A possible early elasmosaurian plesiosaur from the Triassic/Jurassic boundary of Nottinghamshire

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Abstract: The partial remains of a small plesiosaur from the Nottinghamshire Lias, curated in the Natural History Museum at Wollaton Hall, Nottingham, are described. The proportions and sequence of the cervical vertebral centra suggest that it is an early elasmosaur. More detailed identification is problematic because of the limited material available.

Background

This paper describes the partial skeleton of a small plesiosaur (Wollaton Hall Natural History Museum, Nottingham NOTNH 1987.G.60). The specimen was presented to the Nottingham Museum by W. Stafford Esq. (then President of the Nottingham Natural History Society) in 1894. Its provenance is recorded as "Cropwell". Little other information is available.

Several small limestone quarries are known to have existed in the last century along the escarpment between the villages of Cotgrave (SK 64 35) and Cropwell Bishop (SK 68 35), though no exposures were visible at the date of writing. Given that these quarries were exploiting limestone, it is unlikely that excavation would have proceeded to any significant depth into vertebrate-bearing horizons within the underlying mudstones of the Penarth Group (cf. Sylvestor-Bradley and Ford, 1968). This specimen is thus most likely to originate from the lowest part of the Lias Group, in the Barnstone Member of the Scunthorpe Mudstone Group (formerly known as 'Hydraulic Limestone Series'). The good preservation of reptiles from these beds has been noted by Sylvester-Bradley and Ford (1968). The lowest 2 metres or so of the Barnstone Member (the pre-*Planorbis* Beds) are of Late Triassic (Rhaetian) age, the remainder Early Jurassic (Hettangian) (Brandon *et al.*, 1990).

Benton and Spencer (1995) record a ?pliosauroid from Cropwell Bishop, as well as '*Plesiosaurus*' from Barnstone Quarry, about 6km to the east. Other Liassic finds recorded from the general area include '?*Plesiosaurus*' from Elston (SK 76 48), and the more extensive marine reptile fauna of Barrow-on-Soar (SK 58 18) (Kent 1980). Other material from the Westbury Formation is documented mainly from south-west England, and less commonly from other regions of Britain (Storrs and Taylor, 1996; Taylor and Cruickshank, 1993).

The abbreviations used for museum names in the remainder of this paper are listed in the Appendix.

The specimen

A label stored with the specimen reads as follows:

'PLESIOSAURUS: 56 vertebrae, paddle and other bones. Cropwell, Notts, Presented by W. Stafford Esq.'

A search of the geological stores at Wollaton Hall has located: 26 cervical vertebrae, 15 dorsal and pectoral vertebrae, 4 sacral vertebrae and 7 caudal vertebrae (a total of 52 vertebrae); the right humerus; the right femur and the proximal end of the left femur; the left ilium and the distal end of the right ilium; a fragment of left coracoid; 3 rib fragments. No cranial material is present.

Most of the material has been stored together in trays. Some items have been on display, and these have been given accession numbers prefixed 1987 G.60. It should be noted that other non-plesiosaurid material in the collection has the same prefix, though it is easily distinguishable from that belonging to this individual.

In general the material is exceptionally well preserved and shows fine surface detail. Five cervical and all dorsal and pectoral vertebrae are badly damaged (e.g. Plate I, 2). In places, pyritic, calcareous mudstone has replaced structures such as disc and spinal chord. Pyrite decay in the mudstone has caused cracking and fragmentation.

Cervical vertebrae. Cervical vertebrae are well preserved in three dimensions with little, if any, distortion. Their correct order can easily be established in the more anterior vertebrae. Starting with the axis, nine anterior vertebrae are preserved in close articulation and show the natural shape of the neck immediately behind the head (Fig. 1). This clear upward curve has been predicted from detailed measurement and analysis of the cervical vertebrae of the Callovian plesiosaurs *Muraenosaurus* and *Cryptoclidus* (Evans, 1993). In others the faces of centra can be matched from fragments of bone preserved on adjacent elements. The relative positions of the more posterior elements can easily be judged from relative sizes, fragments from adjacent vertebrae and to some degree by matching articular faces.

The centra are spool-shaped, slightly waisted and generally rather broader than high. Anterior centra are heavily ornamented, with rugosities around the rims of articular faces, and a well-defined ventral keel. In more posterior vertebrae, the rugosity decreases and the keel becomes less sharp and well defined, disappearing more or less from the 17th backwards.

