids (Benson and Bowdler, 2014; A.J.R., pers. observ. of CAMSM J35344 and OUM J.3300). The combined mediolateral width of the zygapophyses is narrower than the centrum, as in *Colymbosaurus megadeirus* (Benson and Bowdler, 2014). Based on the single, undistorted neural arch base, PMO 222.663 lacks an anteroposterior constriction at the base of the neural spine as in all other cryptoclidids (Benson and Druckenmiller, 2014). In the mid-dorsal vertebrae (Fig. 4E), the transverse processes are placed dorsally with respect to the neural canal and gradually shift ventrally in more posterior vertebrae. In anterior view, the transverse processes are inclined at 30–40° with respect to the horizontal plane, as in the holotype of *Colymbosaurus svalbardensis* (Knutsen et al., 2012a). Due to crushing, it is impossible

to see if the transverse processes sweep posteriorly in lateral view. The rib facets appear oval and are dorsoventrally taller than anteroposteriorly long, but this could be a taphonomic artifact. The posterior-most dorsal vertebra is more circular than the more anterior vertebrae and has short, rectangular transverse processes in anterior view, but it is still separated from the centrum (Fig. 4C).

**Sacral Vertebrae**—Three sacral vertebrae are preserved in PMO 222.663 (Fig. 5A–C) and were identified as those vertebrae in which the centrum and neural arch both contribute to the sacral rib facet (Benson and Bowdler, 2014). However, this state can be difficult to determine in well-ossified adults, such as PMO 222.663, where the neurocentral sutures are fused and the centra poorly preserved. Three pairs of sacral ribs were also identified in PMO 222.663, although an additional sacral rib may also be present (see below). Thus, four sacral vertebrae may have been present, but poor preservation and disarticulation in this area makes this difficult to confirm. Four sacra are present in the holotype of *Colymbosaurus svalbardensis* (PMO A27745) and *Tatenectes laramiensis* (O’Keefe et al., 2011; Knutsen et al., 2012a), whereas three are found in *C. megadeirus* (Benson and Bowdler, 2014).

The order of the sacral vertebrae in PMO 222.663 can be determined by the position of the sacral rib facets, along with other associated vertebrae (O’Keefe et al., 2011). The first sacral was identified by the more dorsal position of the rib facets, compared to the other sacral vertebrae (Fig. 5A). In posterior view, the centrum is mediolaterally wider than dorsoventrally tall. The vertebra interpreted as being the second or third sacral has a more ventrally positioned rib facet than the first (Fig. 5B). The morphology of the sacral rib facets on this vertebra are subcircular rather than dorsoventrally long and anteroposteriorly short, as in the sacra of one of the syntypes in *Colymbosaurus*

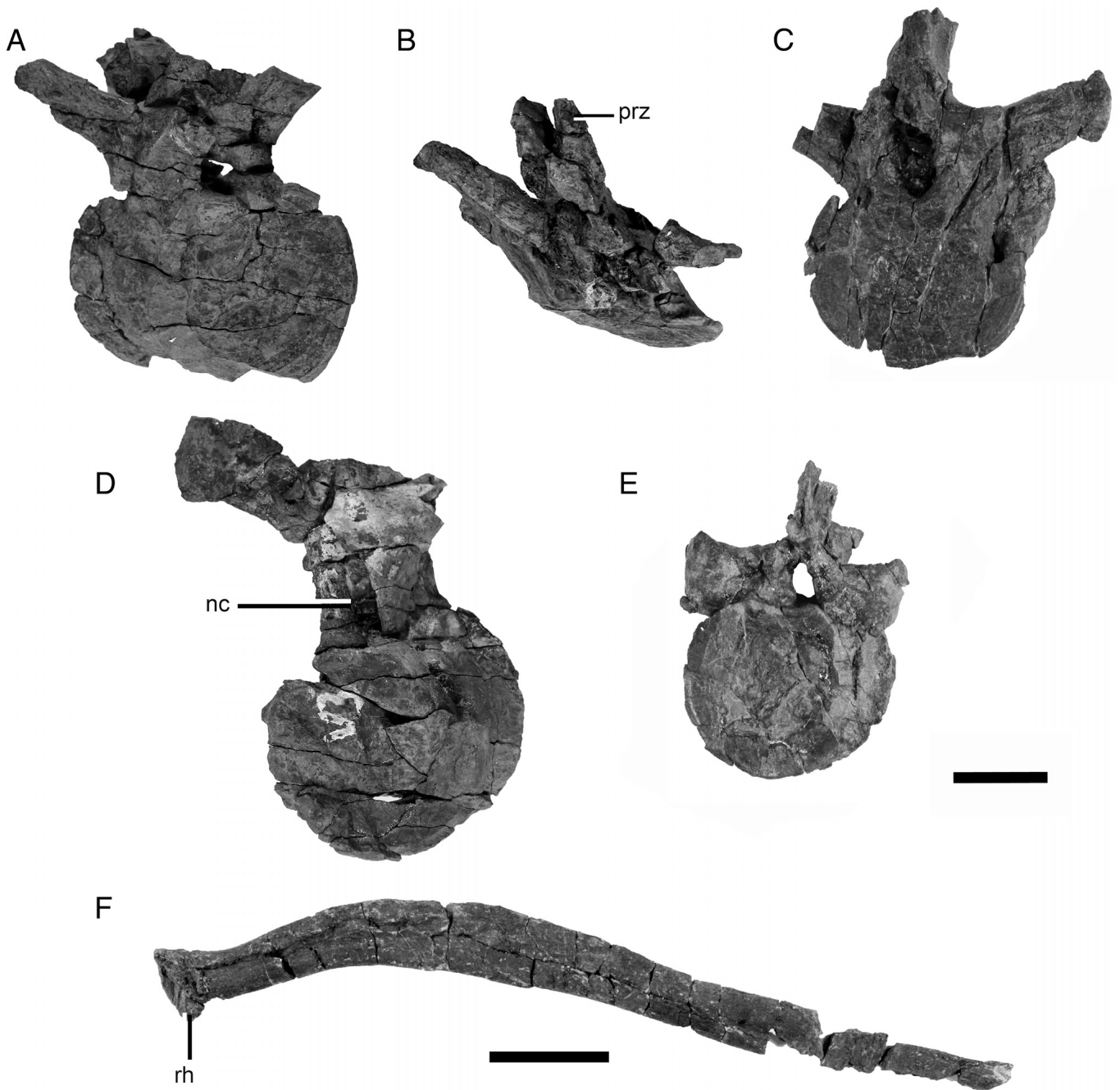


FIGURE 4. Dorsal vertebrae and a partial dorsal rib of PMO 222.663. Mid-dorsal vertebrae in **A**, posterior and **B**, dorsal views; **C**, anterior/mid-dorsal in anterior view; **D**, mid-dorsal in anterior/posterior? view; **E**, posterior-most dorsal in posterior view; **F**, a right dorsal rib in posterior view. **Abbreviations:** nc, neural canal; prz, prezygapophysis; rh, rib head. Scale bars equal 2 cm (**A–E**) and 5 cm (**F**).

*megadeirus* (CAMS J63919) and NHMUK R10062 (Benson and Bowdler, 2014). The posterior-most sacral is the best preserved of the three and was found in articulation with the first caudal vertebra (Fig. 5C). The neural spine is dorsoventrally shorter and nearly anteroposteriorly as long as the centrum, with a slightly posteroventrally sloping apical margin. As in most cryptoclidids, the sacral neural spines are positioned dorsally from the centrum (O’Keefe et al., 2011). This morphology differs from *Pantosaurus striatus*, where the neural spines are significantly posteriorly inclined (Wilhelm and O’Keefe, 2010). A partial sacral rib was found in articulation with this vertebra (Fig. 5C).

Seven partial to complete sacral ribs are preserved in PMO 222.663. Four are complete, two other proximal rib fragments remain in articulation with the centra, and one is incomplete. The most gracile sacral rib (Fig. 5D) was found adjacent to the second or third sacral vertebra, is straight and trilobate in cross-section proximally, and becomes more oval in cross-section distally. The other sacral ribs are straight and elongate and exhibit nearly equal expansion of both the proximal and distal ends. The sacral ribs (Fig. 5E–H) are interpreted as two sets, because these were found in close proximity to each other. Each of the sacral ribs preserved in PMO 222.663 is proximodistally extended and exhibits nearly equally expanded proximal and

