A new plesiosauroid (Reptilia: Sauropterygia) from the Agardhfjellet Formation (Middle Volgian) of central Spitsbergen, Norway

Espen M. Knutsen, Patrick S. Druckenmiller & Jørn H. Hurum

At present, our knowledge of plesiosauroid diversity from the uppermost Jurassic (Tithonian/Volgian) is very limited. Newly discovered material from the Slottsmøya Member of the Agardhfjellet Formation of central Spitsbergen, Svalbard, contributes significant new information on this poorly known interval and helps bridge a temporal gap between better known plesiosaurians from the older Jurassic deposits of Europe, and Cretaceous of North America. The partially articulated skeleton of a juvenile long-necked plesiosaurian, PMO 216.839, is one of the most complete plesiosaur fossils known from Spitsbergen and represents a new taxon, *Djupedalia engeri* gen. et sp. nov. Whilst sharing some similarities with previously described taxa from the Oxford Clay (*Muraenosaurus*, *Tricleidus*, and *Cryptoclidus*) and the Kimmeridge Clay formations (*Kimmerosaurus*) of England, the new taxon can be diagnosed by features of the cervical vertebrae, including centrum proportions and morphology, a very pronounced posterior shift in the neural spines relative to the centrum, fused prezygapophyses and greatly elongated postzygapophyses, as well as extremely short dorsal neural spines and femora that are longer than the humeri. The new taxon can also be distinguished from other newly-described plesiosauroids from Svalbard, thus indicating that several plesiosaurian taxa existed at high paleolatitudes during the Late Jurassic.

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Introduction

Plesiosaurs (Plesiosauria, Sauropterygia) are a clade of secondarily aquatic Mesozoic marine tetrapods that were taxonomically diverse, morphologically disparate, and became geographically cosmopolitan during their long existence throughout the Jurassic and Cretaceous periods (Wiffen & Moisley, 1986; Taylor & Cruickshank, 1994; Storrs, 1994; Cruickshank, 1997; Storrs, 1997; Rieppel, 2000). Their unique body plan includes two pairs of paddle-like limbs, which have been interpreted for use in a mode of subaqueous locomotion ranging from paddling to underwater flight (De La Beche & Conybeare, 1821; Conybeare, 1824; Andrews, 1913; Watson, 1924; Tarlo, 1957; Robinson, 1975; Tarsitano & Reiss, 1982; Godfrey, 1984; Halstead, 1989; Reiss & Frey, 1992; Lingham-Soliar, 2000; Massare & Sperber, 2001; Long *et al.*, 2006; Carpenter *et al.*, 2010). Traditionally, the clade has been divided into a long-necked, small-headed, plesiosaur morphotype and a short-necked, large-headed, pliosaur morphotype. However, recent phylogenetic and morphometric studies suggest that a continuum of body plans are found in Plesiosauria, and that these body plans may have arisen independently at multiple times in the clade (Cruickshank, 1994; O'Keefe, 2001, 2002; Druckenmiller & Russell, 2008; Ketchum & Benson, 2010; Vincent, 2010).

Recent fieldwork in the uppermost Jurassic Agardhfjellet Formation in Svalbard, Norway, has uncovered numerous remains of plesiosaurians and ichthyosaurs, many of which represent new taxa that help to fill a temporal gap between the better known Middle to Upper Jurassic formations of Europe (e.g., the Oxford and Kimmeridge Clay formations of England) and the Lower to Upper Cretaceous forms of North America. In addition to increasing our understanding of diversity and geographic distribution of marine reptiles during this time, these new discoveries contribute greatly to our understanding of the faunal composition of Late Jurassic marine ecosystems, particularly at high paleolatitudes.

In the summer of 2009, the semi-articulated remains of a long-necked plesiosaur (PMO 216.839) were excavated by the University of Oslo Natural History Museum from the Slottsmøya Member (Middle Volgian to Early Valanginian) near Janusfjellet mountain (Figure 1). The specimen is one of the most complete marine reptiles ever found in this highly fossiliferous unit, and represents a new taxon, which is described herein.

Geological setting

The vast majority of marine reptile finds collected during the 2004-2012 field seasons occur in the Slottsmøya Member of the Agardhfjellet Formation. The Agardhfjellet Formation comprises part of the Adventdalen Group (Parker, 1976), a thick succession of Middle Jurassic to Lower Cretaceous sedimentary rocks that crops out extensively in central Spitsbergen. The Agardhfjellet Formation is underlain by shallow-shelf to marginal marine sandstone and shale of the Wilhelmøya Formation (Kapp Toscana Group). The Rurikfjellet Formation overlies the Agardhfjellet Formation and together they make up the Janusfjellet Subgroup (Parker, 1976), which consists of several hundred metres of organic-rich, clayey and silty sediment.

Four named members are recognised in the Agardhfjellet Formation, of which the Slottsmøya Member is the uppermost (Dypvik et al., 1991a). The Slottsmøya Member conformably overlies the Oppdalsåta Member and is overlain by the Myklegardfjellet Bed (i.e., base of the Rurikfjellet Formation; Birkemajer 1980). The Slottsmøya Member, which averages 55 to 60 metres in thickness in the study area, consists of dark-grey to black silty mudstone, often weathering to paper shale, discontinuous silty beds, with local occurrences of red to yellowish sideritic concretions as well as siderite and dolomite interbeds (Dypvik et al., 1991a; Hammer et al., 2011; Collignon & Hammer, 2012). The Slottsmøya Member was deposited in an open marine environment under oxygen-deficient settings (Nagy et al., 1988; Dypvik et al., 1991b). Paleogeographic reconstructions for Svalbard during the Kimmeridgian to Valanginian interval place paleoshorelines several hundred kilometres to the north and west (Dypvik et al., 2002).

The Agardhfjellet Formation ranges from the Middle Jurassic to the Lower Cretaceous based on macrofossils (mostly ammonites: Parker, 1976; Ershova, 1983; Wierzbowski et al., 2011), foraminifera (Nagy & Basov, 1998) and palynology (Løfaldli & Thusu, 1976; Bjærke, 1978). The Slottsmøya Member is largely Volgian in age, but recent work in the study area indicates that the unit becomes condensed up-section, with the top of the member lying at or close to the Volgian-Ryazanian boundary (Nagy & Basov, 1998; Hammer et al., 2011), or as young as the Boreal Valanginian (Collignon & Hammer, 2012). The specimen described here, PMO 216.839 occurs in either the *Dorsoplanites maximus* or the *D. ilovaiskyi* zone, corresponding the middle Volgian. Precise age correlations between Upper Jurassic and Lower Cretaceous units of the Boreal and Tethyan regions remain controversial (Ogg, 2004; Hammer et al., 2011; Gradstein et al., in press). However, the Middle Volgian age assigned to this specimen accords with an informally defined Middle Tithonian or Early Portlandian age in the Tethyan region (Gradstein et al., in press).

To further quantify the stratigraphic occurrence of the vertebrate remains, a laterally continuous, sideritic horizon rich in ammonites (especially *Dorsoplanites* sp.) and bivalves, and a similarly continuous yellow silt bed were used as upper and lower marker beds, respectively, against which the stratigraphic position of each skeleton was measured. The yellow silt bed was set as 0 m. The *Dorsoplanites* marker bed occurs 27 m above this yellow layer and 21 m below the top of the Slottsmøya Member (Myklegardfjellet Bed; see Collignon and Hammer, 2012), and occurs in the Middle Volgian *D. maximus* or *D. ilovaiskyi* zone. The vertical position of each vertebrate specimen was recorded with a Leica TCR 110 total station with <1 cm error at 100 metre distance and later
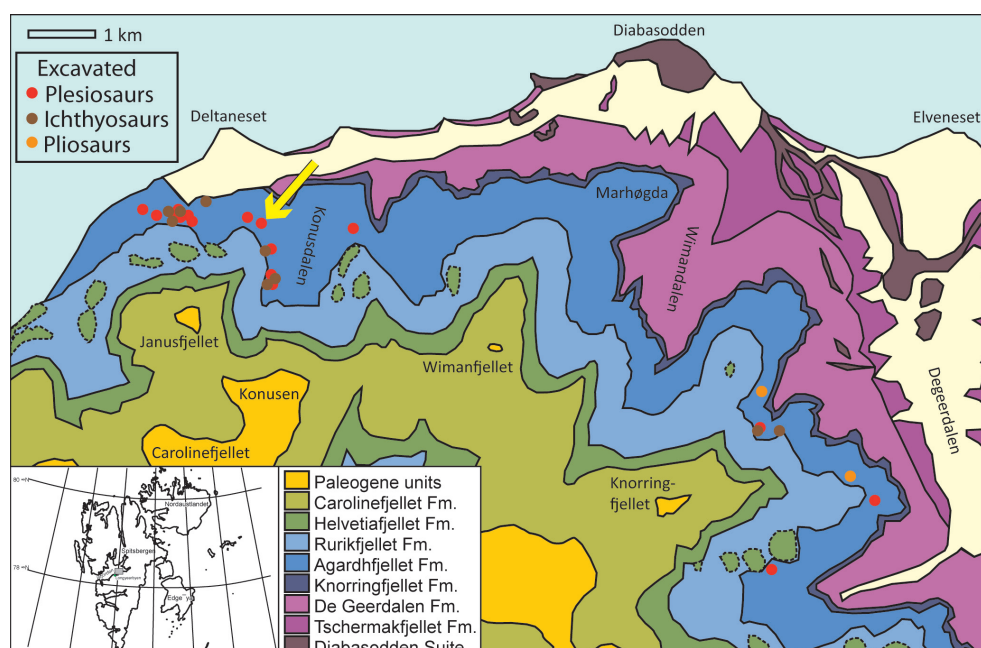

Figure 1. Map of field area showing the locations of excavated plesiosaur, pliosaur and ichthyosaur skeletons. The location of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) is indicated by the yellow arrow. Redrawn and adapted from Dallmann et al. (2001).*

corrected with respect to dip. The specimen described here (PMO 216.839) was found 20 metres below the *Dorsoplanites* bed.

Material and methods

A morphometric analysis of the cervical vertebral column of PMO 216.839 was performed in order to understand size variation within the preserved portion of the vertebral column and ultimately to provide an approximate estimate of the total number of cervical vertebrae in this taxon. Ventral length, and posterior height and width were measured for each individual centrum (supplementary material). The atlas-axis is not included in the analyses and therefore not assigned a number. Cervical centra posterior to this are labelled 1-38, but the actual position in the neck is only known for centra 1-17. The dimensions of distorted centra were estimated by plotting the values of their undistorted dimensions against position in the neck. A regression line was calculated for each plot, with the slope of each line providing the conditional mean increase in size from one vertebral centrum to the next. The adjusted values of the distorted centra (supplementary material) along with original dimensions of undistorted vertebrae were used for analysing the changes in centrum shape through the cervical series. Vertebrae 28 to 38 contain numerous fractures that inflate the overall dimensions of the centra. Based on the size and number of fractures in the respective planes, 5 mm of length and 15 mm of width were subtracted from the original measurements to give the adjusted values. Values for height were not adjusted as these vertebral centra are also dorsoventrally compressed, and subtracting from this dimension would only serve to give the compressed value for height. Thus, the true height value for these centra is likely to be closer to the measurement including the gap made by the fractures.

The number of cervical centra missing between the two articulated cervical vertebral series preserved in this specimen were estimated using the following equation:

$$n = \Delta x / slope_x$$

where n is the number of missing vertebral centra, Δx is the difference in size of a given dimension for the last centrum before the gap and the first centrum after the gap and $slope_x$ is the slope number for the same dimension (calculated from the trend line). The ratios of the adjusted values for the three dimensions (length, width and height) were compared to each other in a scatter plot to see how the relative sizes change from anterior to posterior in the neck.

Institutional abbreviations

MGUH — Geological Museum in Copenhagen, Denmark
NHMUK — Natural History Museum, London, UK
PMO — University of Oslo Natural History Museum, Norway

Systematic paleontology

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943

Djupedalia gen. nov.

LSID - urn:lsid:zoobank.org:act:6854AA5C-20D8-4C17-8167-85262479389F

Type and only species – *Djupedalia engeri*

Etymology – In honour of Øystein Kåre Djupedal, Norway's Minister of Education and Research from 2005-2007, whose commitment to the Jurassic marine reptile project made the excavations in Svalbard possible.

Diagnosis – As for species.

Djupedalia engeri gen. et sp. nov.

LSID - urn:lsid:zoobank.org:act:2B0CA8EB-B86B-4127-B573-E639DAE0B1AA

Etymology – In honour of Øyvind Enger, long-time PMO volunteer who has been involved in the discovery and collection of marine reptiles in Svalbard for many years.

Holotype – PMO 216.839: semiarticulated skeleton of a juvenile plesiosaur including a partial lower jaw and incomplete left quadrate and squamosal; a partial cervical and dorsal vertebral series; several articulated cervical ribs; disarticulated cervical and dorsal neural arches; disarticulated dorsal ribs and gastralia; an incomplete pectoral girdle and two partial forelimbs; both pubes and one incomplete hindlimb.

Type locality – The northeastern slope of Janusfjellet, Spitsbergen, Svalbard, Norway (78.33689°N 15.85945°E).

Type horizon and age – 20 metres below the *Dorsoplanites* Bed, Slottsmøya Member, Agardhfjellet Formation, Janusfjellet. *Dorsoplanites ilovaiskyi* to *Dorsoplanites maximus* ammonite zones, Middle Volgian (Tithonian; Nagy & Basov, 1998; Collignon & Hammer, 2012; Gradstein *et al.* in press).