The articular faces of the centra are usually concealed by hard matrix, but can be seen on nos. 2, 3, 8 and 12-20. They are typical of those of
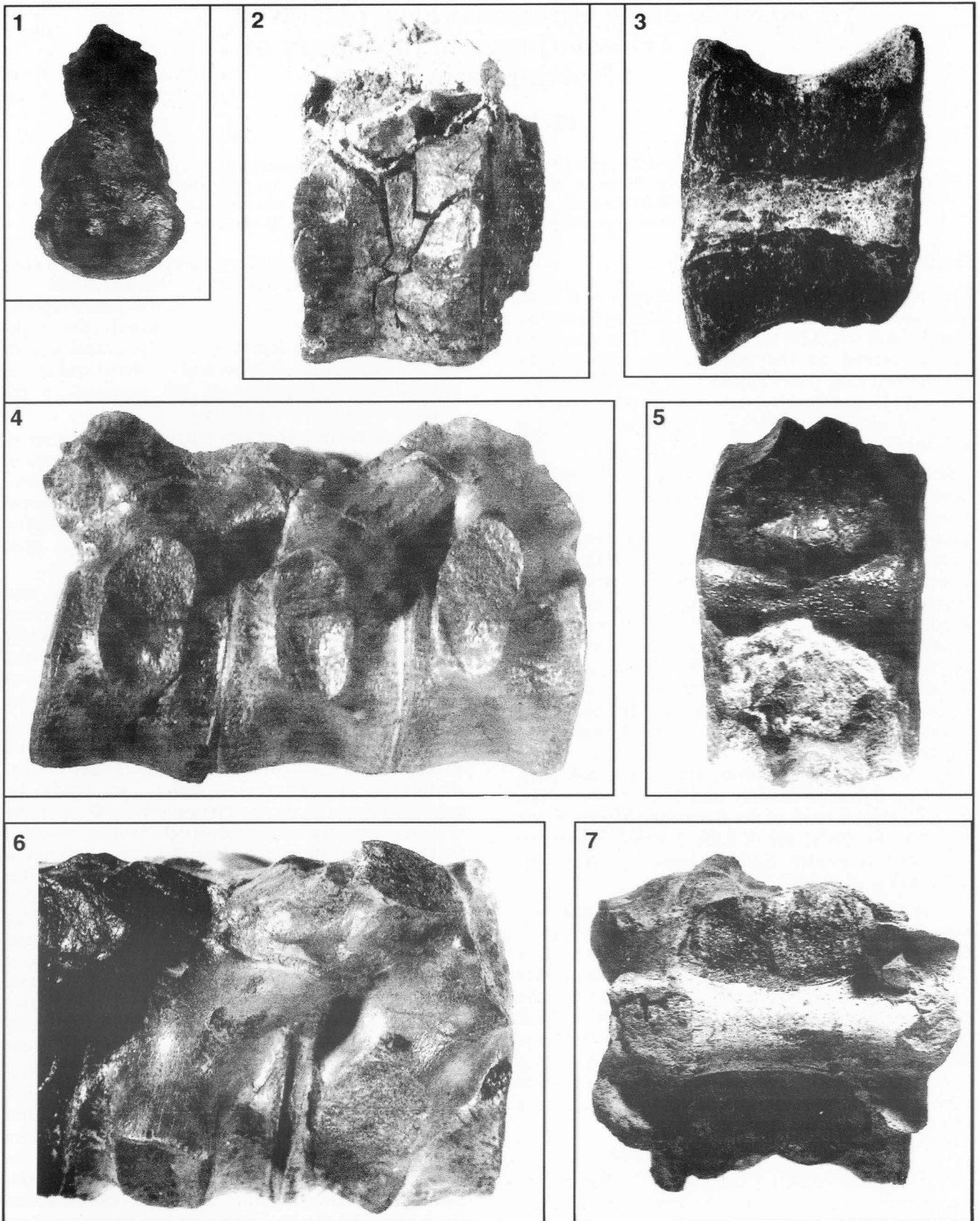
Plate I. NOTNH 1987.G.60. All photographs are natural size. 1. Articular face of cervical centrum (NOTNH 1987.G.60.8) showing paired pits (width 22mm). 2. Dorsal vertebra (NOTNH 1987.G.60.57) showing damage (height 64mm). 3. Base of neural canal (dorsal vertebra NOTNH 1987.G.60.57) (length 48mm). 4. Sacral vertebrae (NOTNH 1987.G.60.24, 25, 42) (length of block 100mm). 5. Base of neural canal (caudal vertebra NOTNH 1987.G.60.28) (length 43mm). 6. Interlocking zygapophyses on sacral vertebrae. 7. Internal cast of neural canal (dorsal vertebra NOTNH 1987.G.60.52) (length 70mm).

elasmosaurs, showing a shallow V-shaped section as opposed to the double sigmoid curve characteristic of cryptoclidids (Brown, 1981; 1994). The faces to the anterior vertebrae are oval or slightly heart-shaped, slightly flattened under the neural canal. There is a shallow depression in the middle of the face in which can be seen a pair of small pits (Plate I, 1). In vertebrae towards the posterior end of the neck, the rims of the articular faces become more rounded and the faces have deep depressions in the middle; these depressions change in shape from oval at vertebra 16 to heart-shaped at no. 24. The five most posterior cervical vertebrae are poorly preserved, having suffered pyrite decay as described above. Two of these appear to be fused, and bear a rib to each centrum on the right side and a single rib to the pair on the left.

Paired rib facets are placed low on the sides of the centrum (Fig. 2). The lower facets are flattened ovals, curved below, flattened above. The upper facets are in the form of a broad-based triangle, the wide base below. All neural arches are fused. The base of each arch runs the full length of the centrum, and extends downwards on the outside to a point extending towards the pointed top of the upper rib facet. In more posterior cervical vertebrae, from no. 16 onwards, the points are joined by a well-defined notch. A similar structure has been noted by Storrs (1997) in a juvenile specimen of *Plesiosaurus dolichodeirus* (YPM-PU 3352).

All cervical vertebrae have paired nutritive foramina on the ventral surface on both sides of, and close to, the keel. A third ventral foramen is present (Fig. 3) on vertebrae 14-18, most prominently on no. 17.

Pre- and post-zygapophyses are large, and extend well beyond the articular faces. Several vertebrae are preserved with fragments of zygapophyses from adjacent vertebrae in articulation. The close match of the articular surfaces of the zygapophyses shows that there was a tight fit up to the 10th vertebra, including a rigid neck. Posterior to this, preservation is less good, and no articulation is preserved until the sacral vertebrae.