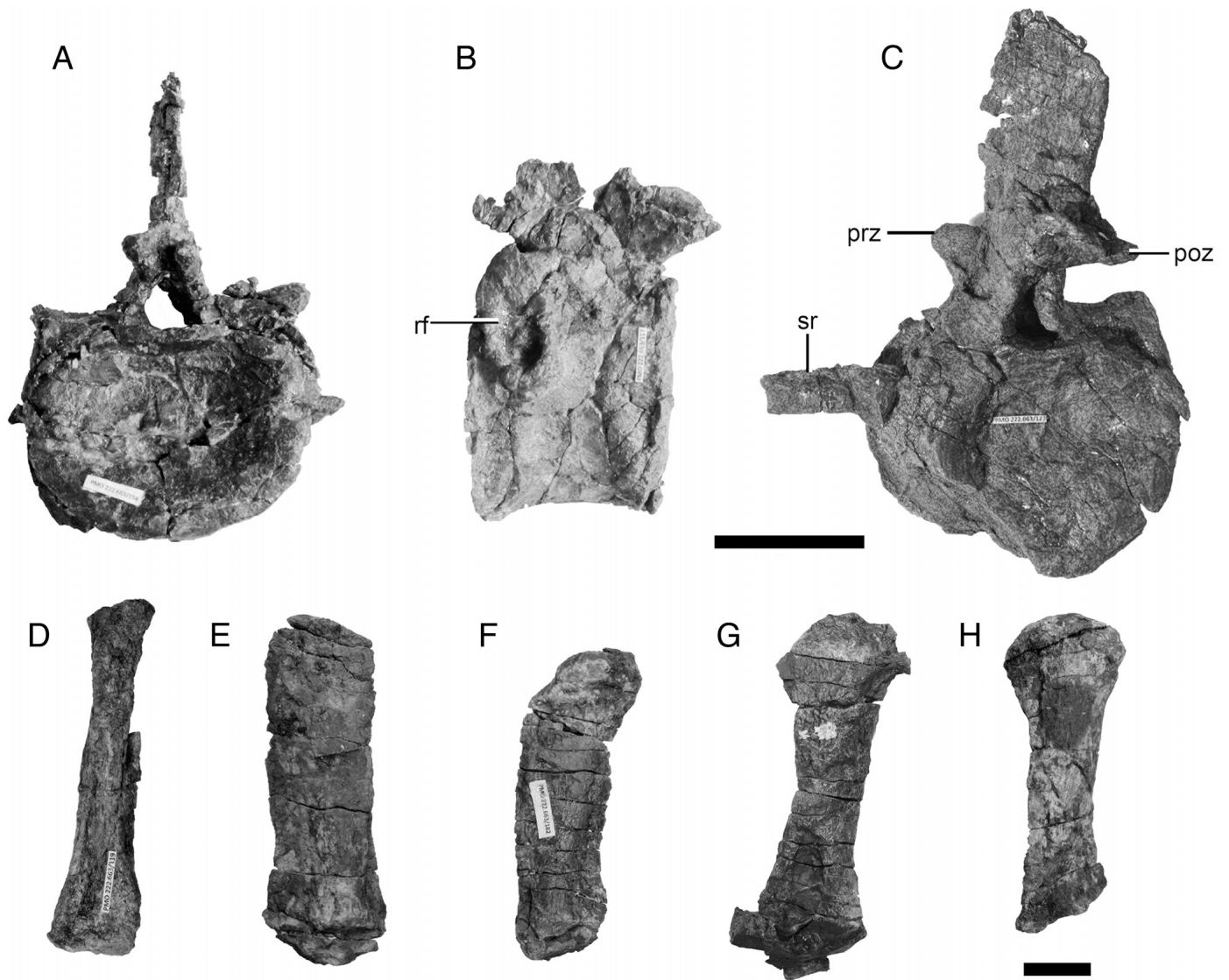


FIGURE 5. Sacral vertebrae and ribs of PMO 222.663. **A**, first sacral vertebra in posterior view; **B**, second or third sacral vertebra in lateral view; **C**, posterior sacral vertebra in posterolateral view; **D–H**, sacral ribs. **Abbreviations:** **poz**, postzygapophysis; **prz**, prezygapophysis; **rf**, rib facet; **sr**, sacral rib. Scale bars equal 5 cm (**A–C**) and 2 cm (**D–H**).

distal ends. This differs from the spatulate sacral ribs found in *Tatenectes laramiensis* and *Pantosaurus striatus*, which have anteroposteriorly expanded distal ends in dorsal view (Wilhelm and O’Keefe, 2010; O’Keefe et al., 2011). Additionally, PMO 222.663 differs from *Cryptoclidus eurymerus*, in which the proximal end is dorsoventrally thicker than the distal end (Brown, 1981).

**Caudal Vertebrae**—The 24 caudal vertebrae preserved in PMO 222.663 represent the most complete plesiosauroid tail known from the Slottsmøya Member and consist of an articulated anterior series and several disarticulated mid- and posterior caudals (Fig. 6). In general morphology, the centra are pentagonal and mediolaterally wider than dorsoventrally tall, as in the holotype for *Colymbosaurus svalbardensis* (PMO A27745) and *C. megadeirus* (Knutsen et al., 2012a; Benson and Bowdler, 2014). Paired subcentral foramina are present ventrolaterally. All caudals possess chevron facets, except the first centrum preserved in the series. Similar to the holotype of *C. svalbardensis* (PMO A27745; Knutsen et al., 2012a), the chevron facets are triangular in ventral view, with the apex pointing anteriorly

(Fig. 6B), in contrast to oval facets seen in *C. megadeirus* (Benson and Bowdler, 2014). The facets slightly protrude from the ventral surface, but they are recessed in PMU 24781, an historical specimen from the Slottsmøya Member, suggested to resemble *Colymbosaurus* by Kear and Maxwell, (2013). As in both *C. svalbardensis* and *C. megadeirus*, the chevron facets are shared between adjacent vertebrae (Fig. 6E). An anterior ridge on the chevron facet is present in *C. megadeirus* and also NHMUK R10062 (A.J.R., pers. observ.) but is absent in PMO 222.663.

The neural arches on the anterior caudal vertebrae are well preserved (Fig. 6A). These are posteriorly angled, so the posterior margin of the neural spine is dorsal to the anterior third of the succeeding centrum, similar to the holotype specimen of *Colymbosaurus svalbardensis* (PMO A27745; Knutsen et al., 2012a). The neural spine is slightly taller than the dorsoventral height of the centrum (Table 1). On the sixth vertebra in the articulated caudal series, an anteriorly oriented process extends from the pedicel of the neural arch; this structure may be a taphonomic artifact or possibly a pathology (Fig. 6E). This process is fused to the pedicel and appears broken distally (Fig. S1). The

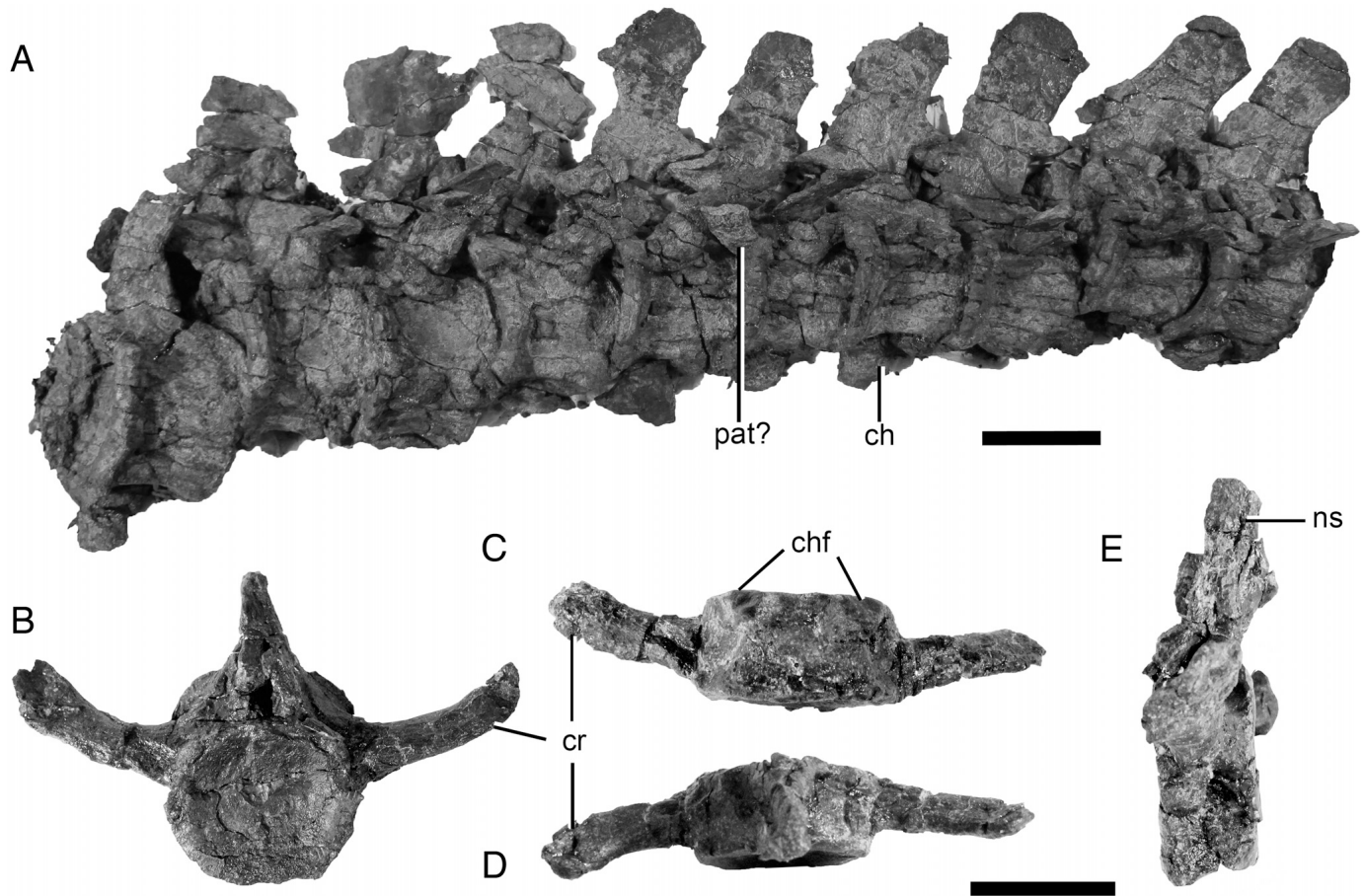


FIGURE 6. Selected caudal vertebrae of PMO 222.663. **A**, the articulated anterior caudal series; mid-caudal vertebra in **B**, anterior, **C**, ventral, and **D**, dorsal views; **E**, mid-caudal in lateral view. **Abbreviations:** **ch**, chevron; **chf**, chevron facet; **cr**, caudal rib; **ns**, neural spine; **pat?**, pathology? Both scale bars equal 5 cm.

caudal ribs are fused to the centra and are gracile. The ribs terminate in a sharp point, which differs from the spatulate morphology observed in *Cryptoclidus eurymerus* (PETRM R283).