Differential diagnosis – plesiosauroid with the following autapomorphies and unique character combinations: Paroccipital process is 0.6 times the height of the exoccipital-opisthotic; exoccipital does not participate in the occipital condyle (in contrast to *Kimmerosaurus*); dorsal margin of the quadrate angles ventrally at 40 degrees (70 degrees in *Spitrasaurus*); pterygoid ramus of quadrate angles anteriorly at an angle of 55 degrees to a line drawn mediolaterally through the quadrate condyle (90 in *Spitrasaurus*, and 80 in *Kimmerosaurus*); lateral condyle of the quadrate is larger than the medial (reverse in *Spitrasaurus*); mandible

is slender, containing approximately 25-30 teeth, and 1-2 pairs of symphyseal teeth (more than *Tricleidus*, less than *Kimmerosaurus*); atlas centrum participates in the rim of the atlantal cup; rib facets present on both atlas and axis; a minimum of 40 strongly biconcave cervical centra (54 estimated; more than in *Cryptoclidus*, *Muraenosaurus* and *Colymbosaurus*; less than in *Spitrasaurus*); anterior cervical centrum length and height approximately equal and less than width (approximately 0.7-0.8 times; unlike *Kimmerosaurus* and *Muraenosaurus*); dorsoventral height of cervical neural spines approximately equal to anteroposterior length; cervical neural spines posteriorly shifted so that their anterior margins are in line with the posterior margin of the base of the neural arch (located directly above the centrum in *Kimmerosaurus* and *Colymbosaurus*, significantly less posteriorly shifted in *Cryptoclidus*, *Tricleidus*, *Muraenosaurus* and *Spitrasaurus*); prezygapophyses fused along the midline (unfused in *Cryptoclidus* and *Kimmerosaurus*); postzygapophyseal facets not united along the midline (united in *Spitrasaurus*); postzygapophyses long, approximately equal to neural arch pedicel in anteroposterior length (shorter in *Spitrasaurus*, *Cryptoclidus*, and *Muraenosaurus*); cervical rib facets reniform and distinctly elevated above the ventral surface of the centrum (not elevated in *Spitrasaurus*); anterior cervical ribs with anteriorly projecting process at the distal end (absent in *Spitrasaurus*); height of dorsal neural spines approximately equal to height of neural canal (significantly taller in *Cryptoclidus* and *Muraenosaurus*); clavicles triangular in

shape, with a straight anterior margin and concave posterior margin; anteroposterior width of interclavicle constricted in sagittal plane, compared to lateral rami, appearing "pinched"; femora are significantly larger than the humeri (reverse is true in *Cryptoclidus* and *Muraenosaurus*, subequal in size in *Tricleidus* and *Spitrasaurus*); both forelimbs and hindlimbs contain three elements in the epipodial row (two in *Cryptoclidus* and *Muraenosaurus*); epipodials anteroposteriorly broader than long.

Taphonomy

PMO 216.839 was preserved dorsal side up in a black, finely laminated mudstone, with the skeletal elements in approximate sequence from anterior to posterior (Figure 2). The specimen shows varying degrees of dorsoventral compression, being only minor in the anterior region of the neck; however, some of the dorsal vertebral centra are so heavily compressed in the anteroposterior plane that they are reduced to thin plates, possibly due in part to the young ontogenetic state of the specimen. The cervical series is broken into two major parts approximately midway along the neck. Compression has also resulted in the collapse of the dorsal surfaces of both proximal and distal limb elements, but not of the ventral surfaces. The elements of the abdominal region appear to have undergone more disarticulation than the anterior region prior to burial. There is no indication of scavenging or epifauna
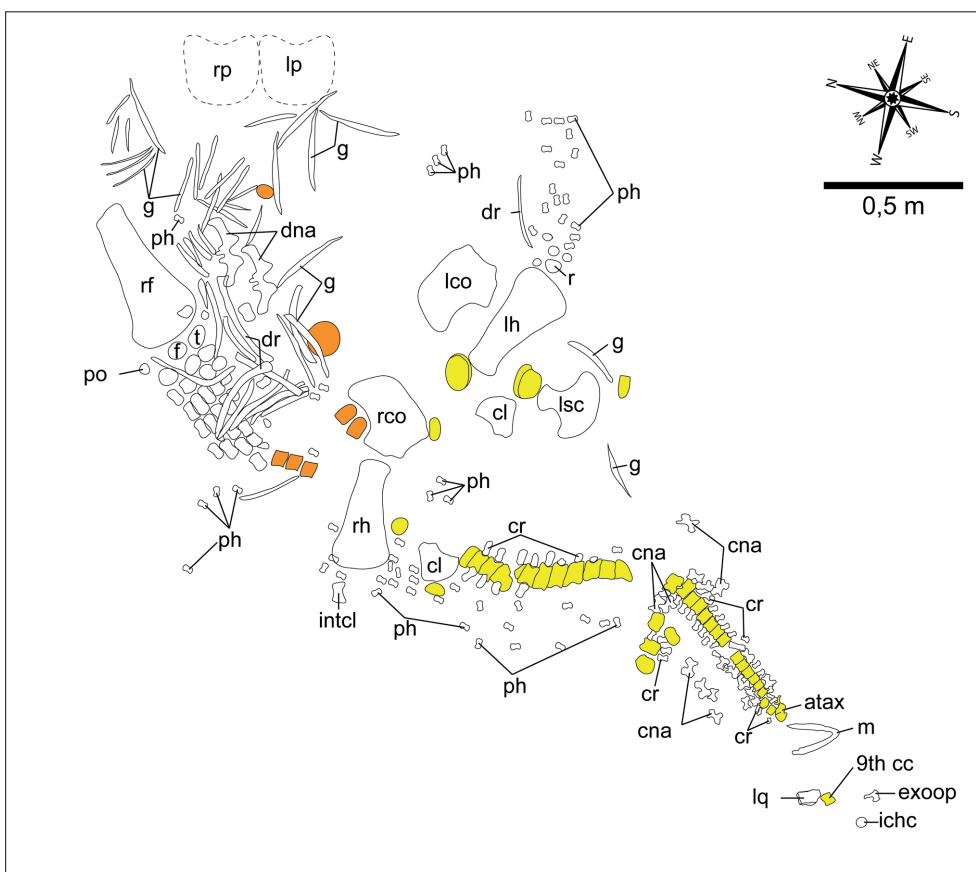

Figure 2. Quarry map of Djupedalia engeri *gen. et sp. nov. (PMO 216.839). The neck is largely separated into two major articulated series of vertebrae. Cervical vertebral centra are coloured yellow, and dorsal vertebral centra are coloured orange. Approximate outline of pubes shown as dashed lines. atax=atlas-axis, cl=clavicle, cna=cervical neural arch, cr=cervical rib, dna=dorsal neural arch, dr=dorsal rib, exoop.=exoccipital-opisthotic, f=fibula, g=gastralia, intcl=interclavicle, ichc= ichthyosaur vertebral centrum, lco=left coracoid, lh=left humerus, lp=left pubis, lq=left quadrate, lsc=left scapula, m=mandible, ph=phalanx, po=postaxial ossicle, r=radius, rco=right coracoid, rf=right femur, rp=right pubis, t=tibia, 9ᵗʰ cc=9ᵗʰ cervical centrum.*

on the bones. An isolated ichthyosaur vertebral centrum was found near the cranial remains of PMO 216.839.

Ontogeny

Brown (1981) divided Late Jurassic plesiosaurians into three ontogenetic stages – juvenile, adult and old adult – based on the degree of ossification in various skeletal elements like vertebrae, limbs and girdles. The lack of fusion between neural arches, cervical ribs and vertebral centra in the holotype specimen of *Djuepdalia* is consistent with Brown's (1981) definition of a juvenile specimen. So too is the lack of separation between the trochanter/tuberosity and the capitulum, and the rounded distal margins of the propodial. This general lack of advanced ossification also explains the rounded morphology of the epipodials and mesopodials, which are distinctly faceted in positively adult specimens of other species from the same locality (Knutsen *et al.*, 2012(a)). It is noteworthy that both clavicles and interclavicle are present in PMO 216.839, suggesting that their absence in

juvenile specimens of other taxa from this locality cannot solely be attributed to ontogenetic status. Although the juvenile status of this specimen makes comparisons with other taxa potentially problematic, especially with respect to the girdle and limb elements, other features less influenced by age remain taxonomically useful and allow us to recognise autapomorphies and unique character combinations diagnostic for this new taxon.

Anatomical description

Cranium

An isolated right exoccipital-opisthotic and the left quadrate is preserved in PMO 216.839. The exoccipital-opisthotic (Figure 3) is small with a dorsoventral height that is two times its mediolateral width along its ventral surface (not including the paroccipital process). The paroccipital process is gracile, approximately 0.6 as long as the height of the exoccipital-opisthotic, expands slightly in
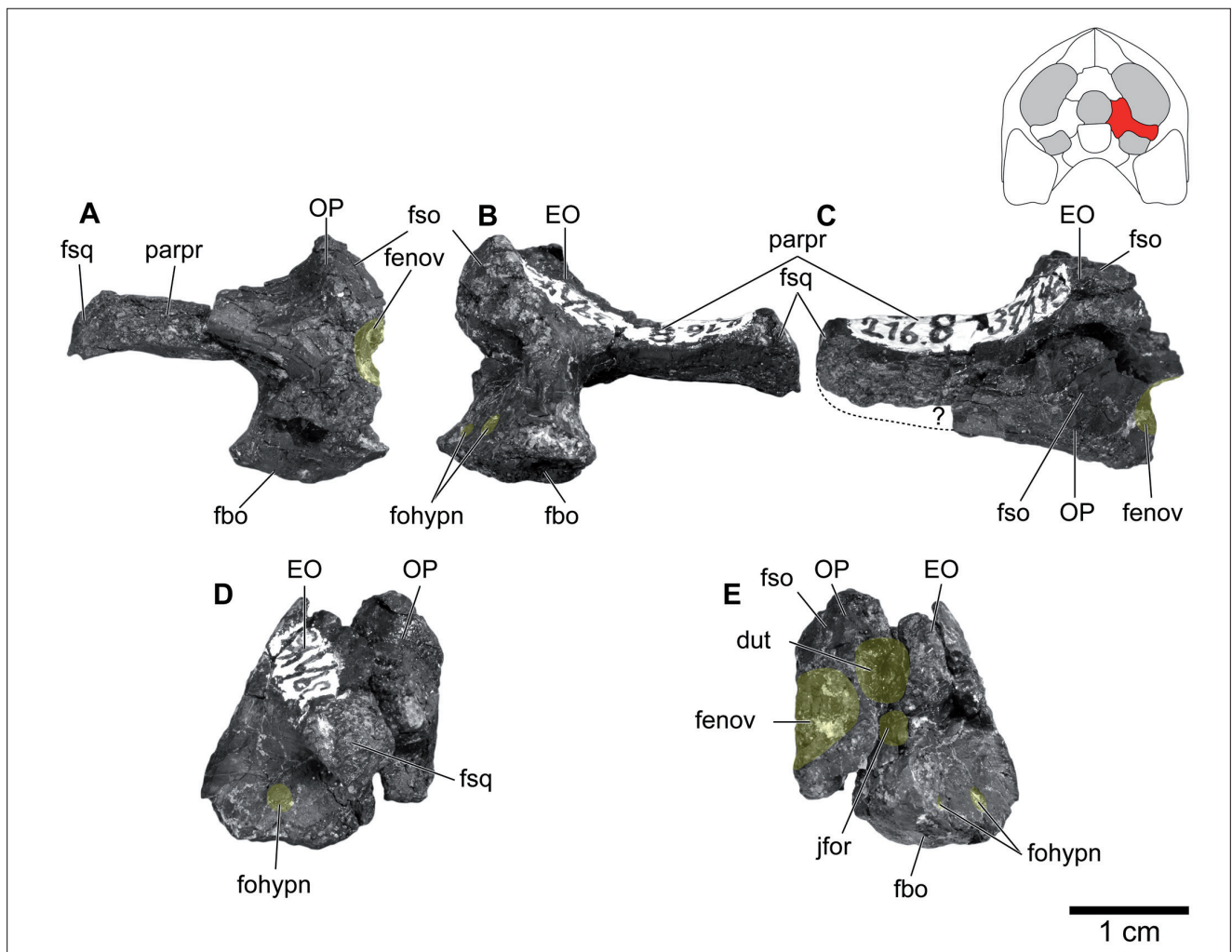

Figure 3. The right exoccipital-opisthotic of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in anterior (A), posterior (B), dorsal (C), lateral (D) and medial (E) view. dut=depression for utriculus, EO=exoccipital, fbo=facet for basioccipital, fenov=fenestra ovalis, fohypn=foramen for hypoglossal nerve, fsq=facet for squamosal, fso=facet for supraoccipital, jfor=jugular foramen, OP=opisthotic, parpr=paroccipital process.*

width and height distally, sub-circular in cross-section, positioned in the dorsal half of the exoccipital-opisthotic, and is angled perpendicular to a line drawn from the lateroventral to the laterodorsal margins of the exoccipital-opisthotic.

The exoccipital and opisthotic, of which the former is the larger, appear to be incompletely fused, possibly as a result of the animal's young ontogenetic state. The jugal foramen perforates the region where the two elements are sutured. Medially, the exoccipital bears at least two foramina interpreted as branches of the hypoglossal nerve, and another on the lateral side. Ventrally, the exoccipital bears a large facet for the basioccipital. There is no indication of a facet for the occipital condyle. The opisthotic contribution to the margin of the fenestra ovalis is smoothly concave and positioned medially in the ventral half of the element. The depression for the utriculus is smaller than the fenestra ovalis and forms a shallow concavity in the area between the exoccipital and opisthotic.

The left quadrate (Figure 4) possesses a roughened, dorsoventrally elongate facet along its posteromedial surface for contact with the pterygoid, and a lateral facet for the squamosal. In ventral view, the quadrate condyle has two distinct articular surfaces, of which the lateral is the largest. In dorsal and ventral views the pterygoid ramus of the quadrate projects anteriorly, at approximately 55 degrees to a line drawn mediolaterally through the condyle (Figure 4B). In posterior view, the dorsal margin is squared off laterally, and slopes ventromedially at an angle of 40 degrees (Figure 4C). There is no indication of a quadrate foramen.