Analysis of dimensions of cervical vertebrae. The good three-dimensional preservation of the cervical vertebrae of this specimen gives the opportunity for detailed analysis of the dimensions of the neck. Most Liassic vertebrate specimens are mounted for display within their original matrix, making it impossible to obtain accurate measurements.

Brown (1994) has redefined the two long-necked plesiosaur families, Elasmosauridae and Cryptoclididae. Diagnostic features differentiating the two families relate in the main to skull anatomy, but include the shape of the articular faces as mentioned above. In addition, the elasmosaurs are distinguished by having more elongated anterior cervical vertebrae. In his earlier publication, Brown (1981) plots the vertebral length index (VLI = the ratio of ventral length to the average of posterior width and height) for three individuals of

Cryptoclidus. Figure 4 plots these data, and adds data from several specimens of the elasmosaur *Muraenosaurus* as well as other individuals of *Cryptoclidus* (sources of measurements are given in Table 1). This shows a clear differentiation between the two families not only in the proportions of the centra, but more significantly in the variation of VLI along the length of the neck. In elasmosaurs the ratio increases sharply from the most anterior vertebra, reaching a peak around the 12th, then decreasing steadily towards the body. In cryptoclidids, the VLI is more or less constant until about the 20th vertebra, after which it decreases gradually then rises again just before the neck meets the body.

Figure 5 plots cervical VLI for NOTNH 1987.G.60 against curves showing the averages for each family computed from the measurements in Figure 4. This shows clearly that the VLI sequence matches closely that for elasmosaurs. However, the limited size of the dataset for these charts limits the statistical significance of these results and a more detailed investigation into the vertebral columns of the Plesiosauroidea would be required for a rigorous validation.

Dorsal and pectoral vertebrae. Parts or all of at least 19 dorsal and pectoral vertebrae are present, though their poor preservation has obliterated most morphological features. Where transverse processes are preserved they are very low, hardly separated from the centra. The neural canal is preserved as an internal cast on some vertebrae, giving rise to a surface texture (Plate I, 3). In other cases, an internal cast of the channel is preserved (Plate I, 7).

Sacral vertebrae. Three sacral vertebrae are preserved (Plate I, 4) as a sequence of three perfectly preserved centra, welded together by a thin layer of matrix which has replaced intervertebral discs. The close interlocking of the zygapophyses (Plate I, 6) and the very thin discs suggests that this part of the vertebral column was rigid, though the possibility that this is the result of taphonomic processes cannot be discounted.

Caudal vertebrae. Caudal vertebrae are shorter and broader than the cervicals, and generally more rounded and smoother in appearance. Their preservation is good, and fine surface detail can be seen. The shape of the centra tends to pentagonal, with a horizontal ventral surface forming one side of the pentagon. The rib facets are oval, and located high on the centra in contact with the neural arch facets. Most neural arches are fused. The stippled texture of the internal surface of the neural canal can be seen where neural arches are missing (Plate I, 5). Haemapophyses are only discernible as pairs of slight ridges on the underside of anterior caudal centra. On more posterior centra, they form facets on both anterior and posterior rims of the articular faces.