The two posterior-most caudals differ significantly from the rest of the series. The centra are fused via the caudal ribs and part of the neural canal floor (Fig. 7). The posterior-most vertebra is compressed so that the posterior face of the centrum is angled posterodorsally, and the chevrons are fused to the centrum. Unlike the fused posterior caudal vertebrae in *Cryptoclidus eurymerus* NHMUK R8575, those of PMO 222.663 bear caudal ribs, although in the posterior-most vertebra these are significantly reduced. A neural arch is not present, as is often the case in posterior vertebrae (Wilhelm, 2010). This structure may represent a pygostyle-like structure similar to that seen in the posterior caudal series of various plesiosaurs outside Cryptoclididae, such as *Albertonectes* and *Rhomaleosaurus zetlandicus* (Kubo et al., 2012; Smith, 2013). The presence of a fused pygostyle structure in adults has also been suggested to be a synapomorphy of Cryptoclididae (Benson and Druckenmiller, 2014).

The morphological variation throughout the caudal series also provides insight into the possible presence of a tail bend in PMO 222.663. Caudal series are well known from three genera of cryptoclidids: *Cryptoclidus* (e.g., NHMUK R8575), *Muraenosaurus* (e.g., NHMUK R2864), and *Pantosaurus* (USNM 536965; Wilhelm, 2010; Wilhelm and O’Keefe, 2010). The latter has a slight downward bend of the tail starting at the fourth caudal, indicating a tail bend (Wilhelm and O’Keefe, 2010). The presence of a tail bend is difficult to confirm in PMO 222.663 due to

the vertebral compression. However, the neural spines angle posteriorly from the mid-caudal vertebrae, resulting in a slight ventral displacement of the vertebrae (Fig. 6E). Following Smith (2013), this morphology could be indicative of a downward tail bend in PMO 222.663.

**Dorsal Ribs and Gastralia**—Numerous disarticulated dorsal ribs and rib fragments are preserved in PMO 222.663. Five complete or near-complete ribs are preserved, all of which have single-headed proximal ends (although crushed). A single proximal end of an undistorted rib is preserved, bearing an oval facet for articulation with the transverse process (Fig. 4F). The ribs are bilobate in cross-section and gradually become more oval-shaped distally. The most complete and undistorted dorsal rib from PMO 222.663 is likely from the mid-dorsal region and measures approximately 50 cm in total length, lacking the distal-most end. This is slightly longer than those in *Colymbosaurus* indet. (NHMUK R10062; 40–47 cm), which has approximately the same overall body size. The ribs of PMO 222.663 are strongly curved throughout, differing from the weaker curvature observed in NHMUK R10062 (A.J.R., pers. observ.), *Djupedalina engeri*, and *Tatenectes laramiensis* (O’Keefe et al., 2011; Knutsen et al., 2012c).

Several complete gastralia are preserved in PMO 222.663, along with several other probable fragments. These are dorso-ventrally curved as in *Cryptoclidus* and *Muraenosaurus* (Andrews, 1910; Brown, 1981) and have grooves along the articulating surfaces of the adjacent gastralia. The majority of these are proximodistally short, curved, and tapering, similar to those



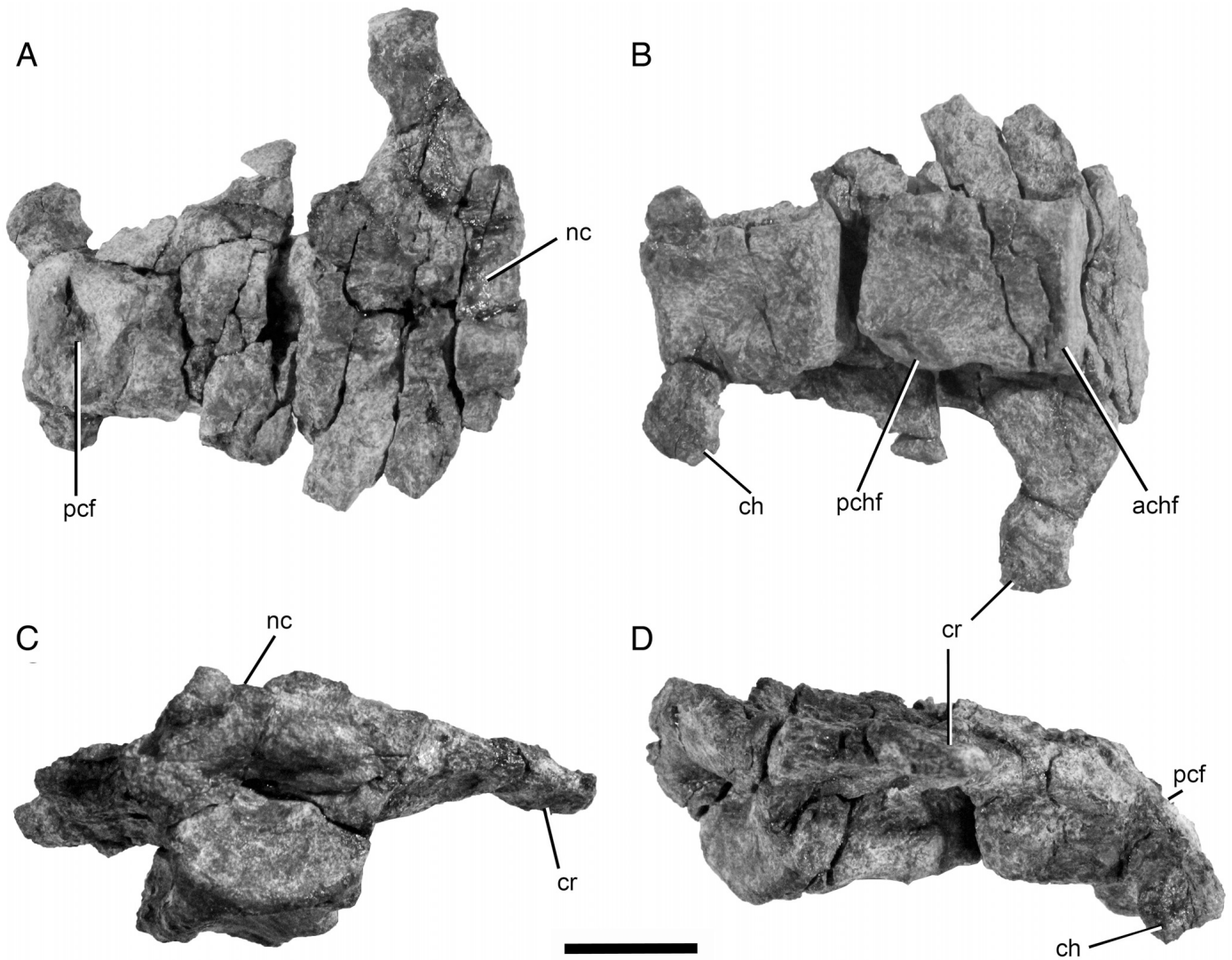


FIGURE 7. Two posterior-most caudal vertebrae of PMO 222.663 in **A**, dorsal, **B**, ventral, **C**, anterior, and **D**, lateral views. **Abbreviations:** achf, anterior chevron facet; **ch**, chevron; **cr**, caudal rib; **nc**, neural canal floor; **pcf**, posterior centrum face; **pchf**, posterior chevron facet. Scale bar equals 2 cm.

preserved in other cryptoclidids (Andrews, 1910; O’Keefe et al., 2011). There is no obvious evidence that these are pachyostotic as seen in *Tatenectes laramiensis* (Street and O’Keefe, 2010; O’Keefe et al., 2011).

#### Appendicular Skeleton

**Pectoral Girdle**—A partial pectoral girdle is preserved in PMO 222.663. It consists of an incomplete clavicle-interclavicle complex and coracoids (Fig. 8). The fragments interpreted to be the clavicle-interclavicle complex are partially fused, making interpretation difficult (Fig. 8C, D). This complex is rarely preserved in Late Jurassic cryptoclidids, and tentative identifications are based partly on morphology and partly on their proximity to other pectoral elements (Brown, 1981). The nearly complete left clavicle is wing-like, with a smooth ventral surface and a pitted dorsal surface, presumably for articulation with the scapula. The interclavicle is fully fused to the clavicles and appears as a bulge on the visceral surface between the two clavicles. On the left clavicle, the anterior margin is convex and the posterior margin is concave. The medial margin is straight and tapered towards the midline and approaches but does not contact the right

clavicle. The lateral margin is more gently rounded than that seen in *Cryptoclidus eurymerus* and *Tricleidus seeleyi* (Andrews, 1909; Brown, 1981). Clavicle-interclavicle complexes are only known from three other Kimmeridgian–Tithonian cryptoclidids and only a single plate-like element is known from the Oxfordian cryptoclidid *Tatenectes laramiensis* (O’Keefe and Street, 2009). In NHMUK R10062 (Brown, 1984), the clavicles differ from those of PMO 222.663 in being triangular and having a foramen perforating one of the elements. The clavicle or interclavicle element preserved in *T. laramiensis* is more square and anteroposteriorly longer in dorsal view than the short and wide element seen in PMO 222.663. However, in the holotype of *Djupedalina engeri* (PMO 216.839), the partial clavicle closely resembles the nearly complete clavicle of PMO 222.663 in being ‘wing-like’ with a concave anterior margin (Knutsen et al., 2012c).