The mandible is dorsoventrally compressed and preserves the nearly complete left and right dentaries (Figure 5), but the mandibular symphysis is not preserved. The dentary bears a ventral cleft along much of its length that likely accommodated the angular or splenial, but the extent to which either was involved in the mandibular symphysis is not possible to discern due to damage anteriorly. Due to taphonomic factors, only ten alveoli are discernible in the middle of the right dentary, and none in the left. Because the preserved fragments of the left and right dentary of PMO 216.839 are of equal length, it is therefore reasonable to believe that they disarticulated from the posterior elements of the mandibular ramus, rather than being fractured at this point. If so, the preserved portion of the dentaries would have accommodated an estimated 25 - 30 teeth based on the dimensions of the alveoli. At the time of collection the mandibular
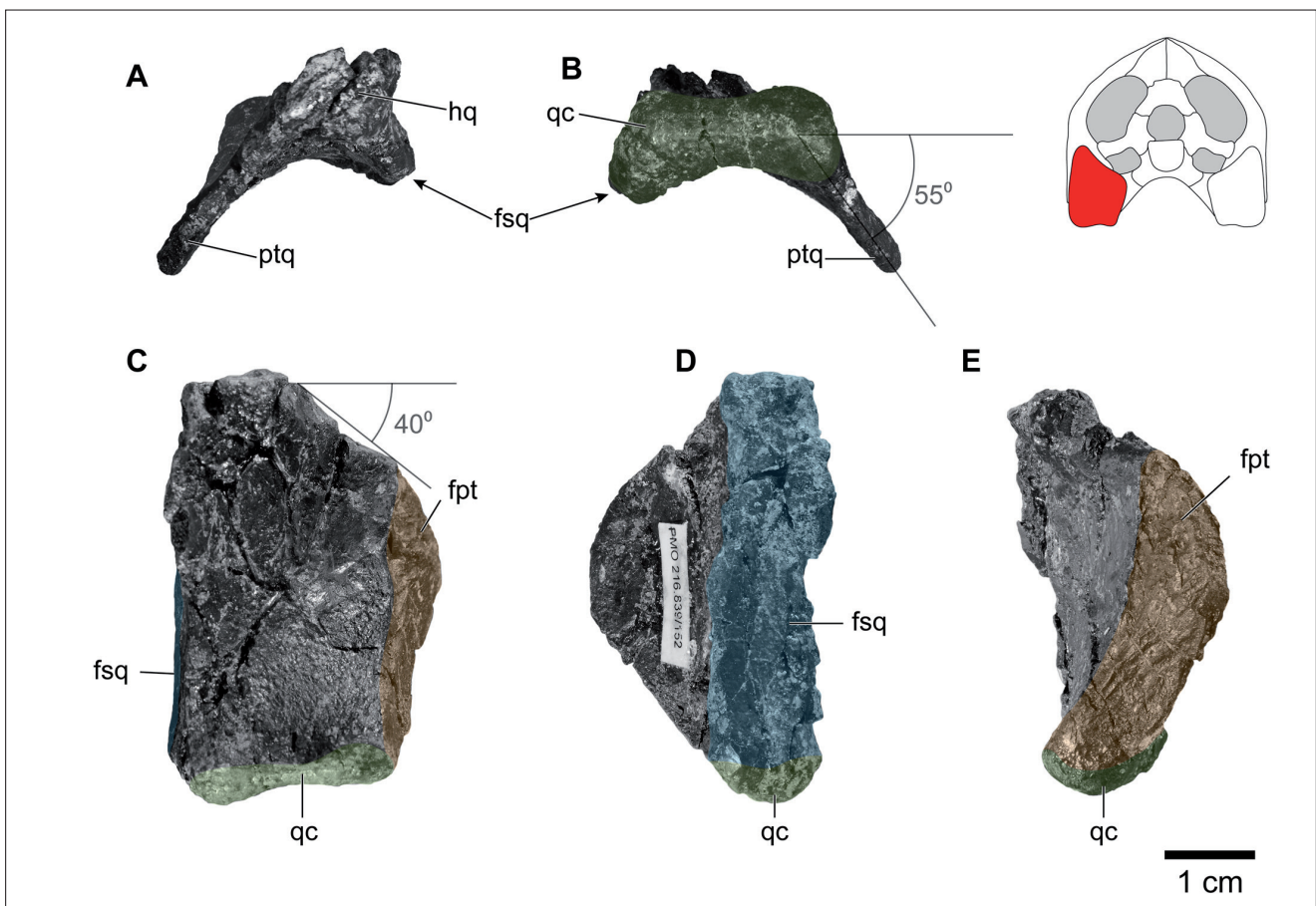

Figure 4. The left quadrate of Djupedalia engeri gen. et sp. nov. (PMO 216.839) in dorsal (A), ventral (B), posterior (C), lateral (D) and medial (E) views. fpt=facet for pterygoid, fsq=facet for squamosal, hq=head of quadrate, ptq=pterygoid ramus of quadrate, qc=quadrate condyle.

symphysis was observed to be very short, and contained no more than two pairs of teeth (this area was subsequently damaged). No teeth were found in association with PMO 216.839.

Axial skeleton

Most of the preserved cervical series, including the atlas-axis, were found as two articulated segments totalling 40 cervical centra. Twenty neural arches are also present, presumably having been disarticulated from the preserved centra (Figure 2). The anterior segment contains the atlas-axis and 21 centra (see material and methods for explanation of numbering). The ninth centrum has been displaced, leaving a small gap in the articulated column; however, an isolated centrum of appropriate size for this position was found near the quadrate, and is assumed to be the missing ninth. Centra number 18-21 are disarticulated from, but lie immediately adjacent to, the posterior-most centrum in the anterior series, but their exact order is uncertain. There are 11 centra preserved in the posterior segment. Six other isolated medium sized centra were preserved disarticulated from the neck (Figure 2). Based on marked size differences between the posterior-most and anteriormost centra in the anterior and posterior segments, respectively (supplementary material), it

is apparent that there are several centra missing between the two preserved portions (see below). The individual pectoral?/anterior dorsal vertebrae are disarticulated and no sacral or caudal vertebrae are preserved.

A progressive and consistent increase in all (undistorted) dimensions between cervicals 1-21 is observed in PMO 216.839 (Figure 6). Based on the average increase in size in all three dimensions (length, width, height), it is possible to reconstruct the dimensions of distorted cervical centra, and thereby estimate the number of missing centra between the two articulated cervical segments (see Material and Methods). This analysis indicates that as many as 20 vertebrae are missing from this gap. Six of those estimated 20 centra are likely the six medium-sized centra preserved disarticulated from the main series, leaving as many as 14 other unrecovered vertebrae between the articulated segments. By inserting 14 vertebrae between the two articulated series in a scatter plot, the slope of size increase of the anterior articulated segment intersects with the slope of the posterior segment, thus supporting the estimated amount of missing cervicals (Figure 7). Although there is no direct connection between the posterior portion of the neck and the anterior dorsal series (Figure 2), the absolute size of the posteriormost cervical and the anteriormost dorsal indicates
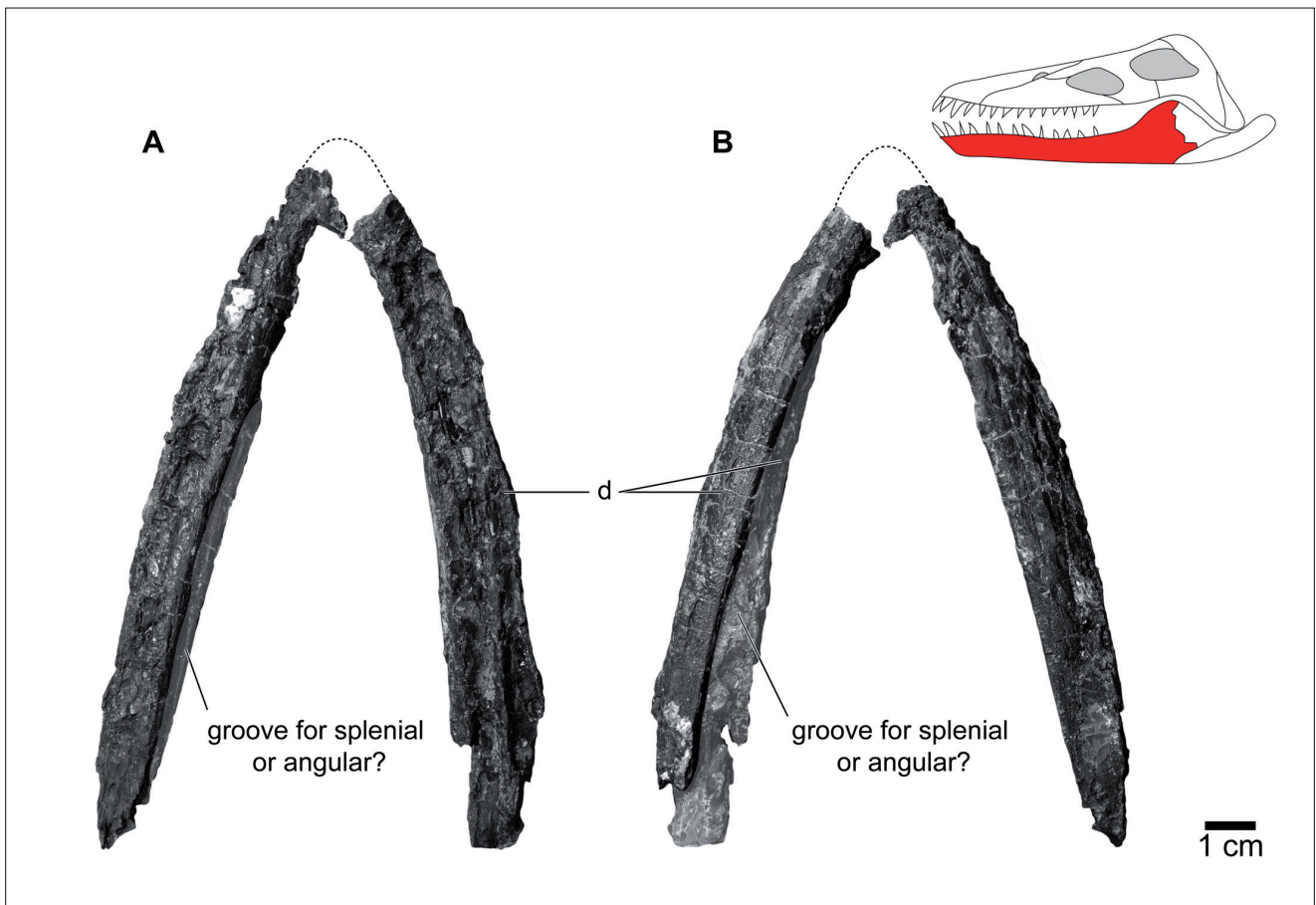

Figure 5. The incomplete dentaries of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in dorsal (A1) and ventral (A2) view. d=dentary.*
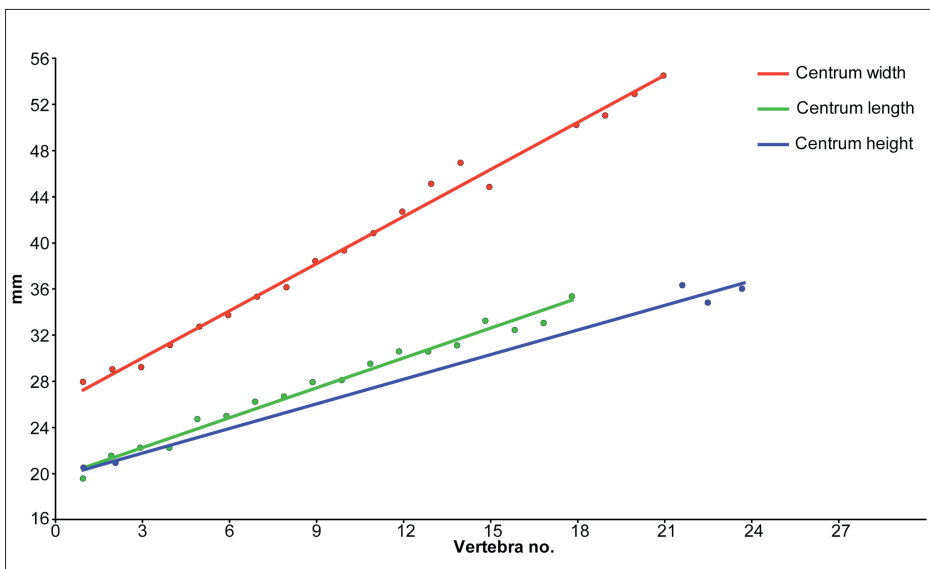
Figure 6. Scatter plot of cervical centrum width (red), length (green) and height (blue) of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in millimetres, and their respective trend lines (for centra in the anterior segment). Slope value for width = 1.362, length = 0.867, height =0.797. R2 value for trend lines: width ~1, length = 0.98, height ~1. Centra 3-17 were ignored with respect to centrum height due to heavy dorsoventral compression, and centra 18-21 were ignored with respect to centrum length due to anteroposterior compression in these particular centra. There is a steady increase in all three dimensions from cervical centrum number 1 to21.*
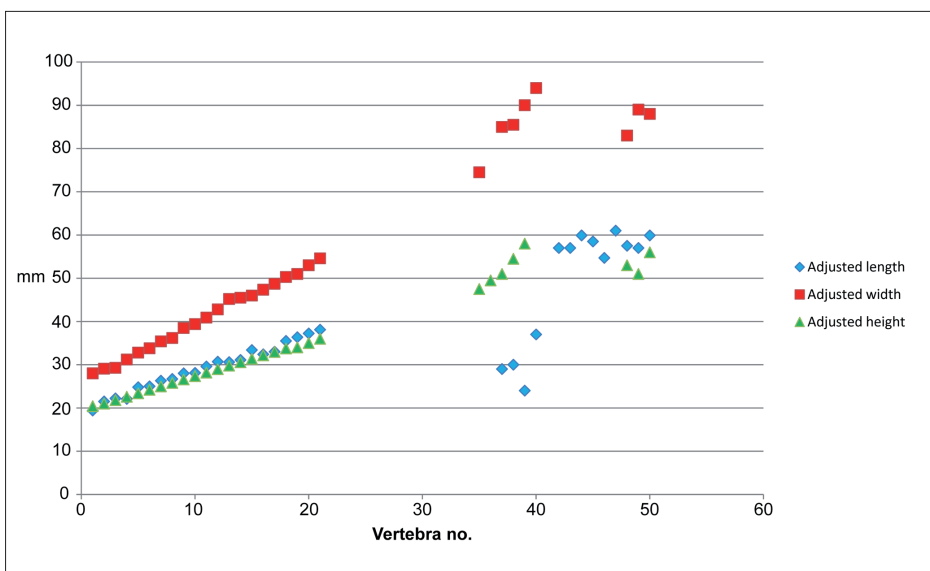