Limb bones. The right humerus is complete and exceptionally well-preserved. The left humerus is missing. The humerus is distinguished from the femur by the curvature of its axis, which is more
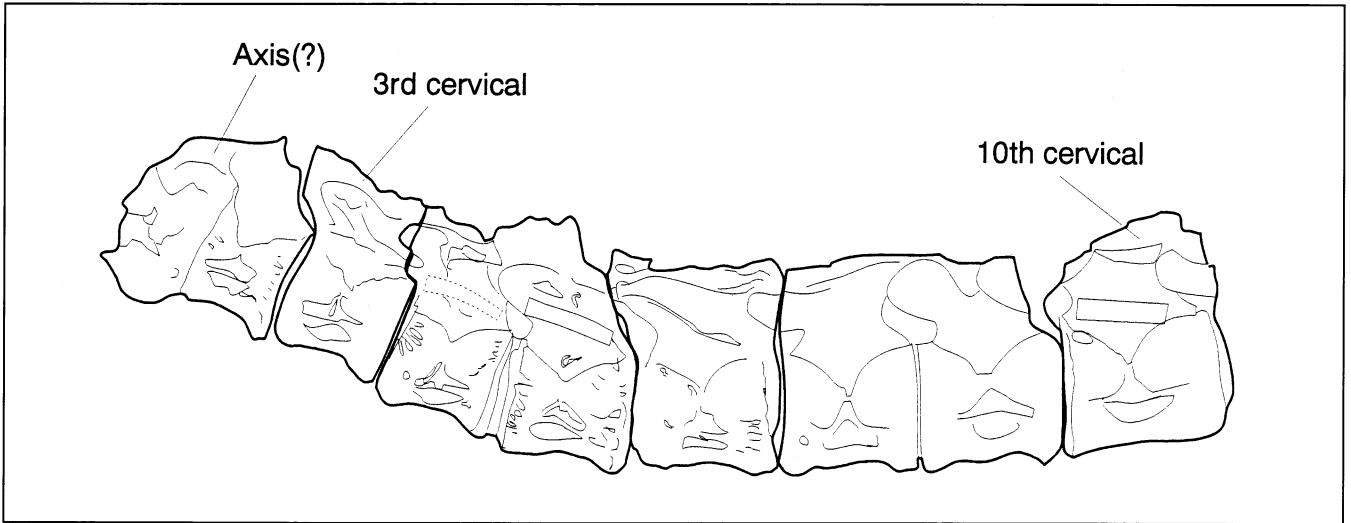
Fig. 1. Cervical vertebrae nos. 2 to 10 of plesiosaur NOTNH 1987.G.60 in left lateral view showing natural curve of neck. Overall length 174mm.
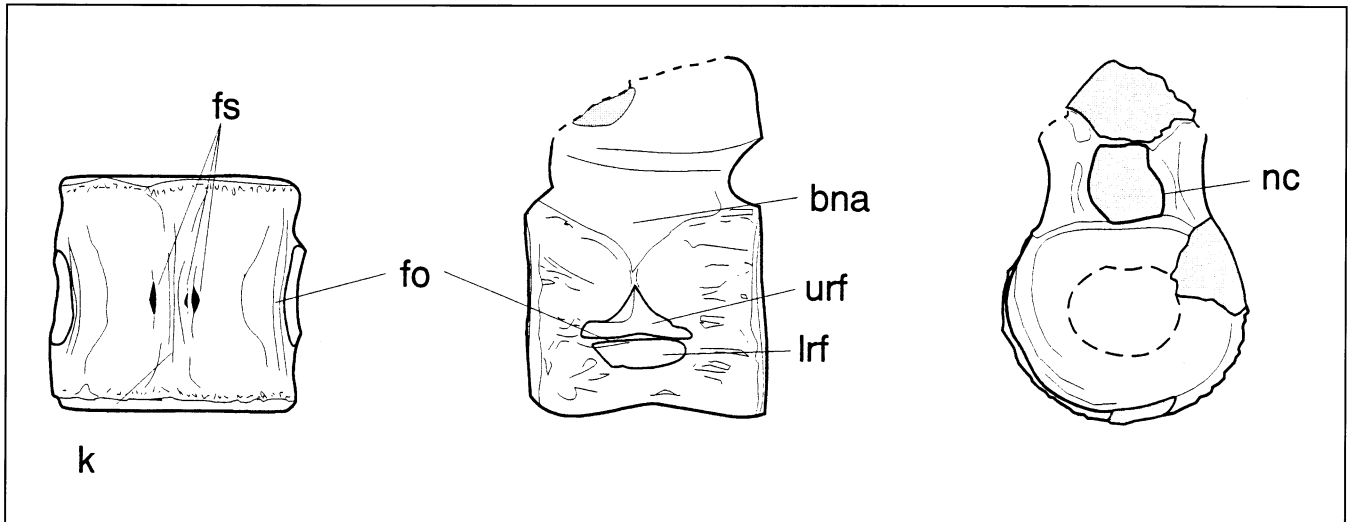
Fig. 2. 13th cervical vertebra (NOTNH 1987.G.60.18) in ventral, left lateral and anterior views. Length 27mm. Abbreviations: bna — base of neural arch; fo — foramen dividing rib-head; fs — subcentral foramen; k — keel; lrf — lower rib facet; nc — neural canal; urf — upper rib facet.
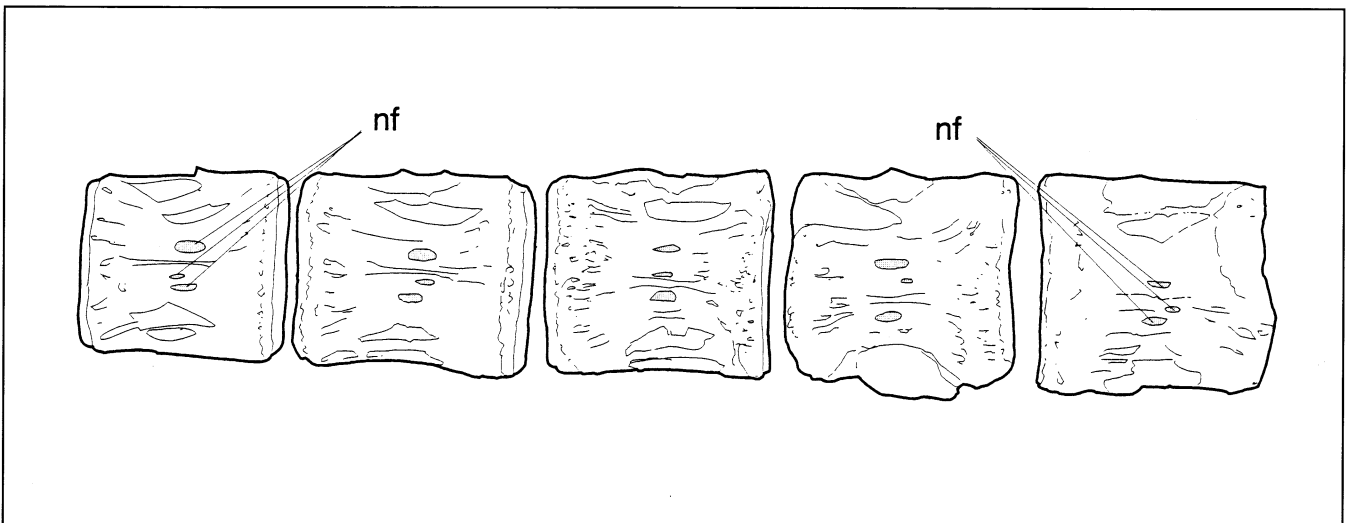
Fig. 3. Cervical vertebrae nos. 14 to 18 of plesiosaur NOTNH 1987.G.60 in ventral view showing third nutritive foramina. Overall length 180mm.