Portions of the left and right coracoids are preserved and dorsoventrally compressed, obscuring their individual morphology (Fig. 8B). However, they preserve complimentary portions, allowing a more complete reconstruction of their overall shape (Fig. 8A). The element interpreted as the right coracoid, based on its close association with the right humerus, consists of much of the anterior end, including part of the medial symphysis and

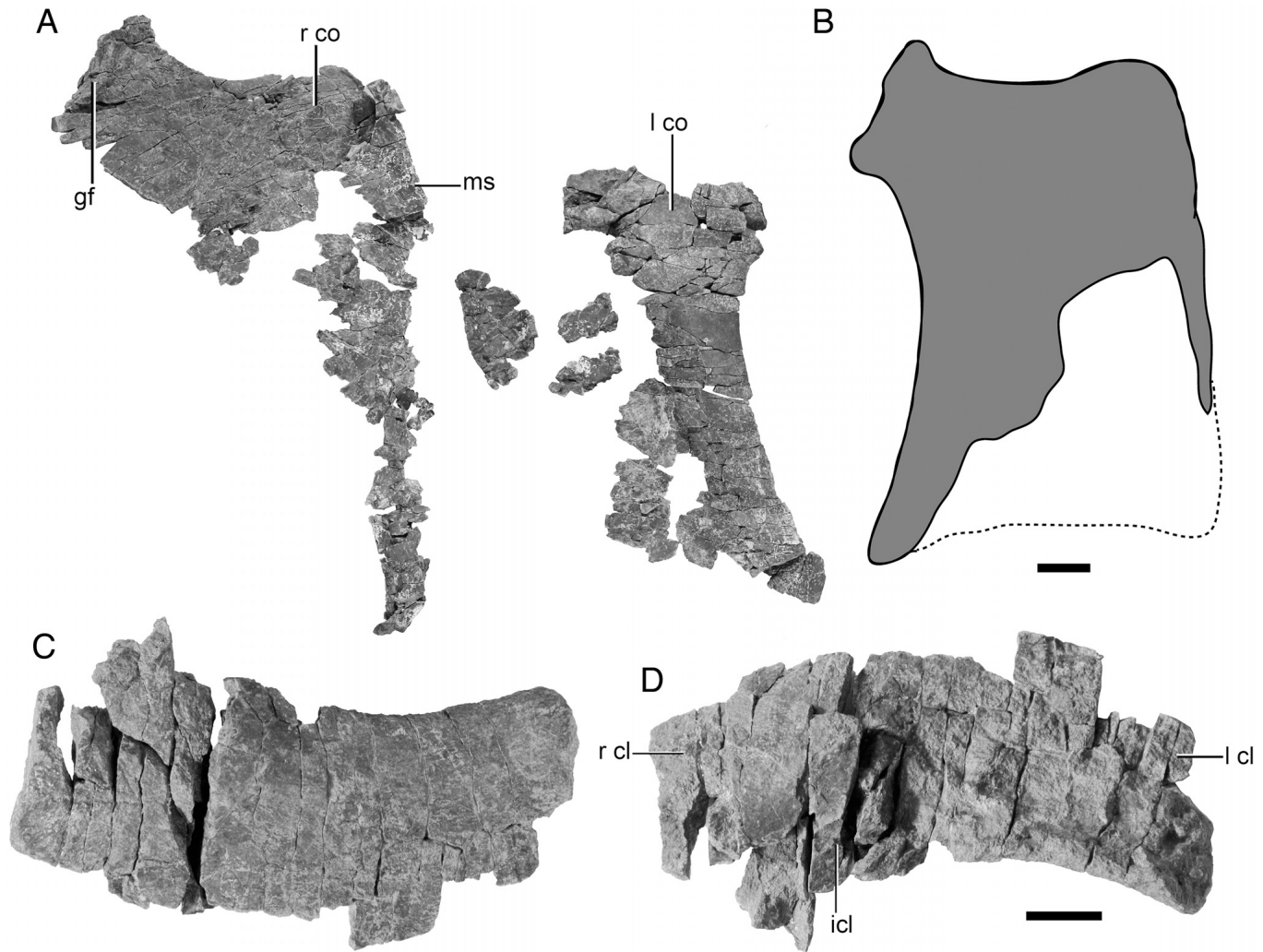


FIGURE 8. The pectoral girdle of PMO 222.663. **A**, the preserved coracoid material reconstructed in approximate life position in ventral view; **B**, reconstructed single coracoid based on the preserved portions of the right and left elements. Clavicle-interclavicle complex in **C**, visceral and **D**, anteroventral views. **Abbreviations:** **gf**, glenoid facet; **icl**, interclavicle; **l cl**, left clavicle; **l co**, left coracoid; **ms**, medial symphysis; **r cl**, right clavicle; **r co**, right coracoid. Scale bars equal 5 cm (**A–B**) and 2 cm (**C–D**).

glenoid. The left coracoid consists primarily of the lateral margin. There is no clear evidence for the presence of an anteromedial process, but this area is damaged and could have been lost. In anterior view, the region between the glenoid and medial symphysis appears level. The anteroposteriorly oriented platform on the ventral surface of the coracoids observed in other colymbosaurines such as *Colymbosaurus megadeirus* (and possibly *Abyssosaurus*; Benson and Bowdler, 2014) is not present. *Spitrasaurus wensaasi* and *Djupedalia engeri* also lack this trait, although the holotype specimens are not fully mature (Knutsen et al., 2012b, 2012c).

**Humerus**—The identity and orientation of the humerus is based on the posterior location of the tuberosity relative to the capitulum. The humeri are well preserved but the proximal regions of the right and to some degree the left humerus are dorsoventrally compressed (Fig. 9). The description is largely based on the better preserved left humerus (Fig. 9B–F). In dorsal view, the humeral shaft constricts immediately distal to the proximal head, remains consistently broad for the first one third of the shaft, and then expands distally. Compared with the femur, the humerus is proximally wider, proximodistally shorter, and possesses a more robust shaft (Table 2). In posterior view, the dorsal surface of the humerus is convex along the length of

the element and flat to slightly concave along the ventral surface. The postaxial margin of the shaft exhibits coarse rugosities along the majority of its length, with the exception of the postaxial flange. There is a single foramen perforating the left humerus mid-shaft along the postaxial surface that is absent in the right humerus, probably due to deformation in this limb (Fig. 9C). Based on a comparison of the relatively smooth bone surface on the right humerus, in addition to computed tomography (CT) scans of the left taken in this region, the ‘swelling’ on the left humerus is likely pathological in origin.

The distal articular surface bears three facets for the radius, ulna, and a postaxial ossicle, respectively, the largest being for the ulna. In contrast, there are two epipodial facets in *Muraenosaurus leedsii* and four in *Pantosaurus striatus* (Andrews, 1910; O’Keefe and Wahl, 2003). In dorsal view, the postaxial flange is considerably more developed than the preaxial flange. A reduced preaxial flange is also present in the referred specimen of *Colymbosaurus* (NHMUK R31787), although the postaxial flange is missing (Benson and Bowdler, 2014). In OUM J.3300 (*Colymbosaurus* indet.), the distal margin is similar to that seen in PMO 222.663 in having a reduced preaxial flange and an enlarged postaxial flange. The greatly expanded postaxial

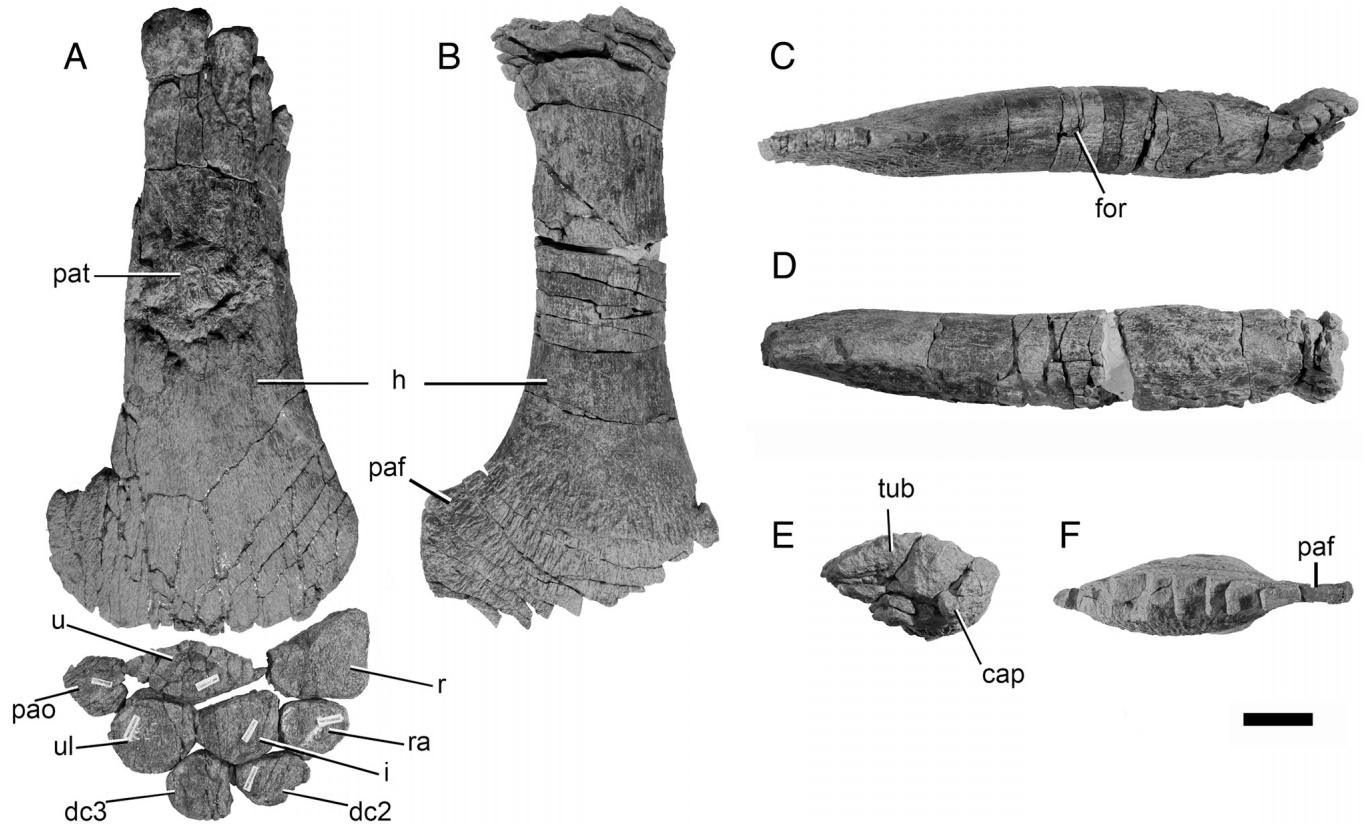


FIGURE 9. Humeri and proximal forelimb elements of PMO 222.663. **A**, right humerus and proximal forelimb elements articulated as found, in dorsal view. Left humerus in **B**, ventral, **C**, anterior, and **D**, posterior views. **E**, proximal and **F**, distal ends of the left humerus. **Abbreviations:** **cap**, capitulum; **dc2**, second distal carpal; **dc3**, third distal carpal; **for**, foramen; **h**, humerus; **i**, intermedium; **paf**, postaxial flange; **pao**, postaxial ossicle; **pat**, pathology; **r**, radius; **ra**, radiale; **tub**, tuberosity; **u**, ulna; **ul**, ulnare. Scale bar equals 5 cm.