Figure 7. Scatter plot of the adjusted values for cervical centrum length (blue), width (red) and height (green) of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in millimetres. The estimated 14 missing vertebrae have been inserted as a gap (22-35) between the preserved cervical vertebrae. The slope of the anterior 21 centra intersects with the more posteriorly preserved centra at approximately cervical centrum number 35. Note the halt in size increase in the posterior centra. Four centra are heavily anteroposteriorly compressed which projects them as outliers in the scatter plot for centrum length.*

that few if any cervical vertebrae are missing from the posterior region of the neck. This is also supported by the lack of increase in size in posterior cervicals (Figure 7), which would be expected when in close proximity to the dorsal region (Knutsen *et al.* in this volume b). Thus, we estimate a total cervical count of approximately 54 and a neck length of approximately 2 metres for PMO 216.839.

The atlas-axis complex (Figure 8A) is somewhat obliquely compressed anteroposteriorly. The fusion between the axial and atlantal centra is incomplete, which is most apparent in right-lateral view where they are distinctly separated. Both the atlantal and the axial centra bear a notochordal pit on their anterior and posterior surfaces, respectively. Rib facets are present on the lateral surfaces of both the atlantal and the axial centra. The atlantal neural arches are not fused to the centrum and do not contact the atlas intercentrum. Thus, the atlantal centrum contributes to the anterior margin of

the atlantal cup. The atlantal intercentrum is not fused to the atlantal centrum. The ventrolateral sides of the atlantal intercentrum are angled medially, forming an anteroventrally projecting lip on which the hypophyseal ridge of the atlantal intercentrum terminates. The posteroventral extent of the atlantal intercentrum is difficult to interpret due to crushing. Dorsally, the atlantal neural arch articulates with the neural arch of the axis. Although incomplete, the axial neural spine is low and anteroposteriorly elongate.

The cervical centra of *Djupedalia engeri* (Figure 8B and C) are somewhat square in profile when seen in lateral view, their length being approximately equal to their height. The centra are also markedly anteroposteriorly short (length < width) and dorsoventrally low (height < width). In articular view, the outline of the centrum is reniform (Figure 8B). Posteriorly, the length to height relationship increases very slightly (i.e., the centra become relatively longer), and there is a visible decrease
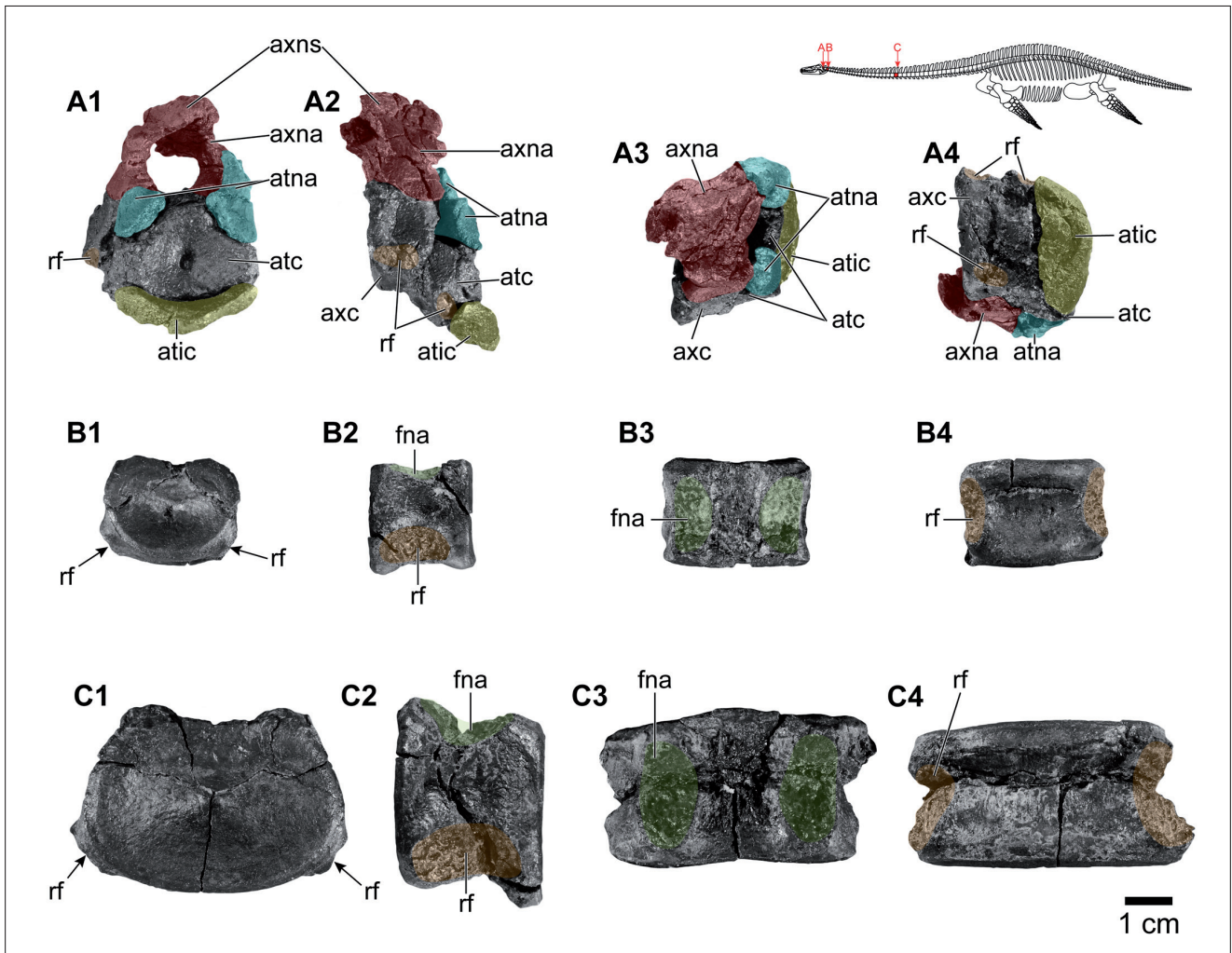
Figure 8. The atlas-axis complex (A), second cervical centrum (B), and twenty-first cervical centrum (C) of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in anterior (A1, B1, C1), right lateral (A2, B2, C2), dorsal (A3, B3, C3) and ventral (A4, B4, C4) views. Centrum C is slightly anteroposteriorly compressed. Atna=atlantal neural arch, atc=atlantal centrum, atic=atlantal intercentrum, axc=axial centrum, axna=axial neural arch, axns=axial neural spine, fna=facet for neural arch, rf=rib facet.*

in height and length relative to width (Figure 9). Width and height continues to increase throughout the cervical series, whilst the increase in length appears to halt around centrum number 45 (Figure 7). The anteriormost cervical centrum is approximately three times smaller in all dimensions than the posteriormost preserved cervical centrum (supplementary material), indicating a great disparity in centrum size throughout the column. All cervical centra are strongly biconcave. The lateral and ventral surfaces of the centra are concave, making the articular rims protrude conspicuously ventrally and laterally from the main body of the centrum. The peripheral margins of the articular surfaces are rimmed by a thin ridge. The rib facets on all cervical centra are shifted posteriorly relative to the middle of the centrum as seen in lateral aspect, are situated on short but distinct pedicels, and bear a reniform articular surface. The inner surfaces of the cervical rib facets are rugose. In lateral view, the facets for the neural arch are triangular (apex facing ventrally) and reniform in dorsal view, giving the neural

canal an hourglass-shaped outline. The lateral and ventral surfaces of all cervical centra are smooth and devoid of a ridge or keel, respectively. The foramina subcentralia are separated by a distance approximately equal to one-fourth of the total centrum width, and become slightly closer to one another posteriorly.

All of the cervical neural arches are laterally compressed. In lateral view, the neural spines of most cervical neural arches are mediolaterally thick and approximately square in outline, although in the anteriormost cervicals, the neural spines are trapezoid in shape, being slightly shorter along their dorsal margin (Figure 10). Notably, the neural spines are shifted posteriorly in relation to the base of the arch, with the anterior edge of the spine being approximately in line with the posterior edge of the neural arch pedicel (Figure 10). Thus, the total length of each individual neural arch is divided into two equally long halves; the anterior half consisting of the prezygapophyses and the base of the arch, and the posterior half
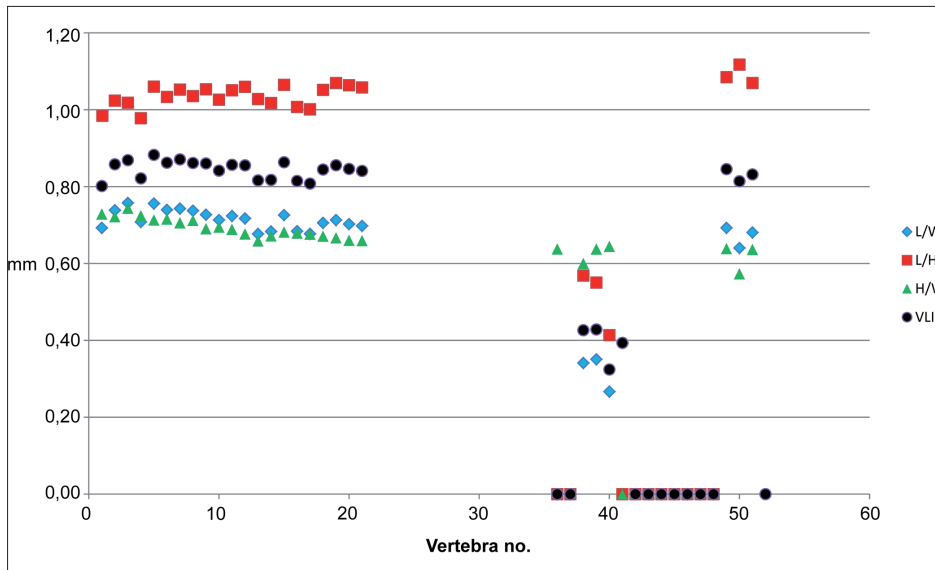
Figure 9. Vertebral proportions of length versus width (blue), length versus height (red) and height versus width (green) for the cervical vertebral centra of Djupedalia engeri *gen. et sp. nov. (PMO 216.839). There is a slight increase in length relative to width, decrease in length relative to width, and a decrease in height relative to width posteriorly in the cervical series, i.e., posterior cervical centra are proportionally the shortest in lateral view and widest in articular view.*
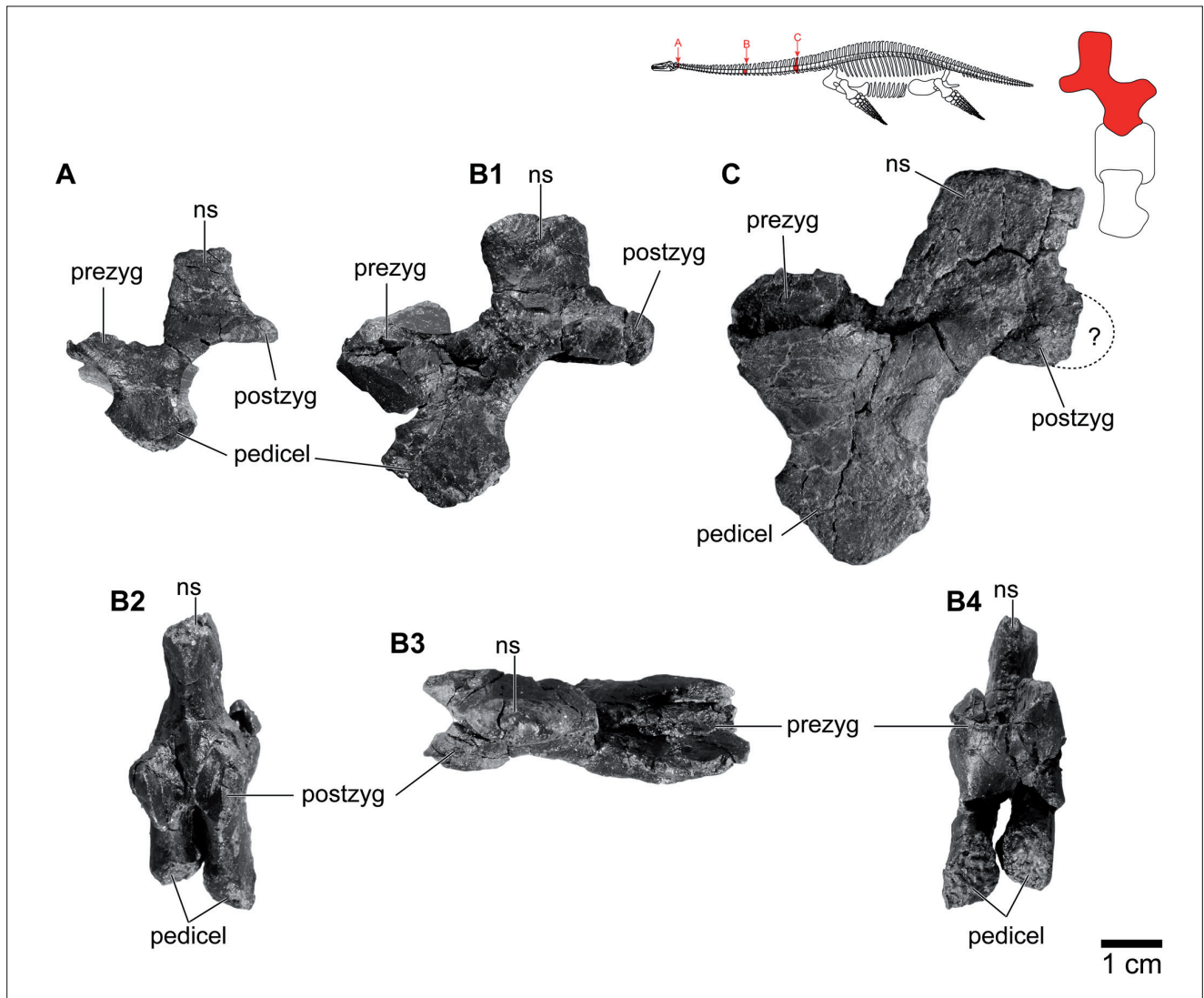
Figure 10. Anteriormost (A), anterior (B) and posterior (C) cervical neural arches of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in left-lateral (A, B1, C) view, and neural arch B in posterior (B2), dorsal (B3) and anterior (B4) views. Some deformation has occurred in the neural spine in 10 A. Note: A, B1 and C are mirrored to align them in anatomical order, but still best show distinguishing characteristics. ns=neural spine, postzyg=postzygapophysis, prezyg=prezygapophysis.*