Ref	Designation	Species	Location	Source
G.60	NOTNH 1987 G.60		Wollaton Hall Natural History Museum, Nottingham	measurements by author
E1	BMNH R 3698	Muraenosaurus beloclis	British Museum (Natural History)	measurements by Mark Evans (Leicester)
E2	LEICS G18.1996	Muraenosaurus ? M.leedsi	New Walk Museum Leicester	measurements by author
E3	BMNH R2863	Muraenosaurus leedsi	British Museum (Natural History)	Evans 1993
C1	BMNH R2860	Cryptoclidus eurymerus	British Museum (Natural History)	Evans 1993
C2	HMG V1104	Cryptoclidus eurymerus	Hunterian Museum, Glasgow	Brown 1981
C3	BMNH R2417	Cryptoclidus eurymerus	British Museum (Natural History)	Brown 1981
C4	BMNH R2860	Cryptoclidus eurymerus	British Museum (Natural History)	Evans 1993

Table 1. Sources of specimens used for VLI determinations in Figures 4 and 5. See Appendix for abbreviations.
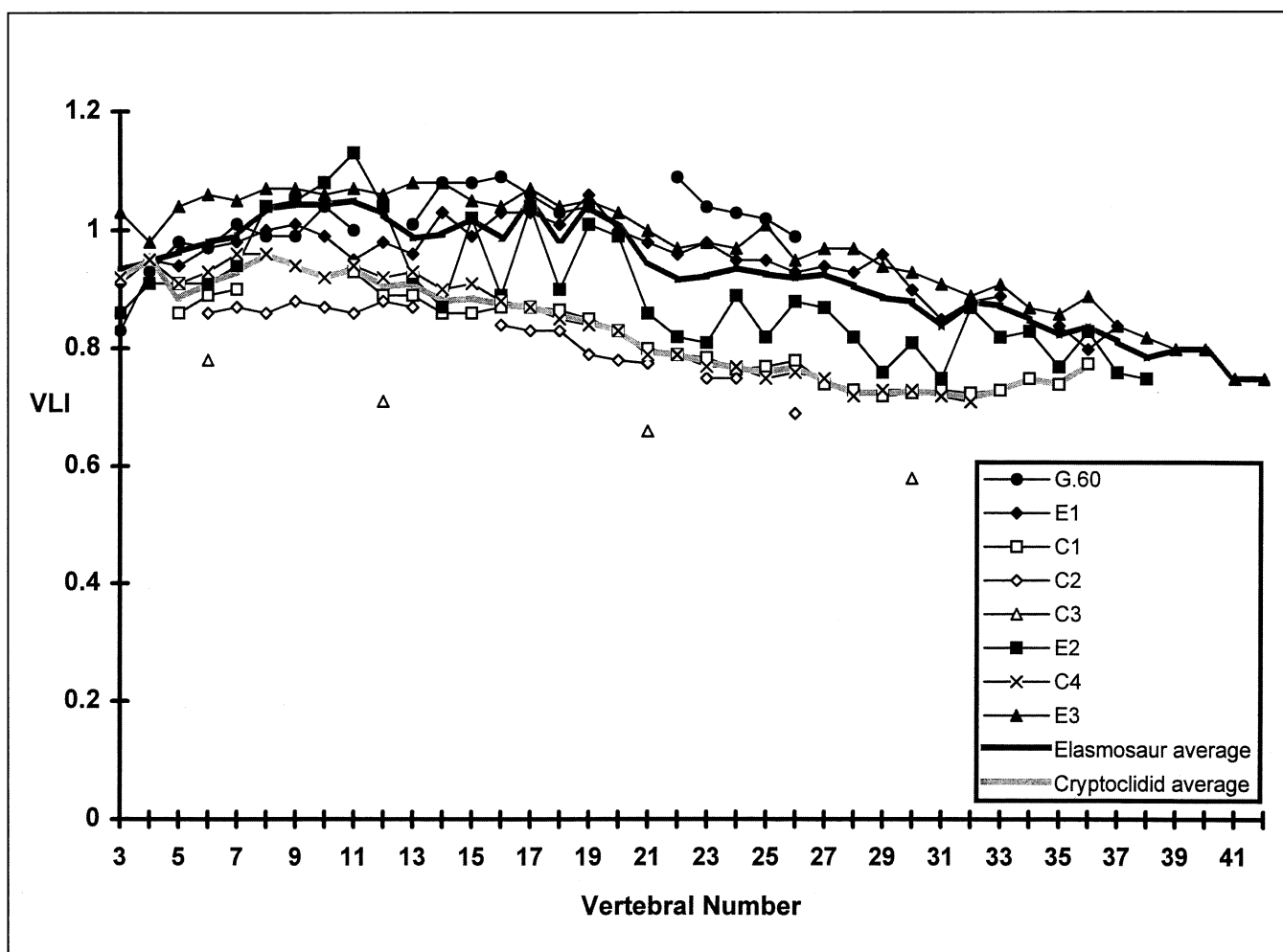