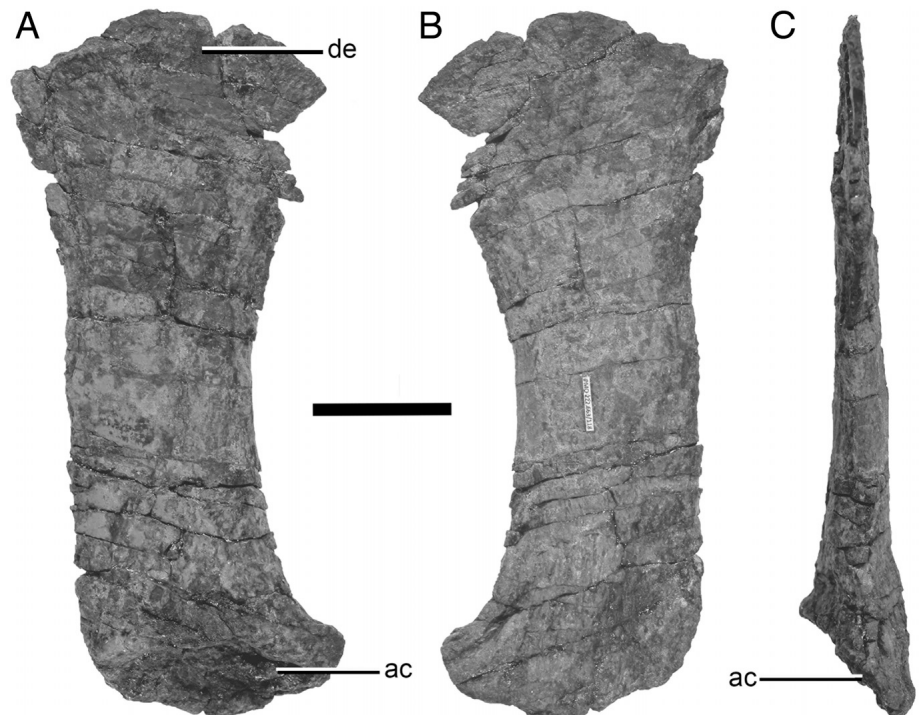


FIGURE 10. Left ilium of PMO 222.663 in **A**, medial, **B**, lateral, and **C**, posterior views. **Abbreviations:** **ac**, acetabular facet; **de**, distal expansion. Scale bar equals 5 cm.

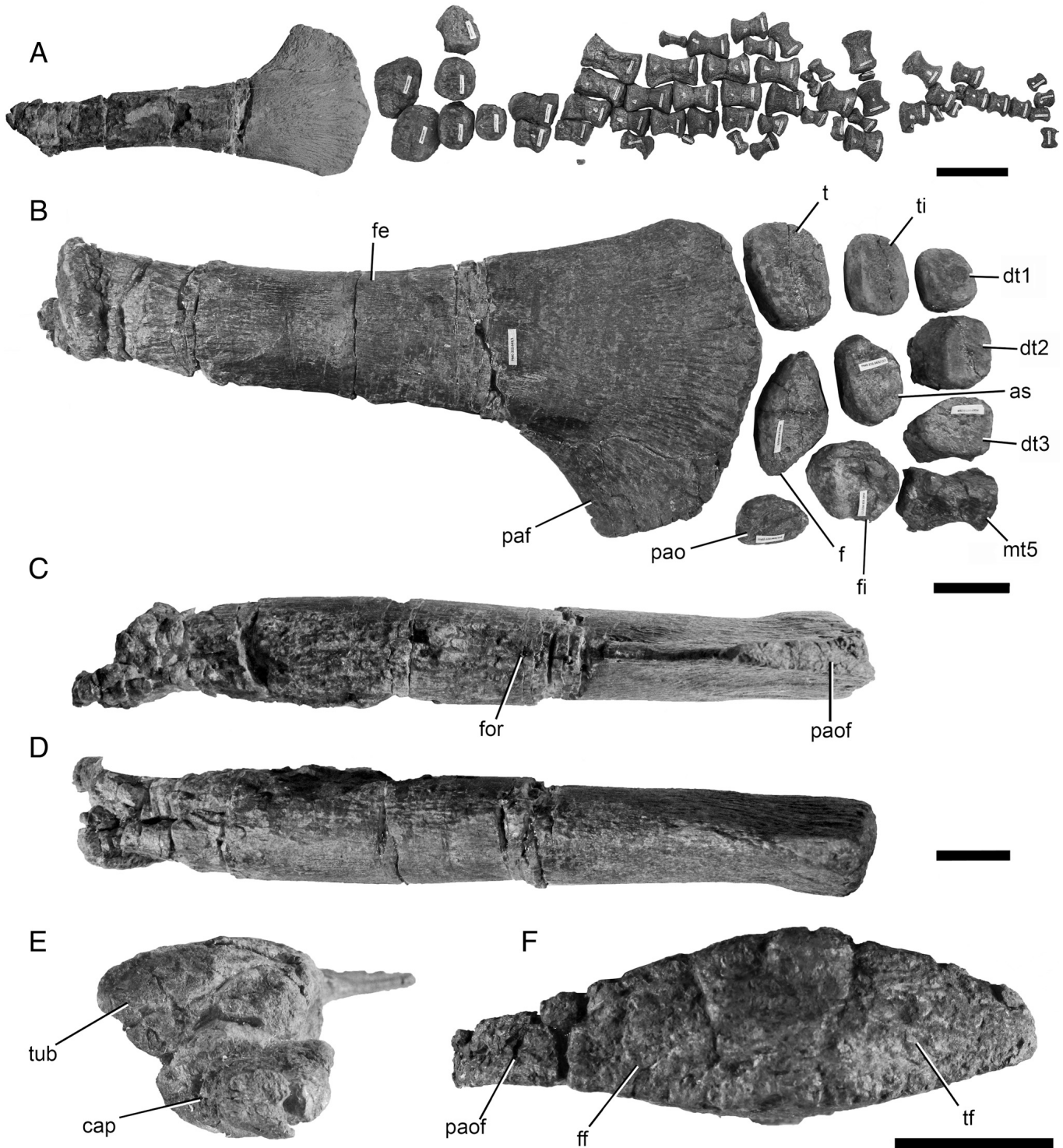


FIGURE 11. Right hind limb of PMO 222.663. **A**, right paddle as preserved in ventral view; **B**, right femur, epipodials, tarsals, and metatarsal IV in dorsal view (reconstructed). Right femur in **C**, posterior, **D**, anterior, **E**, proximal, and **F**, distal views. The identification and position of elements in **B** is based on the more complete paddles of the holotype specimen of *C. svalbardensis* (PMO A27745). **Abbreviations:** as, astragalus; cap, capitulum; dt1, first distal tarsal; dt2, second distal tarsal; dt3, third distal tarsal; dt4, fourth distal tarsal; f, fibula; fe, femur; ff, fibula facet; fi, fibulare; for, foramen; mt5, fifth metatarsal; paf, postaxial flange; pao, postaxial ossicle; paof, postaxial ossicle facet; t, tibia; tf, tibia facet; ti, tibiale; tub, tuberosity. Scale bars equal 10 cm (**A**) and 5 cm (**B–F**).

morphology seen in PMO 222.663 differs from that seen in Callovian cryptoclidids where the pre- and postaxial flanges are significantly expanded (Andrews, 1910; Brown, 1981). *Spitrasaurus larseni* and *Djupedalja engeri* are also subequally expanded,

although this could be due to their younger ontogenetic state (Knutsen et al., 2012b, 2012c).

The right humerus of PMO 222.663 preserves the complete distal edge. It lacks an anteroposteriorly oriented bisecting ridge

TABLE 1. Selected axial skeleton measurements (in cm) for PMO 222.663.

Dorsal vertebrae	DV Height (centrum)	AP Length	ML Width (centrum)	NS Height
Mid-dorsal	7	6	9.2	x
Posterior-most dorsal	7.6	*3.2	9.2	1.9
Sacral vertebrae				
Anterior-most Sacral	6.7	*3.5	9.1	4.9
2/3rd Sacral	*7.4	*5.9	x	x
Posterior-most Sacral	7.1	x	8.0	7.1
Caudal vertebrae				
Anterior-most Caudal	7.0	*2.9	8.7	7.3
Mid-caudal	5.4	x	6.3	5.9
Posterior caudal	2.8	*3.0	3.0	x

\*indicates that the number is an estimation (due to compression), and 'x' indicates missing data. **Abbreviations:** AP, anterior-posterior; DV, dorsal-ventral; ML, medial-lateral; NS, neural spine.

on the distal epipodial facets, previously considered as a diagnostic character for *Colymbosaurus* (Benson and Bowdler, 2014). The distal end of the right humerus is partially fused with the ulna; however, a groove is absent on the proximal articular surface of the right radius, suggesting that the corresponding ridge on the humerus is absent (Benson and Bowdler, 2014). As in other specimens of *Colymbosaurus*, the ulnar facet of PMO 222.663 is anteroposteriorly longer than the radius, similar to *C. megadeirus* (Benson and Bowdler, 2014). The long ulnar facet preserved in *C. megadeirus* and *C. svalbardensis* differs from other cryptoclidids such as *Pantosaurus striatus*, *Cryptoclidus eurymerus*, and *Muraenosaurus leedsii*, in which the radial facet is relatively longer (O'Keefe and Wahl, 2003).