consisting of the neural spine and the postzygapophyses (Figure 10). The anterior and posterior margins of the neural spine bear a sharp, low keel that extends ventrally into the space between the zygapophyses. The ventral margins of the prezygapophysis are fused along the midline forming a U-shaped cup-like suture (Figure 10B3 and B4). In contrast, the articular surfaces of the postzygapophyses are unfused along their midline (Figure 10B2 and B3). The height of the neural canal is approximately equal to the dorsoventral height of the neural spine. The width of the canal cannot be observed due to the lateral compression of the arches, but can be estimated to be nearly equal to its height, based on the distance between the facets for the neural arch on the vertebral centra. In lateral view, the ventral margin of the neural arch pedicel is V-shaped in outline (Figure 10).

All preserved cervical ribs are single headed. The anterior cervical ribs (Figure 11A, B and C) possess an anterodistally directed projection, producing a hatchet-shaped outline in dorsal view. Posteriorly there is a gradual proximodistal lengthening of the cervical ribs. The posterior cervical ribs (Figure 11D and E) curve slightly posteriorly and taper in anteroposterior length to a point. The distal anterior projection is lost in the posteriormost ribs (Figure 11E).

The pectoral centra cannot be distinguished from the dorsals due to crushing. In articular view, the dorsal vertebral centra (Figure 12) are nearly circular in outline. The shape of the lateral and ventral surfaces is not visible due to anteroposterior compaction. The neural arches of the anterior dorsal region (Figure 12A1, A2 and A3) support a very anteroposteriorly short and dorsoventrally low neural spine (approximately equal in height to the neural canal). This feature may be a result of its early ontogenetic state, as neural spines terminate in soft tissue (Brown, 1981; Vincent, 2010). However, this contribution to the total spine length is unknown. The prezygapophyses are fused along much of the midline (the anterior extent is unknown due to poor preservation) and form a broad cup with a flat ventral surface that is mediolaterally wider than anteroposteriorly long. No complete postzygapophyses are preserved. The transverse processes are anteroposteriorly compressed, and their combined width is just under two times the width

Figure 11 - The cervical ribs of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in dorsal (A1, B1, C1, D1, E1) and posterior (A2, B2, C2, D2, E2) views.*

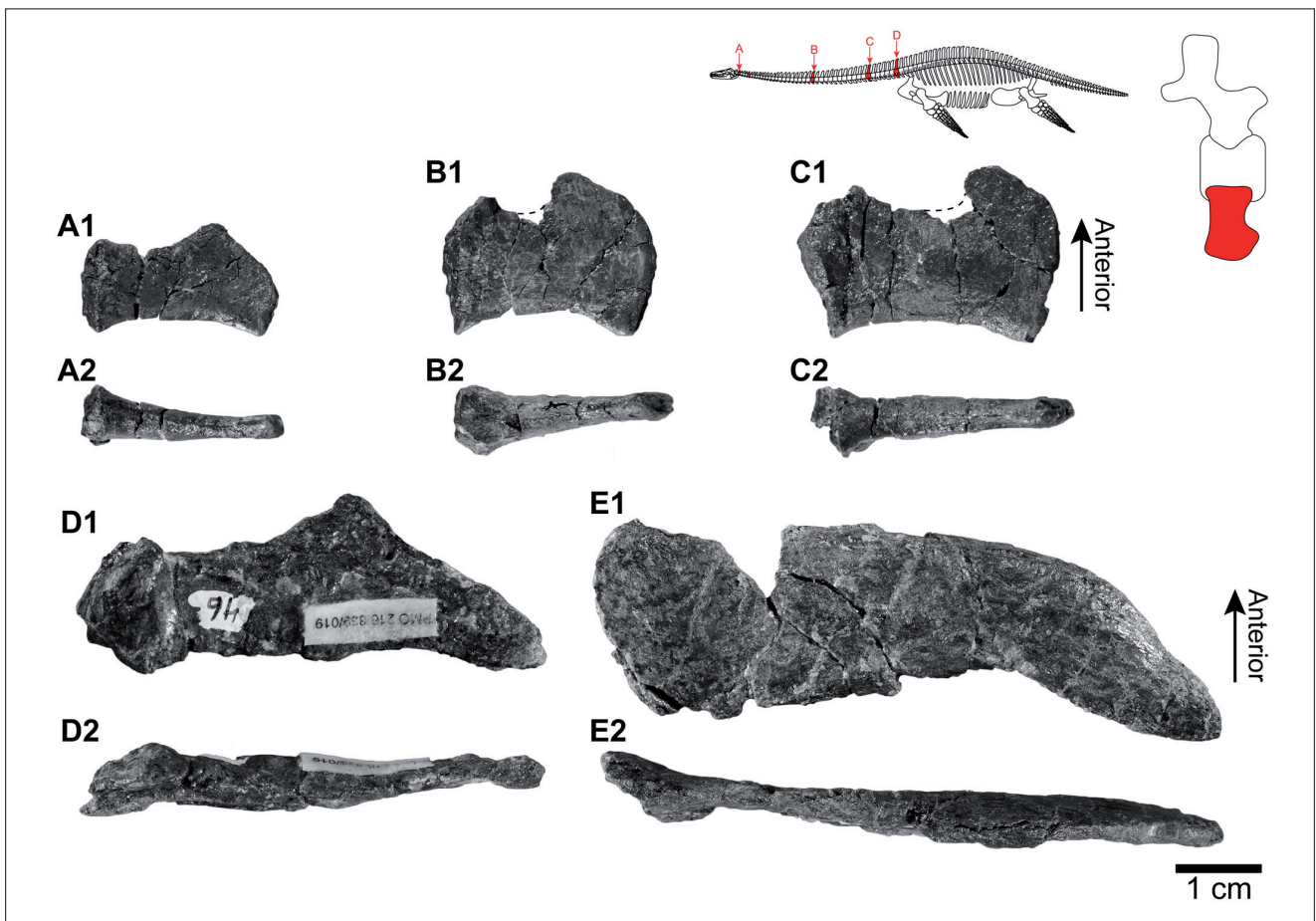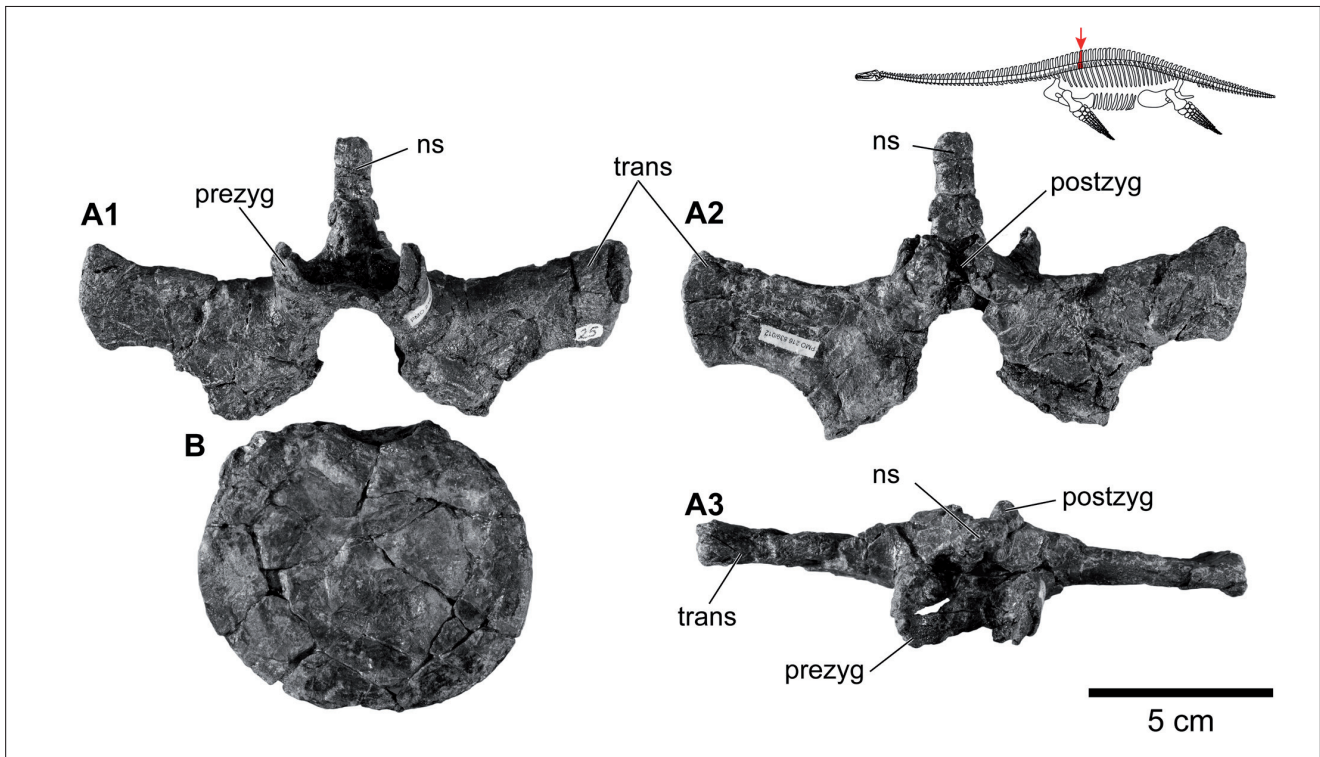*Figure 12. Dorsal neural arch of* Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in anterior (A1), posterior (A2) and dorsal (A3) views, and a dorsal vertebral centrum in articular view (B). The dorsal centrum is anteroposteriorly flattened, obscuring the lateral and ventral morphology. The postzygapophyses are incomplete. ns=neural spine, postzyg=postzygapophysis, prezyg=prezygapophysis, trans=transverse process.*

of the centrum. The processes are very slightly inclined dorsally in anterior view. The outline of the distal end of the transverse processes is uncertain due to the anteroposterior compression of the neural arch, although it appears generally oval in outline.

Several dorsal ribs are preserved, but none in articulation with the vertebral column. They are all anteroposteriorly compressed and possess a slight bend ventrally approximately 5-10 cm from the proximal end.

Pectoral girdle

The disarticulated pectoral girdle (Figure 13) preserves the complete left and right coracoids, left scapula, incomplete left and right clavicles, and a partial interclavicle. Although the girdle is well preserved, it is important to note that our understanding of girdle morphology in this taxon is necessarily limited by the young ontogenetic stage of this individual.

The coracoid (Figure 13A) is approximately 1.5 times longer than the scapula (Table 1). It decreases in dorsoventral thickness posteriorly, and is thickest in the areas of, and between, the medial symphysis and the glenoid. No ventral or dorsal transverse ridges are visible in this area, possibly due to crushing. The coracoid lacks an anteromedial projection, although this might

be further developed in more mature individuals. Laterally, the glenoid facet is approximately 75 percent larger than the scapular facet (Table 1). The medial margin of the coracoid is straight for approximately the anterior two-thirds of its length in dorsal view. The coracoids join their opposites along a thickened medial symphysis, which extends over the anterior three-quarters of its anteroposterior length. The symphysis is dorsoventrally thickest anteriorly and tapers in thickness towards the posterior end. The posterior margin is convex caudad and lacks an embayment. Posterolaterally, the coracoid bears a weakly developed flange or cornu, the lateral margin of which is approximately in line with the glenoid in the parasagittal plane.

The left scapula is complete but has been nearly flattened (Figure 13B) and possesses a dorsal, medial and posterior process. The scapula bears a very weakly developed (nearly absent) lateral ridge. The posterior process of the scapula is thickened in the vicinity of the glenoid. The glenoid facet is equal in length to the coracoid facet (Table 1). The dorsal process is anteroposteriorly broad and dorsally rounded and nearly lacks any posterior slope, although this may have been affected by flattening. On its dorsal surface the medial process of the scapula bears a shallowly depressed shelf for the overlapping portion of the clavicle. When articulated with the coracoids, the scapulae clearly do not contact their opposites along

the midline, nor do they contact the anteromedial processes of the coracoids, although the condition in adult individuals is unknown.