Fig. 4. Comparative chart of vertebral length index (VLI) for Jurassic long-necked plesiosaurs. See Appendix for sources.
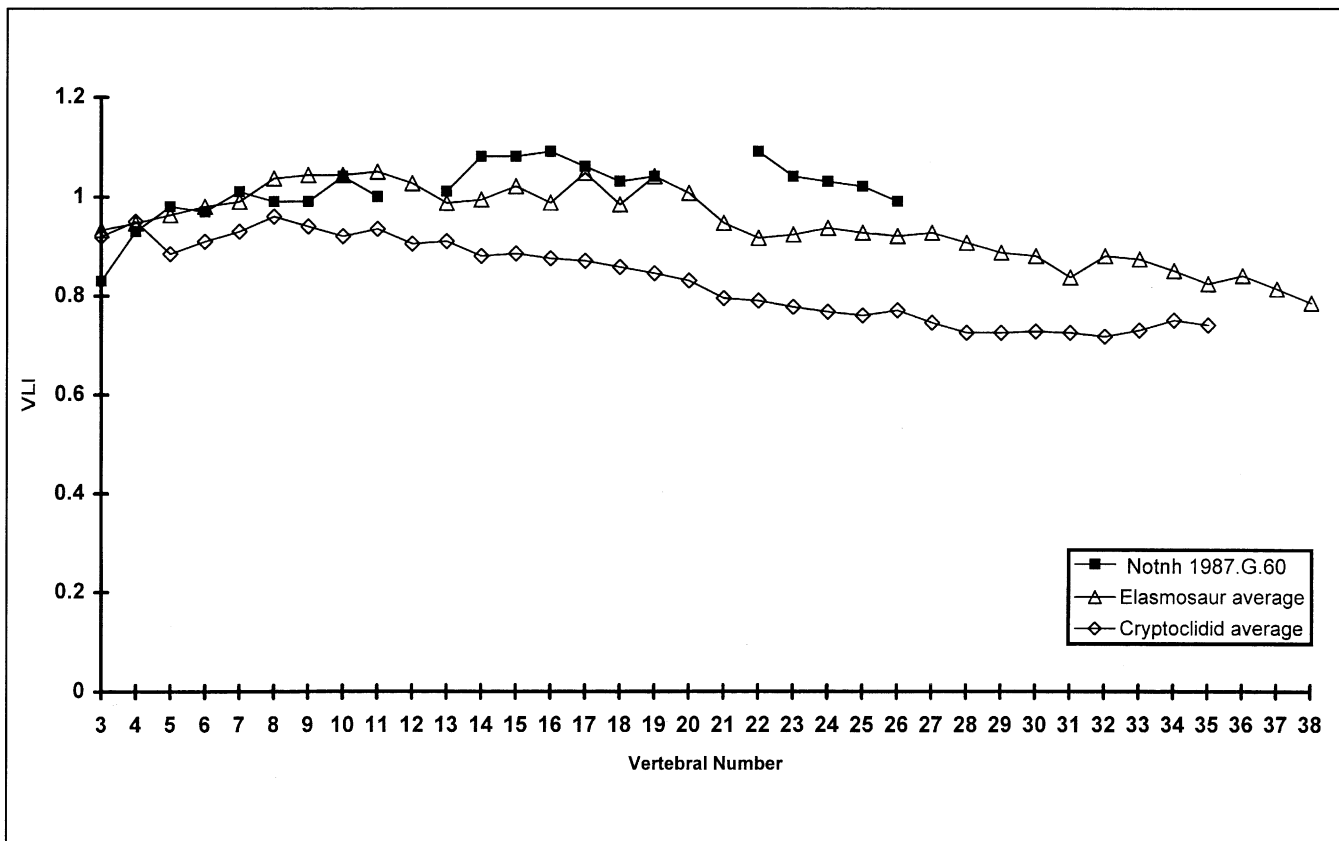
Fig. 5. Vertebral length index for NOTNH 1987.G.60 plotted against elasmosaur and cryptoclidid averages, based on data in Figure 4.
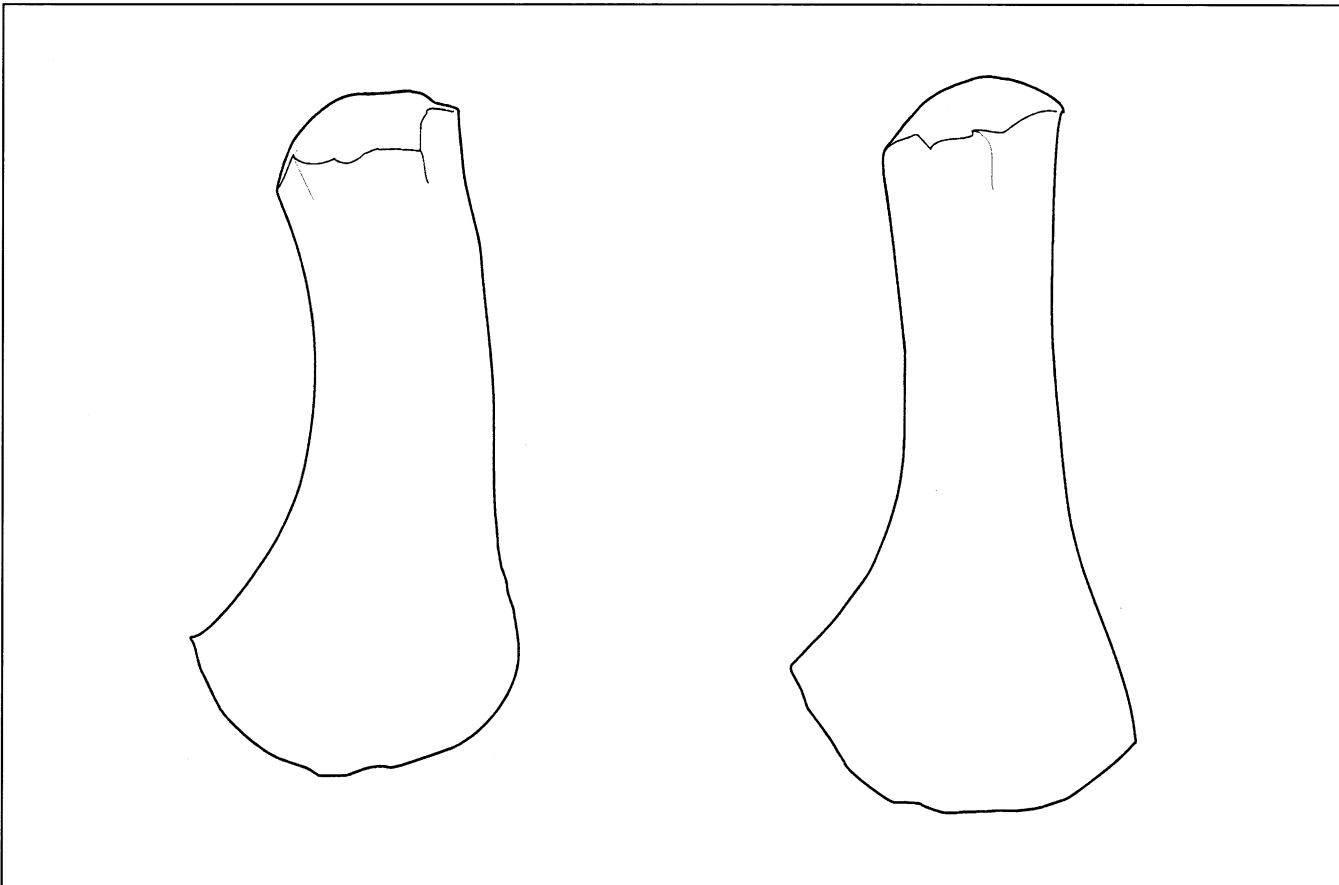