**Epipodials and Mesopodials**—There are three elements in the epipodial row, the radius, the ulna, and a postaxial accessory ossicle, which were preserved in articulation with the right humerus (Fig. 9A). An epipodial foramen (spatium interosseum) is absent in PMO 222.663, unlike Oxford Clay Formation cryptoclidids where an epipodial foramen is present between the radius and the ulna (Andrews, 1910). The radius is trapezoidal in dorsal view, being proximodistally shorter along the posterior margin and in proximal view evenly thick dorsoventrally. The

TABLE 2. Selected measurements (in cm) of the appendicular elements of PMO 222.663.

Element	PD length	Proximal AP width	Distal AP width	Min. shaft AP width
Left humerus	41	11.5	*20.1	8.3
Right humerus	43.7	11.5	22.2	9.5
Left femur	44.2	10.5	*16.2	6.8
Right femur	45	*5.7	19.9	*5.7
	Max. AP length	Max. PD length	Min. PD length	DV proximal thickness
Right humerus elements				
Radius	8.1	6.1	2.5	2.1
Ulna	9.9	4.9	0	x
Post ax. os.	4.5	4.3	x	x
Right femur elements				
Tibia	7.1	5.1	3.9	3.1
Fibular	8.1	5.5	x	3.6
Post ax. os.	3.8	*4.8	x	2.2
Left femur elements				
Tibia	7.6	5.3	x	3.1
Fibular	3.1	5.2	x	2.9
Post ax. os.	3.9	4.9	x	x

\*indicates that the number is an estimation (due to compression), and 'x' indicates missing data. **Abbreviations:** AP, anterior-posterior; DV, dorsal-ventral; PD, proximal-distal.

radius is slightly longer than the ulna proximodistally, but approximately 25% shorter anteroposteriorly (Table 2). This morphology is similar to that seen in OUM J.3300 (*Colymbosaurus* indet.) but differs from *Spitasaurus wensaasi*, *Djupedalid engeri*, and *Pantosaurus striatus* where, in dorsal view, the radius is twice or more the size of the ulna in volume (O'Keefe and Wahl, 2003; Knutsen et al., 2012b, 2012c). Alternatively, in *Muraenosaurus leedsii* and *Cryptoclidus eurymerus*, the radius is proximodistally longer than the ulna, but nearly identical in anteroposterior width (Brown, 1981). The ulna of PMO 222.663 is anteroposteriorly wider than proximodistally long in dorsal view and has a diamond shape. Specimen OUM J.3300 exhibits a similarly anteroposteriorly elongate ulna, although it is not as pointed as in PMO 222.663. These proportions differ from the proximodistally long ulna of *Pantosaurus striatus* and *Tatenectes laramiensis* (O'Keefe and Wahl, 2003; O'Keefe and Street, 2009). The ulnae in *D. engeri* and *S. larseni* are too poorly ossified for comparison (Knutsen et al., 2012b, 2012c).

A postaxial ossicle is preserved in articulation with the humerus and other epipodials in PMO 222.663. This element was positioned directly posterior to the ulna and articulated to the ulnare, giving the element a more distal position than expected for this element. A partial postaxial ossicle is also preserved in *Abyssosaurus nataliae* and resembles the triangular morphology seen in PMO 222.663 (Berezin, 2011). Although a facet for a postaxial ossicle is present in the forelimb of *Pantosaurus striatus* and *Tatenectes laramiensis*, the element is not preserved in the holotypes or referred specimens (O'Keefe and Wahl, 2003; O'Keefe and Street, 2009). A limb element sharing the same morphology as the postaxial ossicle in PMO 222.663 is preserved in OUM J.3300; however, it is not in articulation and whether this postaxial ossicle is from the forelimb or the hind limb cannot be determined.

There are three elements in the proximal mesopodial row: the radiale, intermedium, and ulnare. The radiale is rounded in dorsal view, and is the smallest of the three. It has four facets: for the radius, the intermedium, and first and second carpals. The intermedium and the ulnare are fused, a feature that has been observed in other adult cryptoclidids (Caldwell, 1997). Given that these elements are dorsoventrally compressed, the fusion could possibly also be taphonomic. The intermedium has six facets: for the radius, the radiale, the ulna, the ulnare, and the second and third carpals. The ulnare has five facets: for the intermedium, the ulna, a postaxial accessory ossicle, the third carpal, and the fifth metacarpal. In the distal mesopodial row, the second and third carpals were identified in articulation with the right paddle. Other fragmentary disarticulated metapodial and phalangeal elements were preserved in association with both forelimbs. There is no evidence for a preaxial row as seen in *Spitasaurus* (Knutsen et al., 2012b).

## Pelvic Girdle

**Ilium**—Both ilia are preserved in PMO 222.663 and were found in the vicinity of their respective limbs (Fig. 10). Other elements of the pelvic girdle were not preserved. The ilia have undergone mediolateral compression, particularly the right ilium. However, because the ilia of PMO 222.663 are compressed, and are incomplete in the holotype specimen of *Colymbosaurus svalbardensis* (PMO A27745), detailed comparative remarks are not possible. In lateral view, the dorsal expansion is only slightly anteroposteriorly wider than the acetabular end, similar to isolated ilia and more complete specimens from the Kimmeridge Clay Formation (e.g., NHMUK R10062, OUM J.3300, CAMSM J29896, and CAMSM J29897). In lateral view, the dorsal margin has subequal anterior and posterior expansions. This differs somewhat from the asymmetrically shaped dorsal portion of the ilium preserved in the holotype of *C. svalbardensis* (PMO A27745), and the more rounded dorsal end of



*Tatenectes laramiensis* and *Pantosaurus striatus* (Wilhelm and O’Keefe, 2010; O’Keefe et al., 2011; Knutsen et al., 2012a). The anterior margin is concave and displays more of the acetabular facet in medial view, as in the majority of cryptoclidids (Andrews, 1910; A.J.R., pers. observ. of NHMUK R7428). The anterior margin differs somewhat in the holotype of *C. svalbardensis*, where the preserved acetabular end and shaft are straight. A midshaft tubercle is absent in PMO 222.663, similar to other specimens *C. svalbardensis* (Knutsen et al., 2012a), but differing from numerous penecontemporaneous specimens from the Kimmeridge Clay Formation (CAMSM J29896, CAMSM J29897) as well as PMU 24781 from the Slotsmøya Member (Kear and Maxwell, 2013), that possess this feature. The torsion of the shaft seen in *Cryptoclidus eurymerus*, *T. laramiensis*, and *M. leedsii* could not be observed in PMO 222.663 due to crushing (Andrews, 1910; Brown, 1981; O’Keefe et al., 2011).

**Femora**—Both hind limbs are well preserved, and the majority of the preserved elements are articulated (Fig. 11). In proximal view, the trochanter is situated directly dorsal to the capitulum. As in PMO A27745 (*Colymbosaurus svalbardensis*), the femur of PMO 222.663 retains the same anteroposterior width until approximately midway along the shaft, where it begins to expand (Knutsen et al., 2012a; Table 2). The femoral shaft of PMO 222.663 does not constrict immediately distal to the capitulum (possibly a taphonomic artifact), although there is a slight constriction in the holotype specimen of *C. svalbardensis* (Knutsen et al., 2012a). This differs from *C. megadeirus* and *Muraenosaurus leedsii*, where a clear constriction is present (Andrews, 1910; Brown, 1981; Benson and Bowdler, 2014).

The distal end of the femur bears three distinct facets: for the tibia, the fibula, and a postaxial ossicle. This differs from PMU 24781, which bears additional single pre- and postaxial facets, and ‘*Plesiosaurus manselii*’, which has two postaxial facets (Hulke, 1870). The tibial and fibular facets are clearly demarcated and pitted and are subequal in anteroposterior length, as in *Abyssosaurus nataliae* (Berezin, 2011), but unlike the larger tibial facet seen in PMU 24781 and in the other referred specimens of *Colymbosaurus svalbardensis* (Knutsen et al., 2012a; Kear and Maxwell, 2013). As in all material referred to *C. svalbardensis* and PMU 24781, an anteroposteriorly oriented ridge bisecting the distal femoral facets is absent in PMO 222.663, unlike some specimens of *C. megadeirus* (Knutsen et al., 2012a; Benson and Bowdler, 2014). Distally, the femur has a well-developed straight-edged postaxial flange, which is angled more posterodistally than in the humeri. The postaxial flange has a relatively shorter postaxial facet than in the humerus.

**Epipodials and Mesopodials**—There are a total of three elements in the epipodial row, the tibia, the fibula, and a single postaxial ossicle, as in *Colymbosaurus svalbardensis*, *C. megadeirus*, *Djupedalia engeri*, and *Spitrasaurus* (Knutsen et al., 2012a, 2012b, 2012c; Benson and Bowdler, 2014), but unlike the two observed in *Cryptoclidus eurymerus*, *Muraenosaurus leedsii*, and *Tatenectes laramiensis* (Andrews, 1910; Brown, 1981; O’Keefe and Street, 2009). A preaxial epipodial element is not present in either hind limb. The tibia and fibula are nearly equidimensional and are both anteroposteriorly wider than proximodistally long (Table 2). The tibia is suboval in dorsal view, with four facets: for the femur, the fibula, the astragalus, and the tibiale, the largest of which is for the femur. Unlike the well-demarcated astragalar facet of the tibia in both species of *Colymbosaurus*, the astragalar facet of PMO 222.663 is diminutive on the right and indistinguishable from the facet for the tibiale on the left (Knutsen et al., 2012a; Benson and Bowdler, 2014). The fibula is triangular in dorsal view and bears five facets: the longest for the femur, two short facets for the tibia and the postaxial ossicle, respectively, and two subequal facets for the astragalus and the fibulare. The postaxial ossicle is triangular and is similar to that seen in the forelimb (Fig. 11B). This element was removed

during excavation of the right hind limb but is preserved articulated on the left. Only an external mold of the postaxial ossicle is known in NHMUK R40640 (*Colymbosaurus* indet.; Brown, 1981; Knutsen et al., 2012a), where it has three subequally sized facets for the femur, the fibula, and the fibulare. Previously, the postaxial ossicle of *C. svalbardensis* was known from the hind limbs of the additional referred specimens, but not the holotype (PMO A27745; Knutsen et al., 2012a). The postaxial ossicle of PMO 222.663 is identical to that in other referred specimens of *C. svalbardensis* (PMO 218.377, PMO 216.838), being triangular and bearing two facets, with the smallest for the fibula.