The better-preserved left clavicle (Figure 13C) is evenly thin in dorsoventral thickness. The clavicle is broadest anteroposteriorly in its medial half, and has a convex and fan-shaped medial margin. The anterior margin is nearly straight, whilst the posterior margin is concave. The lateral portion of the clavicle is strap-like and appears to be incomplete and somewhat crushed on its ventral side.

We interpret an isolated and incomplete element found near the right forelimb to be the interclavicle (Figure 13D). The anteromedial and posteromedial margins of

the element are convex. Laterally, it appears that the element expands in anteroposterior length, producing a bow-tie shaped element in dorsal view. The dorsoventral and anteroposterior orientation of the bone is unclear, although comparison with those found in *Muraenosaurus leedsii* Seeley, 1874b suggest that the flatter, roughened side is dorsal. The opposite surface bears a medially thickened ridge, which is asymmetrical between the left and right lateral sides (possibly resulting from crushing). Both lateral margins are incomplete, although one is more intact and suggests a flat, angled edge.

Gastralia

Several disarticulated gastralia are preserved in the area
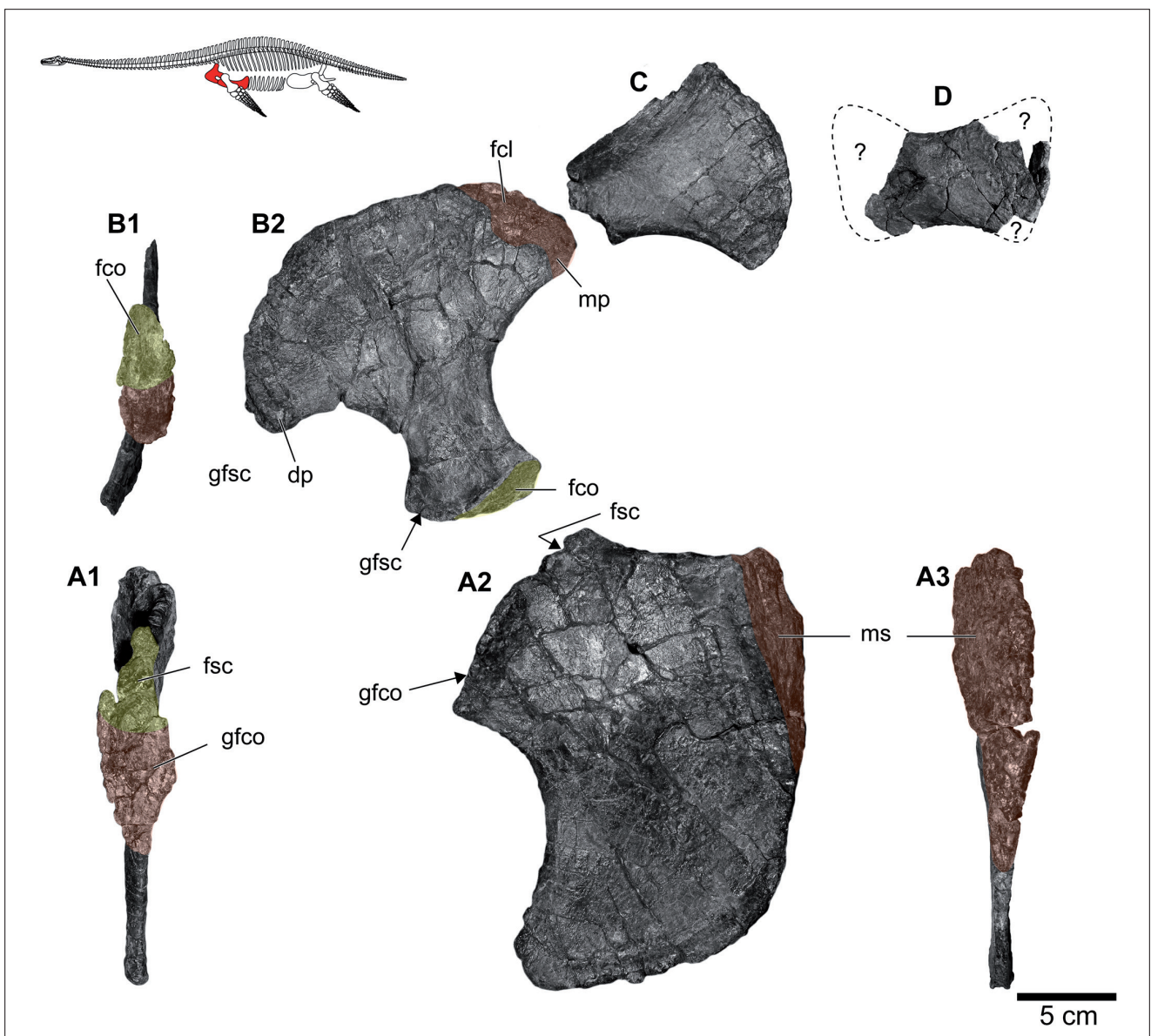
Figure 13. The left pectoral girdle elements of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in dorsal view. The coracoid shown in lateral (A1) and medial (A3) views, the scapula in posterior (B1) view, the clavicle (C) in dorsal view, and the interclavicle (D) in ventral view. dp=dorsal process, fcl=facet for clavicle, fco=facet for coracoid, fsc=facet for scapula, gfco=glenoid facet of coracoid, gfsc=glenoid facet of scapula, mp=medial process, ms=medial symphysis.*

Table 1: Measurements (in mm) of selected skeletal elements of *Djupedalia energi* gen. et sp. nov. (PMO 216.839).

|		Remarks			Remarks
Anterior dorsal vertebra (Figure 11)		Anteroposteriorly compressed	**Fibula**		
Maximum width of centrum	85		Maximum anteroposterior width	50	
Maximum height of centrum	70		Maximum proximodistal length	30	
Ventral length of centrum	25				
Maximum height of neural arch	75		**Coracoid**		
Maximum width of neural arch	154		Maximum anteroposterior length	240	
Height of neural spine	35		Maximum length between medial symphysis and glenoid	180	
Anteroposterior length of neural spine	20	From more posterior vertebra.	Maximum lenght between medial symphysis and posterolateral cornu	135	
			Length of glenoid facet	70	
Left humerus			Length of scapular facet	40	
Maximum proximodistal length	300		Length of medial symphysis	~150	
Maximum distal anteroporsterior width	160		Maximum height of medial symphysis	35	
Maximum proximal anteroposterior width	90				
Anteropsterior width mid shaft	100		**Scapula**		
			Maximum anteroposterior length	165	
Radius		From right limb.	Maximum anterior width	180	
Maximum anteroposterior width			Maximum posterior width	70	
Maximum proximodistal length			Maximum posteriro height	30	
			Length of glenoid facet	40	
Ulna			Length of coracoid facet	40	
Maximum anteroposterior width					
Maximum proximodistal length			**Clavicle**		
			Maximum mediolateral width	110	
Right femur			Maximum medial anteroposterior length	105	
Maximum proximodistal length	375		Maximum lateral anteroposterior length	50	
Maximum distal anteroporsterior width	190				
Maximum proximal anteroposterior width	80		**Interclavicle**		Incomplete.
Anteropsterior width mid shaft	120		Maximum mediolateral width	?	
			Maximum lateral anteroposterior length	?	
Tibia			Minimum medial anteroposterior length	45	
Maximum anteroposterior width	60				
Maximum proximodistal length	40				
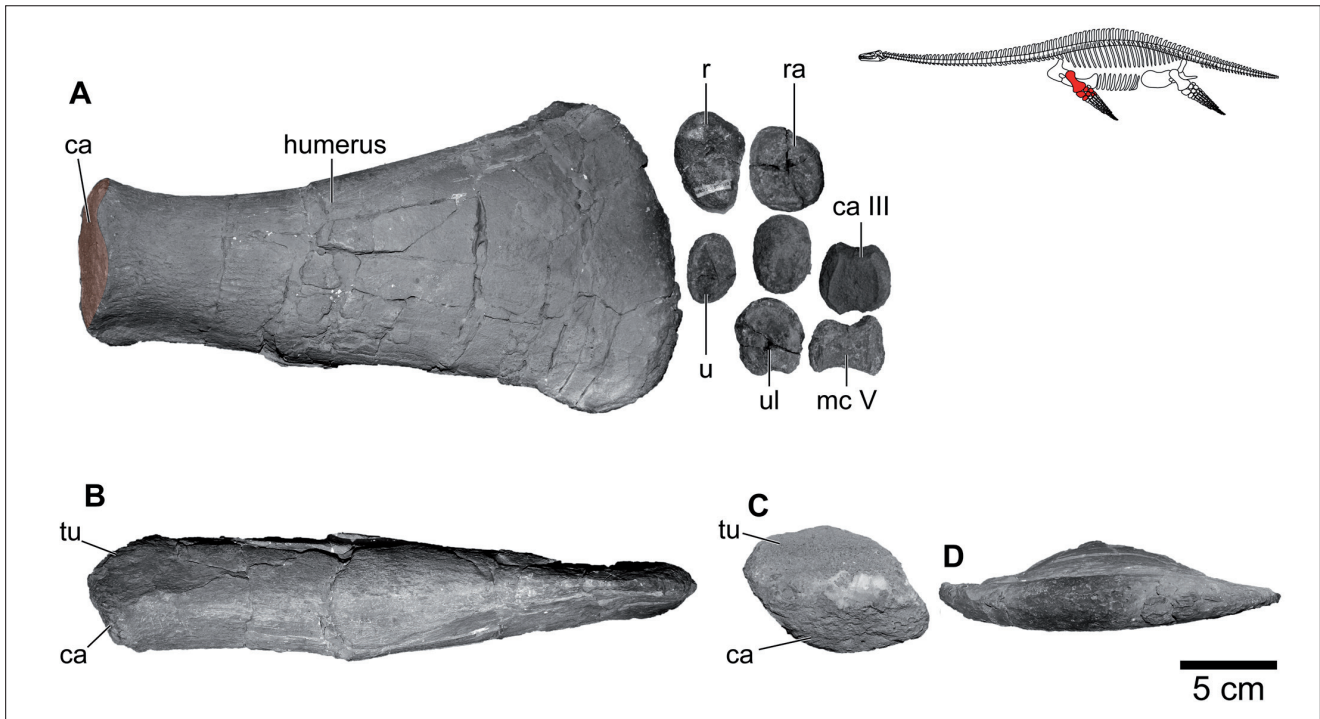
Figure 14. The incomplete left forelimb of Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in ventral (A), anterior (B), proximal (C) and distal (D) views. ca=capitulum, ca III=3ʳᵈ carpal, mcV=5ᵗʰ metacarpal, r=radius, ra=radiale, tu=tuberosity, u=ulna, ul=ulnare. The epipodials and mesopodials have been rearticulated for the illustration.*

between the hindlimb and the pelvic girdle. Simple boomerang-shaped gastralia are interpreted as medial elements, whereas more complexly curved bones are lateral elements. All gastralia exhibit a groove, which interlocks with other gastralia of the same row. As preserved, it is not possible to determine the number of gastral elements in each row.

Forelimb (Figure 14)

Two incomplete and disarticulated forelimbs are preserved in association with the pectoral girdle (Figure 2). The bones distal to the humerus of the left limb remain in approximate association with the propodial, but both distal portions of the forelimbs are disarticulated (Figure 2). Dorsoventral compression has depressed the right humerus, thereby revealing the shape of the internal endochondral cone (for explanation of the term, see Liebe & Hurum, 2012). The humeri are distinctly proximodistally shorter and distally narrower pre- and postaxially than the femur (Table 1). In dorsal view, the humerus distally expands steadily pre- and postaxially from the capitulum, and terminates in a rounded convex margin that lacks distinct epipodial facets. In proximal view, the tuberosity is shifted posteriorly in relation to the capitulum, and is only very slightly separated from it, consistent with its early ontogenetic state (Brown, 1981). In ventral view, the capitulum exhibits a pronounced rim where it meets the humeral shaft; in contrast, the

tuberosity lacks a distinct rim and passes smoothly onto the shaft. The proximal portion of the shaft exhibits some longitudinal ridges on the ventral surface, which are interpreted as insertions for the adductor musculature, but it is otherwise smooth. Distally, there is slightly more expansion posteriorly along the postaxial margin than along the preaxial margin.

The epipodials and mesopodials are poorly ossified, and exhibit rounded edges with weakly developed facets, as is typical of an early ontogenetic stage. The radius bears five facets and is anteroposteriorly wider than proximodistally long. The ulna is triangular with one long proximal facet and two angled distal facets, of which the preaxial is the longest. What is interpreted as the radiale is circular in outline. The radiale contacts distally with the fifth metacarpal, which has an angled proximal end. Upon rearticulating the radius, radiale and humerus, the available space in the epipodial row indicates that a postaxial ossicle may have been present, as is preserved in the hindlimb.

Similar to the hindlimb, the phalanges are short and robust, and generally only slightly narrower in the shaft than the articular ends, although their width may be influenced by dorsoventral compression. Because the distal portions of the forelimb are disarticulated, the morphological variability cannot be described and a phalangeal count is not possible.