Fig. 6. Right humerus and right femur, dorsal view. Length of humerus 200mm, length of femur 190mm.

or less straight on its anterior edge and strongly curved on its posterior edge (Fig. 6). Cruickshank (1996) records the humerus of a *Pistosaurus*-like sauropterygian from the Rhaeto-Hettangian of Barrow-on-Soar, showing a similar morphology. The humerus of NOTMH 1987.G.60 is broad and robust. The head is large, and the articular facet is in the form of a rounded, narrow-based triangle, the base being at the anterior end. It is marked by the rugosity evident of a substantial cartilaginous covering. In section, the shaft is a flattened oval, the same width as the head and approximately one third of its thickness. The distal end is flattened, and flares posteriorly to twice the breadth of the shaft. The articular face is smoothly curved. There are no facets in the bone for radius and ulna, though here again rugosity is evidence of a cartilaginous extension. The lack of pre-axial expansion can be interpreted as a primitive or juvenile characteristic. It shows some surface ornament at distal and proximal ends in the form of shallow, parallel ridges that follow the axial curvature of the bone. The dorsal surface is smooth, and the ventral surface is generally smooth though with some light rugosity near the proximal end, most markedly on the posterior portion.

The complete right, and the proximal end of the left femur are exceptionally well-preserved. The femur is straight and robust, flaring out at the distal end to about twice the breadth of the mid-shaft. The flare extends posteriorly rather more than anteriorly. The head is round in section. The articular facet is rugose. The section of the shaft is oval, rather deeper than the humerus. The distal end is rounded and rugose, with a slight prominence on the curve which may mark the beginning of the ontogenetic development of the sub-division into tibial and fibular facets. The ventral surface is smooth. There are strongly marked rugosities indicating muscle insertions close to the proximal end. These are centred especially on two areas, one slightly in front of the axis, the other in the posterior third.

Analysis of dimensions of limb bones. Table 2 uses the average diameter of the dorsal vertebrae as a reference against which to plot the relative sizes of limb bones for a range of genera. Typically, dorsal vertebrae do not vary very much in diameter within an individual specimen and the diameter of the dorsal vertebral column is determined primarily by structural considerations and therefore related closely to the size of the animal.

The first two columns show that the limb bones are about 20% longer than those of later plesiosaurs. The relative lengths of limb elements falls into the same range as those for the Callovian specimens and show limb bones of roughly the same length. The fourth and fifth columns show the degree to which the distal ends of the bones are flared. This shows that the femur flares roughly to the same degree as the Callovian specimens, whereas the humerus is distinctly narrower. These measurements of proportion may imply an evolutionary progression whereby both limbs shorten, and the humerus

becomes more flared. This would reflect the development of better adaptations to a marine environment, and the unique underwater locomotory method of plesiosaurs (Taylor, 1986). In the absence of a rigorous phylogeny, such conclusions must remain speculative.

Other material. The left ilium is complete and well-preserved. The right ilium is represented by a fragment from the distal end. The ilium is notably slender and curved. The articular face of the head is divided into two well-defined triangular facets, one forming the junction with the ischium, the other forming part of the acetabulum. The head tapers to a narrow shaft, which twists markedly, flares and curves inwards proximally. The anterior quarter of the articular facet is set at an angle of about 45° to the remainder, which is in turn angled at about 80° to the main axis of the bones.