Three proximal mesopodial elements are preserved; the fibulare is the largest, whereas the somewhat smaller astragalus and tibiale are similar in size, consistent with other specimens of *Colymbosaurus svalbardensis* (Knutsen et al., 2012a). The fibulare and the tibiale are suboval in outline, being anteroposteriorly wider than proximodistally long. The fibulare in *C. svalbardensis* is distinct in being anteroposteriorly broader and bearing two offset distal facets, whereas *C. megadeirus* has a single distal facet for the fifth metatarsal (Knutsen et al., 2012a; Benson and Bowdler, 2014). The first distal tarsal appears similar to other cryptoclidids, being small and bearing three facets. Based on the proximal position of the fifth metatarsal in PMO 222.663, it is possible that this element is shifted entirely into the mesopodial row, as in *Djupedalia engeri* and *C. svalbardensis* (Knutsen et al., 2012a, 2012c).

**Metapodials and Phalanges**—Five digits are preserved in the hind limb of PMO 222.663. The proximal edges of the metapodials of the hind limb are more convex in dorsal view compared with those in the forelimb. The phalanges are robust with flat articular surfaces, which in dorsal view become more convex distally throughout the hind limb. The distal-most elements are oval to lunate in dorsal view. The longest digit (the third) has a minimum of 11 articulated phalanges and a large number of disarticulated smaller ones distal to the articulated series (Fig. 11A).

## DISCUSSION

### Phylogenetic Analysis

A modified version of the data matrix of Benson and Druckenmiller (2014) (also used by Benson and Bowdler, 2014) was used in this analysis (Supplementary Data 2, 3). First, we attempted to replicate the results of the original analysis (Benson and Druckenmiller, 2014), which was conducted in PAUP\* (Swofford, 2003), using TNT (version 1.1) (Goloboff et al., 2008). The matrix was built in Mesquite (version 3.10; Maddison and Maddison, 2016). In order to most closely replicate the original search algorithm run in PAUP\*, a New Technology Search was performed in TNT using a combination of both ratchet and tree bisection reconnection (TBR; see Supplementary Data 1 for specific settings). All characters are unordered and equally weighted, and the same wildcard taxa were removed as in Benson and Druckenmiller (2014). *Yunguisaurus* was defined as the outgroup taxon (Cheng et al., 2006). The search resulted in fewer most parsimonious trees (MPTs; 2016) than in the original analysis, but with the same number of steps (1289) and the strict consensus recovered the same topology (consistency index [CI] = 0.304; retention index [RI] = 0.661).

To the Benson and Druckenmiller (2014) matrix were added the scores for two new operational taxonomic units (OTUs), *Colymbosaurus svalbardensis*, based solely on the holotype specimen, and PMO 222.663. Additionally, a small number of scores for other cryptoclidid taxa were modified (Supplementary Data 2; score changes detailed in Supplementary Data 1). A second matrix was also prepared that combined the scores for *C. svalbardensis* and PMO 222.663 as a single OTU (Supplementary Data 3). Bremer support and a bootstrap percentages were

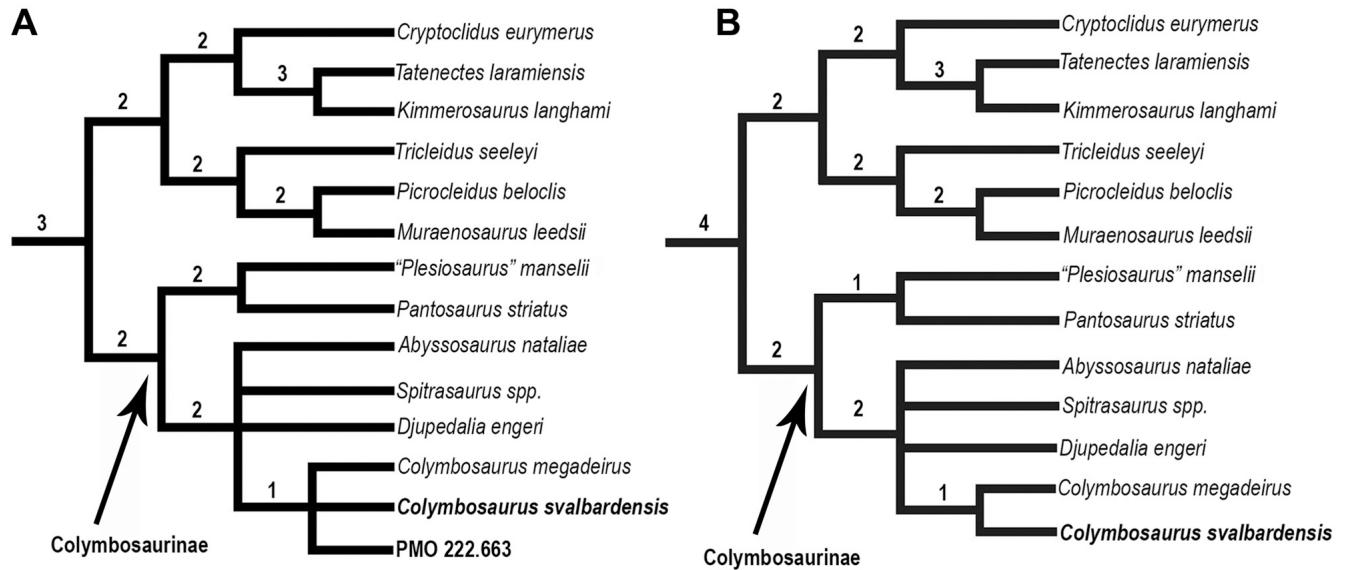


FIGURE 12. The results of the phylogenetic analysis of Cryptoclididae. **A**, strict consensus of 576 MPTs with PMO 222.663 and *Colymbosaurus svalbardensis* scored as separate OTUs (CI = 0.304, RI = 0.661); **B**, strict consensus of 576 MPTs, with a composite scoring of PMO 222.663 and *Colymbosaurus svalbardensis* (CI = 0.303, RI = 0.663). Bremer support values are given above the internodes.

calculated in TNT. Bremer support values are presented in Figure 12; however, bootstrap values for all nodes within Cryptoclididae were less than 50% and are not shown.

The analysis of the first matrix yielded 576 MPTs with 1290 steps. The strict consensus tree recovered PMO 222.663, *Colymbosaurus svalbardensis*, and *C. megadeirus* in a polytomy and as the sister taxon to (*Spirasaurus* spp. + *Djupedalia* + *Abyssosaurus*) within Colymbosaurinae (Fig. 12A). The analysis of the second matrix yielded 576 MPTs, with 1289 steps and the strict consensus tree recovered the same topology, with *C. svalbardensis* (composite scoring) and *C. megadeirus* as sister taxa (Fig. 12B). The topology for the other cryptoclidids was identical to that presented in Benson and Bowdler (2014).

### Diagnostic Characters of *Colymbosaurus*

Multiple Kimmeridge Clay Formation specimens that have been or possibly are referable to *Colymbosaurus* exhibit a large amount of variation in several aspects of their morphology. This variation must be taken into account when reevaluating diagnostic features of the genus.

Characters relating to the length to height ratio and the lack of a lateral ridge on the cervical vertebrae (characters 153 and 154, respectively; Benson and Druckenmiller, 2014) have been studied in *Colymbosaurus megadeirus* (Benson and Bowdler, 2014) but are currently unknown in *C. svalbardensis* (including PMO 222.663). With regards to cervical length to height dimensions, there is a greater degree of intraspecific variation in this character than was previously recognized, particularly regarding which region of the cervical series is measured. In NHMUK R10062, the preserved anterior and posterior cervical vertebrae have a length to height ratio <0.7, but the ratio increases slightly in the mid-cervical vertebra. In OUM J.3300 and the syntype CAMSM J.29596–29691, J.59736–J.59743 (referred to by Benson and Bowdler, 2014 as CAMSM J.29596ect.), this ratio is close to 1.0 in the anterior cervicals, and this value steadily decreases to 0.8 in the mid-cervical vertebrae. This illustrates that more consistent results are found when measurements are limited to the mid-cervical series where there is less variation among specimens referred to *Colymbosaurus*.

One of the most variable features of the genus relates to the morphology of the postaxial flange of the propodials (Fig. 13), defined in the diagnosis of Benson and Bowdler (2014:1054) as “propodials with a large posterodistal expansion bearing a postaxial ossicle facet of subequal size to the epipodial facets.” Most other colymbosaurines, including *Abyssosaurus nataliae*, *Spirasaurus wensaasi*, *S. larseni*, *Djupedalia engeri*, and ‘*Plesiosaurus*’ *manselii*, also possess a postaxial flange (Hulke, 1870; Berezin, 2011; Knutsen et al., 2012a, 2012b, 2012c). Thus, to help further distinguish *Colymbosaurus* from penecontemporaneous taxa, we have modified the diagnosis to denote ‘an extended postaxial flange, which is significantly larger than the preaxial flange, bearing a single postaxial ossicle facet of subequal size to the epipodial facets.’ Further, the specification of a single postaxial ossicle facet distinguishes *Colymbosaurus* from the taxonomically problematic material of ‘*P.*’ *manselii* (NHMUK PV OR40106), which also has a large postaxial flange but bears discrete facets for two postaxial accessory ossicles on the humerus (Hulke, 1870).