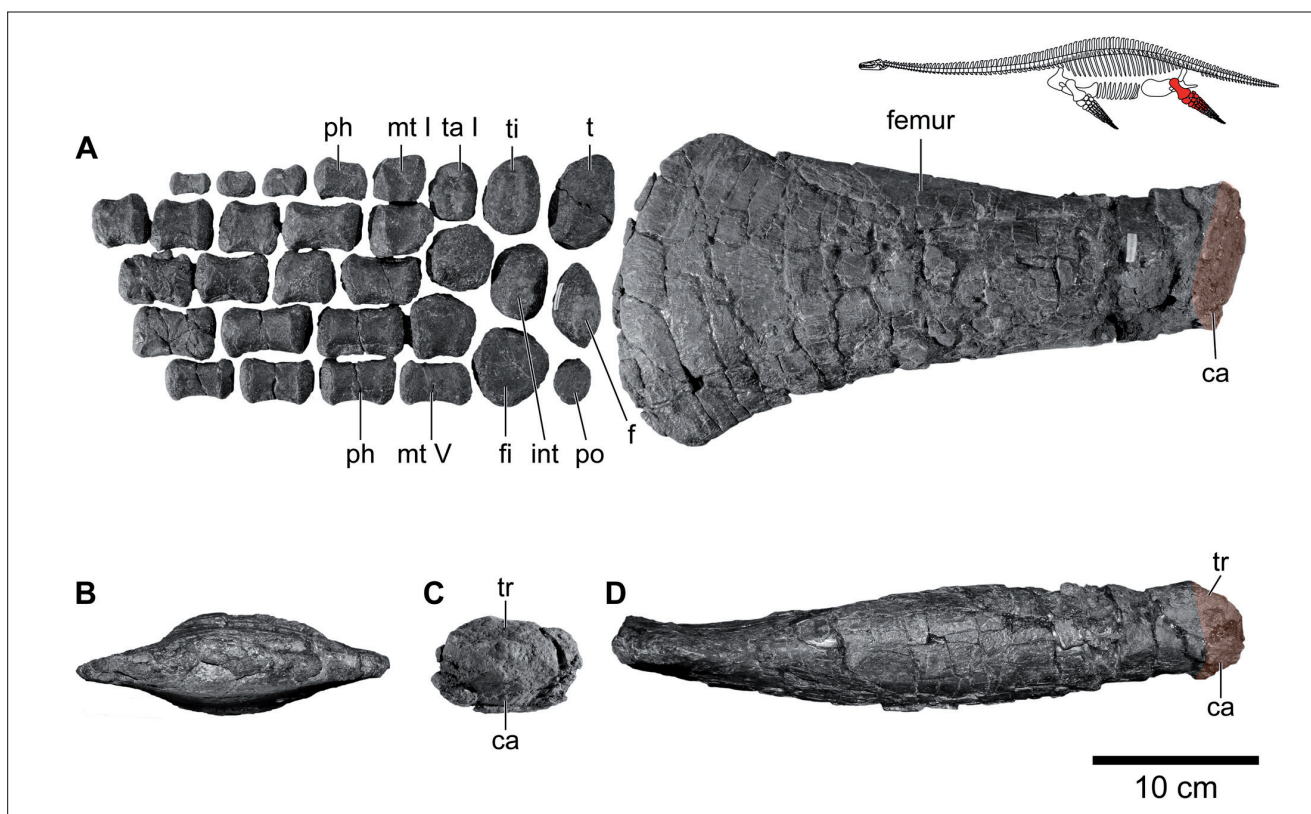*Figure 15. The incomplete right hindlimb of* Djupedalia engeri *gen. et sp. nov. (PMO 216.839) in ventral (A), distal (B), proximal (C) and anterior (D) views. ca=capitulum, f=fibula, fi=fibiale, int=intermedium, mt=metatarsal, ph=phalanx, po=postaxial ossicle, t=tibia, ta=tarsal, ti=tibiale, tr=trochanter.*

Pelvic girdle

The incomplete right and left pubes are the only portion of the pelvic girdle preserved. The lateral, anterior and medial margins of the left pubis can be discerned and indicate that the bone is slightly wider than long, that its anterior margin is convex, and it lacks any conspicuous anterolateral projection. The area of the acetabulum is incomplete in both pubes.

Hindlimb (Figure 15)

The right hindlimb is well preserved and articulated down to the proximal phalanges. The femur is proximodistally longer and anteroposteriorly broader than the humerus, but otherwise mirrors the overall shape and characteristics of the distal and proximal ends, as well as the ventral rugosities on the proximal part of the femoral shaft. However, in contrast to the humeral tuberosity, the trochanter lies directly dorsal to the capitulum in proximal view.

The shape of the epipodials is broadly equivalent to that of the forelimbs, but they are overall larger in size (Table 1). The hindlimb also preserves a circular postaxial ossicle in the epipodial row. The fifth metatarsal is shifted almost completely in line with the distal mesopodial row.

The general phalangeal morphology is also similar to that of the forelimbs, but also larger in overall size. The largest phalanges are found in digits two, three and four, possibly indicating that these were the longest digits. The phalanges of digit two are the shortest and most robust, whilst those of digit five are the most slender phalanges in the limb. Digit one appears to be almost complete and the shortest of the digits.

Discussion

Comparisons of vertebral dimensions

Brown (1981) developed a method for comparing vertebral dimensions along the axial column by comparing the average diameter of the centrum to its length and position in the body, named the vertebral length index (VLI). He then plotted these data in order to easily compare the curves for different individuals and concluded that the results had both intra- and interspecific significance. This method of comparing vertebral dimensions was later applied by other authors (e.g., Brown *et al.*, 1986; Smith, 2007; also discussed by O'Keefe & Hiller, 2006). However, a limitation of this method is that by comparing centrum length to average width and height, there is an implicit assumption that the vertebral centra are circular (or nearly so) in articular view. In many cases this is not true for cervical vertebrae, which can often be wider than tall (pers. obs. EMK, PSD). A hypothetical example for a vertebra that is wider than tall is given below (Table 2). Here, centrum length and height have a constant relationship (0.75) to each other, but using Brown's (1981) interpretation of the VLI values, we conclude that the anterior centra in this example are proportionally the longest. The same conclusion would be drawn when comparing length relative to width. The discrepancy can be attributed to the relationship between height and width (H/W). VLI is insensitive to this variability because it uses the average value between height and width. Therefore, it is possible for two plesiosaurs with very differently shaped vertebral centra to have the same VLI value; for example, one individual may have cervical centra in which the height equals the width, and the length equals the width (or the height), whereas another with the same VLI has vertebral centra in which the width is twice the height and the length is one-and-a-half times the height.

O'Keefe & Hiller (2006) noted that the VLI of elasmosaurids has the highest value in the mid-section of the neck. This fits well with observations for *Djupedalia engeri* and *Spitrasaurus wensaasi* (Knutsen *et al.*, 2012(b)), which show that the increase in cervical centrum length ceases near the midpoint of the neck, whereas width and height continue to increase. However, since width has a higher value and appears to increase more rapidly than height in these two taxa, width would have a larger influence on the VLI values than height.

Given the limitations of the VLI, we recommend that more meaningful conclusions regarding the relative proportions of vertebral centra may be drawn from independent comparisons of length to height and length to width (presented for *Djupedalia engeri*; Figure 9). Likewise, the relationship between width and height should also be assessed independently in order to more fully appreciate variation in vertebral dimensions and ontogenetic changes throughout the vertebral column, as intended by Brown (1981). For *D. engeri*, the cervical vertebral centra can be interpreted as being equally long and tall if observed in lateral view, whilst being relatively short if viewed dorsally or ventrally. This emphasizes the importance of specifying from which view an element is examined when discussing shape and relative dimensions. O'Keefe & Hiller (2006) argued that the vertebral dimensions of individual or a small number of cervical centra should not be used as a taxonomic character, as this appears to vary within the neck and both ontogenetically (getting relatively longer in adults) and intraspecifically. However, most of the cervical series is known for *Djupedalia engeri*, allowing a more accurate description of dimensions and variability in these along the neck. Furthermore, the relative length of cervical centra in *D. engeri* is not used as a main characteristic in distinguishing it from its comparators, so a possible increase in relative length for adult individuals (as in the elasmosaurids described by O'Keefe & Hiller, 2006) would not have much influence on this relationship.

Centrum no.	Length	Width	Height	L/H	L/W	VLI	H/W
1	3.38	5	4.5	0.75	0.68	0.71	0.90
2	3.75	6	5	0.75	0.63	0.68	0.83
3	4.13	7	5.5	0.75	0.59	0.66	0.79
4	4.50	8	6	0.75	0.56	0.64	0.75
5	4.88	9	6.5	0.75	0.54	0.63	0.72
6	5.25	10	7	0.75	0.53	0.62	0.70
7	5.63	11	7.5	0.75	0.51	0.61	0.68
8	6.00	12	8	0.75	0.50	0.60	0.67
9	6.38	13	8.5	0.75	0.49	0.59	0.65
10	6.75	14	9	0.75	0.48	0.59	0.64

Table 2: Hypothetical dimensions and ratios for a plesiosaur with vertebral centra that are wider than tall.

Another potentially useful comparison of cervical vertebral dimensions is the relative change in size from the anteriormost to the posteriormost cervical centrum, here named "cervical disparity". This will yield three ratios (change in length, width and height), which can be compared to other specimens. For *D. engeri* this number is approximately three for all dimensions, whereas for *Spitrasaurus wensaasi* (Knutsen *et al.*, 2012(b)) this number is approximately two. Thus, there is a proportionately greater increase in the size of vertebrae throughout the cervical series of *D. engeri* than for *S. wensaasi*.

Comparison to other taxa

Djupedalia engeri is compared to relevant contemporary (Tithonian/Volgian) taxa from the Slottsmøya Member, including *Colymbosaurus svalbardensis* (Persson, 1962) Knutsen et al., 2012(a) and *Spitrasaurus wensaasi* Knutsen *et al.*, 2012(b). *D. engeri* is also compared to *Cryptoclidus* Seeley, 1892, *Tricleidus* Andrews, 1909 and *Muraenosaurus* Seeley, 1874b from the Oxford Clay Formation (Callovian) and *Kimmerosaurus* Brown, 1981 and *Colymbosaurus* Seeley, 1874a from the Kimmeridge Clay Formation (Kimmeridgian and Tithonian), all from the UK. Only cranial and anteriormost cervical material is available for *Kimmerosaurus*, whilst only postcranial material is known for *Colymbosaurus*. Brown *et al.* (1986) discussed the possibility of *Kimmerosaurus* and *Colymbosaurus* being conspecific, but concluded that this was contingent on the discovery of a greater amount of overlapping material. The phylogenetic status of *Muraenosaurus* is contentious; it may be either a basal elasmosaurid (e.g., Bardet *et al.*, 1999; Gasparini *et al.*, 2003) or more closely related to Jurassic cryptoclidids (*sensu* Brown, 1981) such as *Cryptoclidus* and *Kimmerosaurus* (Ketchum & Benson, 2010). An incomplete cryptoclidian plesiosaur, *Vinialesaurus caroli* (De la Torre and Rojas, 1949) has also been reported from the Oxfordian part of the Jagua Formation in Cuba (Gasparini *et al.*, 2002). The type specimen consists of the anterior portion of the skull, the mandible and an associated atlas-axis. Another

partial juvenile postcranial skeleton (MGUH 28378) is known from lower Kimmeridgian strata on Milne Land in Greenland. These remains were first descried by von Huene (1935) as *Apractocleidus aldingeri*, but the genus is now considered to be a junior synonym of *Cryptoclidus* (Brown, 1981). Most recently, Smith (2007) redescribed this specimen and concluded that it belongs to the cryptoclidians (based on its relative cervical vertebral dimensions), but is indeterminable at the genus level. Potential comparators also include Upper Jurassic plesiosaurians from Russia; however, Storrs *et al.* (2000) did not recognise any diagnostic material and considered these taxa *nomina dubia* and these have therefore not been taken into account here.

Cranium

The exoccipital-opisthotic in *Djupedalia engeri* is similar in overall shape to those of *Kimmerosaurus*, *Cryptoclidus*, *Muraenosaurus* and *Tricleidus*. However, the paroccipital process of *Djupedalia* is proportionally shorter than those figured for *Tricleidus* (Brown, 1981), slightly longer than those in *Kimmerosaurus* (Brown, 1981; pers. obs., EMK, PSD), and similar in length to those of *Cryptoclidus* (Andrews, 1910). Brown (1981) noted that the quadrate in *Tricleidus* and *Muraenosaurus* contact the pterygoids anteromedially, thus covering them in posterior view, and that the reverse (pterygoid connects the quadrate posteromedially) is true in *Kimmerosaurus*. This character was, however, somewhat confusingly presented by Brown (1981), and remains questionable (Druckenmiller & Russell, 2008). The quadrate of *Kimmerosaurus langhami* shows faint, dorsoventrally oriented ridges on the pterygoid facet (Brown, 1981; pers. obs., EMK). Similar ridges are also present on the posteromedial surface of the quadrate of *Djupedalia*, suggesting that it had a similar quadrate-pterygoid articulation to *Kimmerosaurus*, but different than that of *Tricleidus* and *Muraenosaurus*. The configuration is unknown in *Cryptoclidus* (Brown, 1981). The quadrate of *Djupedalia* differs from that of *Spitrasaurus* in having a dorsal margin that is less steeply

inclined mediolaterally (40 versus 70 degrees). In *Djupedalia*, the pterygoid ramus of the quadrate for articulation with the pterygoid is angled 55 degrees relative to a line drawn mediolaterally through the condyle in ventral view, whereas in *Spitrasaurus* this angle is approximately 90 degrees and 80 degrees in *Kimmerosaurus*, although this difference might be influenced by compression. On the quadrate condyle of *Djupedalia*, the lateral facet is larger than the medial facet, similar to the situation in *Kimmerosaurus*. This is the reverse of what is observed in *Spitrasaurus*. The dentary of *Djupedalia* is more gracile than that of *Muraenosaurus* and *Tricleidus*, and is more similar to that of *Kimmerosaurus* and *Cryptoclidus*. The 25-30 dentary teeth estimated for *Djupedalia* are most similar to those of *Cryptoclidus* (24-27), greater than *Tricleidus* (17) and *Muraenosaurus* (19-22), but fewer than in *Kimmerosaurus* (36; Brown, 1981; Brown 1993).