Girdles are represented by a single, poorly preserved fragment of coracoid. Three fragments of rib show that these were thick and apparently pachyostotic, circular or sub-triangular in section. The single preserved rib head is that of a dorsal rib. The head face is oval.

Discussion

The proportion and sequence of the cervical vertebral centra suggest that it is an early elasmosaur, but the limitations of the material available do not allow for identification at the generic level. The triangular form of the bases of the neural arches in NOTMH 1987.G.60 resembles that described on two immature cervical vertebrae of uncertain taxonomy (BMNH 2055, Lydekker 1889) and also from a series of vertebrae from the Linksfield erratic (Rhaeto-Hettangian), Morayshire, Scotland (Taylor and Cruickshank, 1993). In the latter, the upper part of the upper rib facet is generally irregular in form, though with a slight tendency towards the triangular. Taylor and Cruickshank (1993) also refer to other similar material recorded from the Rhaetian of Aust Cliff, Avon. Reference to the V-shaped neurocentral suture on a juvenile specimen of *Plesiosaurus dolichodeirus* has been made above (Storrs, 1997). This is regarded as an ontogenetic feature, and may be equally applicable to unrelated genera.

Taking into account missing vertebrae and cranial material, the overall length of the animal represented by the Cropwell remains is estimated at between 1.4 and 1.6m. This is small, but not uniquely so. The fused neural arches and unfused rib heads of this individual suggests that it was not fully grown. In comparison, Storrs (1995) describes a juvenile '?*Plesiosaurus*' estimated at between 1.25 and 1.5m in length, though with cervical vertebrae that are much shorter in proportion to their breadth.

Hawkins (1834) figures the complete articulated skeleton of *Thalassiodracon hawkinsi* (as *Plesiosaurus triatarsostinus*) giving an overall length of 5'6" (1.7m). The general form of the limb bones is

		H/av.Ø	F/av.Ø	H/F	F L/W	H L/W
NOTNH 1987.G.60		615%	602%	102%	52%	47%
LEICS G18.1996	*Muraenosaurus*	486%	451%	108%	45%	58%
BMNH R.2421	*Muraenosaurus*	515%	478%	108%	51%	60%
BMNH R.2428	*Muraenosaurus*	470%	424%	111%	56%	62%
BMNH R.2463	*Muraenosaurus*	500%				
BMNH R.2425	*Muraenosaurus*	459%	436%	105%	56%	65%
BMNH R.2539	*Triclidus*	450%	470%	96%	55%	57%
BMNH R.2412	*Cryptoclidus*	561%	522%	107%	61%	75%
BMNH R.2417	*Cryptoclidus*	473%	486%	97%	57%	63%
BMNH R.2420	*Cryptoclidus*	563%	512%	110%	59%	74%

Key

H/av.Ø	Length of humerus/average diameter of dorsal vertebrae
F/av.Ø	Length of femur/average diameter of dorsal vertebrae
H/F	Length of humerus/length of femur
F L/W	Length of femur/maximum width of femur
H L/W	Length of humerus/maximum width of humerus

(Sources: NOTNH 1987.G.60 and LEICS G18.1996 — measurements by the author, others from Andrews (1910)

Table 2. Comparison of relative limb dimensions for long-necked plesiosaurs. See appendix for abbreviations.

similar to the Cropwell specimen, though the articular facets for the radius, ulna, tibia and fibula are more clearly defined, possibly an ontogenetic feature. As the cervical vertebrae of Hawkins (1834) specimen are deeply embedded in matrix, there is no way of determining the VLI. Storrs and Taylor (1996) illustrate the 5th cervical vertebra of *T. hawkinsi*. This differs in form and proportion from those for the Cropwell specimen, though this might again be explained as an ontogenetic feature. The cervical centra of NOTNH 1987.G.60 are significantly more elongated than those of the specimen of *Plesiosaurus dolichodeirus* described by Owen (1865).

Summary

The specimen described in this paper exhibits a range of characteristics that seem to rule out its inclusion in any currently described genera of Lower Jurassic plesiosaur other than '*Plesiosaurus*'. However, this genus has tended to become a 'catch-all' for any specimen which cannot be included in other genera. Storrs and Taylor (1996) and Storrs (1997) have started the process of breaking '*Plesiosaurus*' down into a range of genera, which should lead to a better understanding of the evolutionary relationships of the long-necked plesiosaurs.

The concentration, especially in recent years, on skull morphology has tended to play down the importance of post-cranial anatomy as a diagnostic element in plesiosaur taxonomy. There is a tendency, especially in the long-necked plesiosaurs for heads to become detached from bodies prior to fossilisation, which can make the association of cranial to post-cranial anatomy problematic. Complete, articulated specimens exist, though these were collected mainly in the last century and are in display mounts which make impossible the detailed analysis of dimensions used in this paper. Given these constraints, plotting of VLI along the length of the neck seems to provide a potentially useful tool to distinguish elasmosaurs and cryptoclidids and may throw light on the early evolution of these families.

Acknowledgements

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Appendix

The following abbreviations apply to the museum specimens referred to in this paper:

BMNH — British Museum (Natural History), London;

LEICS — New Walk Museum, Leicester (formerly Leicester Museum and Art Gallery);

NOTNH — Natural History Museum, Wollaton Hall, Nottingham;

YPM-PU — Yale Peabody Museum — Princeton University.