The presence of an anteroposteriorly oriented ridge bisecting the distal articulating facets of the propodials has also been used as a diagnostic character of *Colymbosaurus* (Brown, 1981; Benson and Bowdler, 2014). An anteroposteriorly bisecting ridge on the distal end of the propodials is observed on the propodials of numerous specimens of *Colymbosaurus*, including *C. ‘richardsoni*’ (NHMUK R1682) and *Colymbosaurus* indet. (OUM J.3300 and NHMUK R31787; Benson and Bowdler, 2014). However, the bisecting ridge shows varying degrees of anteroposterior exposure on other ‘*Colymbosaurus*-like’ propodials from the Kimmeridge Clay Formation, including some that appear to lack the ridge altogether. Eighteen propodials (isolated and associated) from the Kimmeridge Clay Formation that have been either referred to *Colymbosaurus* or otherwise resemble *Colymbosaurus* on the basis of overall propodial morphology or associated material were examined in the course of this study. The left humerus and right femur of PMO 222.663, left femur of PMO 216.838, and the right femur of PMO A27745 were also included for comparison. Of the 22 propodials examined, nine had a well-defined anteroposteriorly oriented ridge present on both epipodial facets, four had a ridge on one of the epipodial facets,



FIGURE 13. Humeri (upper row) and femora (bottom row) of referred specimens of *Colymbosaurus*. **A**, left humerus (reversed) of PMO 222.663 (*C. svalbardensis*); **B**, right humerus of NHMUK 10062 (*Colymbosaurus* indet.; photo used with permission); **C**, right humerus of OUM J.3300 (*Colymbosaurus* indet.); **D**, right femur of PMO A27745 (holotype of *C. svalbardensis*); **E**, right femur of PMO 222.663 (*C. svalbardensis*); **F**, left femur of PMO 216.839 (*C. svalbardensis*); **G**, right femur of OUM J.3300 (*Colymbosaurus* indet.); **H**, right femur of CAMSM H29654 (*C. megadeirus*). Scale bar equals 10 cm.

and nine lacked the ridge altogether (Table S1). Additionally, MANCH LL.5513–14, which preserves both femora, has a recognizable ridge on the left femur, but not on the right.

After reexamination of PMO 218.377, one of the referred specimens of *Colymbosaurus svalbardensis* (Benson and Bowdler, 2014; fig. 10A), the presence of an anteroposteriorly oriented bisecting ridge on the distal humeral facets is equivocal. This ridge is also clearly absent in all other propodials of specimens referable to *C. svalbardensis*, including PMO 222.663. The potential utility of this feature also needs to be judged in the light of other factors, including taphonomic compression (CAMSM J29739, NHMUK R6317) and ontogenetic and/or individual variation (MANCH LL.5513–14). A similar feature has also been observed in other uncompressed cryptoclidid propodials from the Oxford Clay Formation (CAMSM J67072, GLAHM V1807, MANCH LL.14975, LEICS 413.1956/40, NOTNH FS5879) and a non-cryptoclidid propodial from the Kimmeridge Clay Formation (OUM J.13837). These observations suggest that the presence of an anteroposteriorly oriented bisecting ridge may prove valuable in a broader evolutionary context. Given that this character is equivocal on the holotype of *C. svalbardensis* (PMO A27745), is absent on two of the referred specimens of this species (PMO 222.663, PMO 216.838), and is variable in extent and presence in Kimmeridge Clay Formation specimens of *Colymbosaurus*, we do not consider this to be a reliable diagnostic character for the genus. However, it is possible that the presence of this feature could be diagnostic at a less inclusive taxonomic level, possibly for *C. megadeirus*.

Based on a broad examination of material from both the U.K. and Svalbard, we provide new diagnostic features for *Colymbosaurus* relating to the morphology of the mid-caudal vertebrae and the ulna and fibula.

As described above, the middle caudal centra of *Colymbosaurus* are subrectangular due to the presence of a flat ventral surface

with widely spaced, low chevron facets located ventrolaterally (Benson and Druckenmiller, 2014). The middle caudal centra of *Colymbosaurus* are distinctive among cryptoclidids in that their chevron facets project slightly from the ventral surface and are not positioned in a deep groove (PMU 24781) or are not significantly venterolaterally projecting (e.g., *Cryptoclidus eurymerus*; Andrews, 1910; Kear and Maxwell, 2013). The mid-caudal centra of *Colymbosaurus* also have a flat ventral margin in anterior view, compared with the more rounded morphology in *Cryptoclidus eurymerus*, *Muraenosaurus leedsii*, and *Pantosaurus striatus* (Andrews, 1910; Wilhelm and O’Keefe, 2010).

In referred specimens of *Colymbosaurus* where an ulna is present (PMO 222.663, OUM J.3300), the element is conspicuously anteroposteriorly wider than the radius, and proximodistally short. This differs from the ulna in *Muraenosaurus leedsii* and *Pantosaurus striatus*, where this element is significantly anteroposteriorly shorter than the radius, and from ‘*Plesiosaurus*’ *manselii*, where the ulna and the radius are subequal in length (Hulke, 1870; Andrews, 1910; O’Keefe and Wahl, 2003).

A unique morphology of the fibula is also observed in *Colymbosaurus megadeirus* (CAMSM J29654–91, CAMSM J59736–43), *Colymbosaurus* indet. (OUM J.3300), and *C. svalbardensis* (PMO A27745, PMO 216.383, PMO 218.377, PMO 222.663), in which this element is pentagonal to nearly triangular, with symmetrical preaxial and postaxial margins. The fibula lacks a spatium osseum and has subequal facets for the fibulare and the intermedium, differentiating *Colymbosaurus* from all other cryptoclidids. This particular morphology is noted in Knutsen et al. (2012a) as one of the characters justifying the referral of the *C. svalbardensis* material to *Colymbosaurus*. Although some specimens of *Cryptoclidus eurymerus* also exhibit a pentagonal fibula, these are anteroposteriorly longer than those seen in *Colymbosaurus* and possess a clear spatium osseum (Andrews, 1910; Brown, 1981).

### New Autapomorphies for *Colymbosaurus svalbardensis*

In addition to the holotype specimen, PMO A27745, Knutsen et al. (2012a) also included PMO 216.838 and PMO 218.377 in the hypodigm of *Colymbosaurus svalbardensis*. The inclusion of the new specimen described here, PMO 222.663 (also found at nearly the exact same stratigraphic horizon as PMO 216.838), provides the opportunity to recognize two additional autapomorphies from the dorsal vertebrae and the hind limbs.

The neural canal of the dorsal vertebrae in the holotype specimen and PMO 222.663 is conspicuously ovate and dorsoventrally taller than wide when compared with the more rounded, equidimensional neural canals observed in *Colymbosaurus megadeirus* and other plesiosauroids from the Kimmeridge Clay Formation (Benson and Bowdler, 2014; A.J.R., pers. observ. of OUM J.55482). The presence of this character in multiple specimens suggests that this is not simply a taphonomic artifact but is the true morphology and can be recognized as a new autapomorphy of the species. A second possible autapomorphy pertains to the relative anteroposterior expansion of the femoral head relative to the femoral shaft, as seen in either dorsal or ventral view (Fig. 13). In all specimens of *C. svalbardensis*, the anteroposterior width of the femoral shaft is nearly the same as that of the proximal end. In contrast, the anteroposterior width of the shaft is conspicuously less than that of the proximal end in *Colymbosaurus* material from the Kimmeridge Clay (NHMUK R31787, OUM J.3300, NHMUK 10062; Benson and Bowdler, 2014). This feature also does not seem to be the result of a taphonomic bias given that a marked constriction between the humeral head and shaft is present in the newly referred specimen of *C. svalbardensis*, PMO 222.663.

### Affinities of NHMUK R10062 to *Colymbosaurus svalbardensis*

Specimen NHMUK R10062, a partial skeleton including much of the vertebral column and associated girdle and limb elements, was originally named *Colymbosaurus 'portlandicus'* by Brown (1984) and was subsequently referred to Plesiosauroidea incertae sedis by Benson and Bowdler (2014). Based on the newly amended diagnosis, NHMUK R10062 shares three diagnostic features of *Colymbosaurus* and can be referred to this taxon: (1) the mid-caudals are pentagonal in anterior view, with widely spaced chevron facets; (2) the humerus has a large postaxial expansion at least twice as large as the preaxial expansion, bearing a single postaxial ossicle facet of subequal size to the epipodial facets; and (3) although the ulna is not preserved, the ulnar facet on the humerus is longer than the radial facet.

It is noteworthy that NHMUK R10062 also shares several features with *Colymbosaurus svalbardensis*. The neural canal of the mid-dorsal vertebrae is taller than wide, although not to the degree observed in specimens of *C. svalbardensis* from the Slottsmøya Member (Knutsen et al., 2012a). Additionally, it shares the same morphology of the posterior margin of the ischium, which is abruptly squared-off and mediolaterally broad. This suggests that NHMUK R10062 is potentially referable to *C. svalbardensis* and, as such, represents the first specimen of this taxon occurring in the upper Kimmeridge Clay Formation. However, in the absence of additional overlapping material, we refrain from formally referring the specimen to *C. svalbardensis*.

### Survival of Colymbosaurinae into the Cretaceous

The Slottsmøya Member of central Spitsbergen preserves a high diversity of colymbosaurine plesiosauroids (*Djupedalina engeri*, *Spirasaurus larseni*, *S. wensaasi*, and *Colymbosaurus svalbardensis*) that lived close to or likely across the Jurassic-Cretaceous boundary at high paleolatitudes (>60°; Torsvik et al., 2002). The taxonomic composition differs from the slightly older Kimmeridge Clay Formation in the United Kingdom, where non-

colymbosaurine plesiosauroids are also found (e.g., *Kimmerosaurus*). Given that the stratigraphically youngest known colymbosaurine is *Abyssosaurus* from the Lower Cretaceous of boreal Russia (Berezin, 2011), and that colymbosaurines are the only known plesiosauroids from the high-latitude deposits of the Slottsmøya Lagerstätte, we propose that this clade may have persisted across the Jurassic-Cretaceous boundary in the Boreal Realm. Ongoing studies relating to the stratigraphy, the diversity, and the phylogenetic relationships of cryptoclidids from the Slottsmøya Lagerstätte and other sites are needed to better understand the timing and nature of extinctions for the clade at the Jurassic-Cretaceous boundary (Benson and Druckenmiller, 2014).

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