Axial skeleton

In *Djupedalia engeri* the atlantal centrum participates in the atlantal rim of the atlantal cup, and bears rib facets as seen in *Cryptoclidus* and *Muraenosaurus* (Andrews, 1910). These characters are unknown for *Tricleidus*, *Kimmerosaurus* and *Colymbosaurus*. The total number of cervical vertebrae is imprecisely known for *Djupedalia* (PMO 216.839), but the 54 estimated for this taxon is less than the 60 recorded for *Spitrasaurus wensaasi*, and much greater than that of *Cryptoclidus* (32 or 35), *Colymbosaurus* (42) and *Muraenosaurus* (44 or 47) (Brown, 1981; Ketchum & Benson, 2010; Knutsen, *et al.*, 2012(b)). The complete cervical count for *Tricleidus*, *Kimmerosaurus* and MGUH 28378 is not known. In marked contrast to *Muraenosaurus* and *Spitrasaurus*, *Djupedalia* lacks a lateral longitudinal ridge on cervical centra. It is unlikely that this is due to the immature status of PMO 216.839, as a lateral longitudinal ridge is present in both referred specimens of *Spitrasaurus*, which are juveniles. In *Djupedalia* the length of the individual neck vertebrae is approximately equal to its height (Figure 9), in contrast to the anterior cervicals of *Kimmerosaurus*, which are shorter than tall, and *Muraenosaurus* and *Spitrasaurus*, where they are longer than tall (Brown, 1981; Knutsen *et al.*, 2012(b); pers. obs. EMK and PSD). Smith (2007) noted that the cervical centrum length of MGUH 28378 is roughly equal to its height. This is only true, however, if height is measured from the ventral margin of the centrum to the ventral border of the neural arch facet, which extends ventrally on the lateral surface of the centrum. If height is measured from the ventral margin of the centrum to its dorsal margin, the length is consistently (~25%) shorter than the height (pers. obs. EMK). Although both *Djupedalia* (PMO 216.839) and MGUH 28378 are skeletally immature, the posterior cervical centra of MGUH 28378 are approximately half the absolute length of those of *Djupedalia* (pers. obs. EMK).

Brown (1981) described the articular faces of the cervical centra of *M. beloclis* as having the same shape as in *M.*

leedsii, although this is clearly not the case, as shown in the illustrations by Andrews (1910; pl. 4 and 7). In *Djupedalia*, the cervical centra are relatively wide as in *Muraenosaurus beloclis* Seeley, 1892 (Andrews, 1910 pl. 7, fig. 5a and 5b), but not as wide as in *Spitrasaurus*, and differ from *M. leedsii*, *Cryptoclidus*, *Tricleidus*, *Kimmerosaurus* and *Colymbosaurus*, in which the cervical centra are more circular in outline in articular view (i.e. width being nearly equal to height) (Andrews, 1910; Brown, 1981; Brown *et al.*, 1986; pers. obs. EMK and PSD)). The widths of cervical centra are unknown for MGUH 28378 due to their preservation. The articular faces of the cervical centra in *Djupedalia* are distinctly concave, similar to *Kimmerosaurus*, but more so than in *Cryptoclidus* and *Colymbosaurus*. The cervical centra of *Tricleidus*, *Muraenosaurus* and *Spitrasaurus* have been described as platycoelous or weakly concave (Brown, 1981; Brown *et al.*, 1986, Knutsen *et al.*, 2012(b); pers. obs.), although the centra of *Muraenosaurus* likely become increasingly concave with advancing age (Brown, 1981).

One of the most characteristic features of *Djupedalia engeri* is the shape of the cervical neural arches, which possess a relatively short and anteroposteriorly broad neural spine that is shifted far posteriorly with respect to its centrum (Figure 10). A similar posterior shift is seen in MGUH 28378; however, the neural spines are incomplete in this specimen, and their shape and length cannot be fully determined (Smith, 2007; pers. obs. EMK). A lesser degree of posterior shifting of the neural spine is seen in *Cryptoclidus*, *Muraenosaurus*, *Tricleidus*, and *Spitrasaurus* (Andrews, 1910; Brown, 1981; Knutsen *et al.*, 2012(b); pers. obs. EMK), such that the posterior margin of the base of the neural arch is approximately in line with the middle of the neural spine. In *Kimmerosaurus*, the cervical neural spines (at least of the anteriormost vertebrae) are positioned directly above its respective centrum (Brown *et al.*, 1986; pers. obs. EMK, PSD), similar to *Colymbosaurus* (Brown *et al.*, 1986, fig.6 a and b). The cervical prezygapophyses of *Djupedalia* are fused along the ventral midline like in *Tricleidus* and *Muraenosaurus*, but contrary to the situation in *Cryptoclidus* and *Kimmerosaurus* (Ketchum & Benson, 2010). The postzygapophyses of *Djupedalia* are separated along their midline (as in *Muraenosaurus*) and are significantly longer than those observed in any of the other taxa mentioned above, with the possible exception of *Kimmerosaurus* (Andrews, 1910; Brown, 1981; Brown *et al.*, 1986).

The distal ends of the anterior cervical ribs of *Djupedalia engeri* bear an anteriorly directed projection like in *Muraenosaurus* (although not as sharply so (Andrews, 1910)) and *Spitrasaurus*. However, the distal margin is convexly rounded in *Djupedalia*, in contrast to the tapering ribs of *Muraenosaurus*. Anterior distal projections on cervical ribs are absent in *Cryptoclidus* and *Tricleidus* and are unknown for *Kimmerosaurus*.

The dorsal vertebral centra of *Djupedalia engeri* are all compressed (in various directions) and do not show any

features that distinguish them from other cryptoclidian plesiosaurs. The dorsal vertebrae of *Colymbosaurus svalbardensis* exhibit a key-hole-shaped neural canal that differs from the circular canal seen in *Djupedalia*. Also, the dorsal neural spines of *Djupedalia* are very dorsoventrally and anteroposteriorly short relative to the size of the neural arch compared to that seen in all other cryptoclidians. The dorsal neural spines of *Djupedalia* are anteroposteriorly and dorsoventrally short compared to those of *Cryptoclidus*, *Muraenosaurus* and *Tricleidus* (Andrews, 1910; Brown, 1981; pers. obs.). A similar situation is seen in *Spitrasaurus*.

Appendicular skeleton

The juvenile state of the holotype of *Djupedalia engeri* places limitations on the number and type of comparisons that can be made between it and adult comparators; however, some features of the pectoral girdle and limbs are less prone to ontogenetic issues, thereby allowing meaningful comparative comments. *Djupedalia* does preserve clavicles and an interclavicle. These elements are also known from *Cryptoclidus*, *Muraenosaurus*, and *Tricleidus*, although the interclavicle is reduced or absent in *Cryptoclidus* and the clavicles may be reduced or absent in *Muraenosaurus* (Brown, 1981). Even though both coracoids and scapulae are preserved in MGUH 28378, the clavicles and interclavicle are not known in this specimen. Both clavicles and interclavicle are also absent (or at least not ossified) in *Spitrasaurus wensaasi* (Knutsen *et al.*, 2012(b)) even though the scapulae and coracoids are well preserved and in articulation. The interclavicular shape interpreted for *Djupedalia* is most similar to that seen in *Muraenosaurus leedsii* and *Tricleidus*, except that *Djupedalia* lacks a posterior process. Brown (1981) noted that the interclavicle of *M. leedsii* is convex ventrally and flat dorsally, which is consistent with the morphology seen in *Djupedalia*. The scapula in the juvenile specimen of MGUH 28378 (Smith, 2007) is also distinctly different in outline from that in *Djupedalia* in that the dorsolateral and medial margins of MGUH 28378 are less curved, and its curved dorsolateral edge is abruptly squared off anterolaterally (pers. obs. EMK). The exact shape of the dorsolateral process is uncertain as it is covered by the left forelimb (Smith, 2007). The scapula of MGUH 28378 also possesses a well developed lateral ridge (scapular shelf), which is nearly absent in *Djupedalia*.

In *Djupedalia engeri* the femur is larger than the humerus (a condition not known to change ontogenetically in plesiosaurs), whist the converse is true in *Cryptoclidus* and *Muraenosaurus*. In *Tricleidus* and *Spitrasaurus* the femur is equal in length or very slightly longer than the humerus (pers. obs. EMK). Sander (1989) described positive allometric growth in the humerus compared to the femur in three pachypleurosaurid taxa. However, a fourth pachypleurosaurid taxon does not show this relationship (Sander, 1989). It is therefore difficult to say whether the proportional differences observed in the fore and hind propodials of *Djupedalia* are due to its ontogenetic immaturity. The three elements preserved in the epipodial rows of *Djupedalia* are the same as those in *Colymbosaurus*, *Tricleidus* and *Spitrasaurus*, but more than the two known to occur in *Cryptoclidus* and *Muraenosaurus*. *Tricleidus*, however, possesses an extra element proximal to the epipodial row, at least in the forelimb (Andrews, 1910; pers. obs. EMK). Brown (1981) noted that even juvenile specimens of *Cryptoclidus* exhibit a proximally and anteriorly expanded radius, which clearly contrasts to the condition seen in *Djupedalia*.

Conclusions

A new plesiosaur taxon, *Djupedalia engeri* gen. et sp. nov. (PMO 216.839), from the Middle Volgian of Svalbard has been shown to share some general features with comparable British Callovian and Kimmeridgian/Tithonian taxa, such as atlas-axis morphology and cervical vertebral dimensions. The little cranial material that is known from the new taxon somewhat resembles that of *Kimmerosaurus*, although significant differences exist to indicate that they are not congeneric. In articular view, the shape of the cervical vertebral centra of *D. engeri* are similar to those of *Muraenosaurus beloclis*, but in lateral view more closely resemble those of *Cryptoclidus*, *Tricleidus*, and *Colymbosaurus*. The cervical neural arch morphology resembles that of MGUH 28378; however, the large temporal gap (Early Kimmeridgian to Middle Volgian), large differences in the scapular morphology, and discrepancies in both relative and absolute dimensions of the posterior cervical vertebral centra make it unlikely that they belong to the same taxon. At this time it cannot be conclusively ruled out that *D. engeri* is a juvenile specimen of the *Colymbosaurus svalbardensis* (known from the same locality), but it is considered highly unlikely given that the overlapping material (primarily from the hindlimbs) shows distinct morphological differences, and that *D. engeri* exhibits large differences in its vertebral morphology compared to other more complete specimens referred to *Colymbosaurus*. *D. engeri* is also distinct from *Spitrasaurus*, a second new genus of long-necked plesiosaur from the Slottsmøya Member in Svalbard with respect to its cranial, axial, pectoral and limb morphology. Therefore, in spite of the juvenile status of the holotype specimen (PMO 216.839) and pending the discovery of conclusive adult material of this taxon, a suite of diagnostic characters permit the erection of a new plesiosauroid taxon. New material from this taxon, preferably adult specimens, will assist in further unravelling the relationship of this species to previously known comparators. This new taxon is only one of many new specimens to have been discovered in the fossiliferous Upper Jurassic strata of Svalbard. Its distinctiveness compared to other described species from the same area shows that several taxa of plesiosauroid plesiosaurians inhabited this area, perhaps at different times.

Supplementary information

Vertebra no.	Length	Width	Height	Adjusted length	Adjusted width	Adjusted height
Atlas-axis	25	25	20	N/A	N/A	N/A
1	19,4	28,0	20,4	19,4	28,0	20,4
2	21,5	29,1	21,0	21,5	29,1	21,0
3	22,2	29,3	19,5	22,2	29,3	21,8
4	22,1	31,2	19,5	22,1	31,2	22,6
5	24,8	32,8	17,4	24,8	32,8	23,4
6	25,0	33,8	18,9	25,0	33,8	24,2
7	26,3	35,4	15,4	26,3	35,4	25,0
8	26,7	36,2	19,9	26,7	36,2	25,8
9	28,0	38,5	20,9	28,0	38,5	26,6
10	28,1	39,4	18,8	28,1	39,4	27,4
11	29,6	40,9	17,2	29,6	40,9	28,2
12	30,7	42,8	21,0	30,7	42,8	29,0
13	30,6	45,2	18,8	30,6	45,2	29,8
14	31,1	47,0	19,2	31,1	45,5	30,6
15	33,4	44,9	20,0	33,4	46,0	31,4
16	32,4	?	23,3	32,4	47,4	32,2
17	33,0	?	28,7	33,0	48,7	33,0
18	35,5	50,3	22,6	35,5	50,3	33,8
19	28,4	51,1	35,4	36,4	51,0	34,0
20	27,6	53,0	35,0	37,2	53,0	35,0
21	28,5	54,6	36,0	38,1	54,6	36,0
22	?	74,5	47,5	N/A	N/A	N/A
23	?	?	49,5	N/A	N/A	N/A
24	29,0	85,0	51,0	N/A	N/A	N/A
25	30,0	85,5	54,5	N/A	N/A	N/A
26	24,0	90,0	58,0	N/A	N/A	N/A
27	37,0	94,0	?	N/A	N/A	N/A
28	?	?	?	N/A	N/A	N/A
29	62,0	?	?	57,0	N/A	N/A
30	62,0	?	?	57,0	N/A	N/A
31	64,9	?	?	59,9	N/A	N/A
32	63,5	?	?	58,5	N/A	N/A
33	59,7	?	?	54,7	N/A	N/A
34	66,0	?	?	61,0	N/A	N/A
35	62,5	98,0	53,0	57,5	83,0	53,0
36	62,0	104,0	51,0	57,0	89,0	51,0
37	64,9	103,0	56,0	59,9	88,0	56,0
38	?	?	?	N/A	N/A	N/A

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