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The first relatively complete exoccipital-opisthotic from the braincase of the Callovian pliosaur, *Liopleurodon*

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Abstract – A newly recognized left exoccipital-opisthotic of a Callovian pliosaur, derived from the Peterborough or lower Stewartby Members of the Oxford Clay Formation of Peterborough, is described and figured. This isolated bone is tentatively identified as belonging to an ‘adult’ individual of *Liopleurodon ferox* that is inferred to have had a skull length of 1.26 metres and an overall body length of 6.39 metres.

Keywords: Jurassic, Callovian, Sauropterygia, Plesiosauria, braincases.

1. Introduction

Pliosaur occipital and braincase elements are rarely preserved, and when present are often damaged or obscured by crushing of the cranial roof and suspensorium against the palate (e.g. Andrews, 1895, 1897, 1909, 1913; L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001). The three-dimensional structure of the pliosaur braincase and its associated nerve and blood vessels is therefore problematic to reconstruct. A rare pliosaur exoccipital-opisthotic complex, CAMSM J.27424 (see below for institutional abbreviations), originally mis-identified in the Museum as belonging to the giant filter-feeding fish *Leedsichthys problematicus* Woodward, 1889, is described and interpreted. Although CAMSM J.27424 is an isolated element, its recognition as a large, well-preserved and almost uncrushed exoccipital-opisthotic complex adds significantly to our understanding of pliosaur braincase anatomy. Prefixes for figured and cited specimen numbers denote the following repositories: CAMSM – The Sedgwick Museum, Cambridge; PETMG – Peterborough Museum and Art Gallery, Peterborough; NHM – The Natural History Museum, London; GPIT – Institut und Museum für Geologie und Paläontologie, Tübingen.

2. Locality and horizon

CAMSM J.27424 was collected in 1909 from a brick pit in Whittlesey, south of Peterborough, England. The brick pits in the Whittlesey area (Fig. 1) currently expose the whole of the Peterborough Member and the lowest few metres of the overlying Stewartby Member of the Oxford Clay Formation (Hudson & Martill,

1994). These ‘deposit-feeder’ shales preserve the *Sigaloceras calloviense* to *Peltoceras athleta* ammonite zones (Martill & Hudson, 1991), and are therefore of Callovian age (161.3 to 157.1 million years ago: Harland *et al.*, 1990). However, whether CAMSM J.27424 originated from the Peterborough Member, or the bottom of the Stewartby Member of the Oxford Clay Formation, cannot be stated definitively. The Stewartby Member is generally considered to be less fossiliferous than the underlying Peterborough Member (Cox, Hudson & Martill, 1992), with Bed 10 of the Peterborough Member (Callomon, 1968) presently identified as the most prolific source of fossil vertebrates in the Peterborough area (Martill, 1986; Hudson & Martill, 1994). However, this is an artefact of modern clay extraction techniques: shale planers are used to remove the clay to a level immediately above Bed 10 of the Peterborough Member, thereby destroying fossils higher in the succession. Older sources indicate that fossils of marine vertebrates have been collected from all levels of the Callovian Oxford Clay Formation in the Peterborough area (e.g. Leeds & Woodward, 1899; Leeds, 1956).

3. The pliosaur braincase

The braincase in Callovian pliosaurs is partially exposed in lateral view through the large temporal fenestrae (Fig. 2), and consists of seven bones: four median and three paired. Dorsally, the supraoccipital (s) surmounts the paired prootics (pr) anteriorly and the paired exoccipital-opisthotics (eo) posteriorly. Each prootic contacts the exoccipital-opisthotic posteriorly, the basisphenoid (bs) anteroventrally, and the basioccipital (bo) posteroventrally. Each exoccipital-opisthotic overlies the basioccipital ventrally, the

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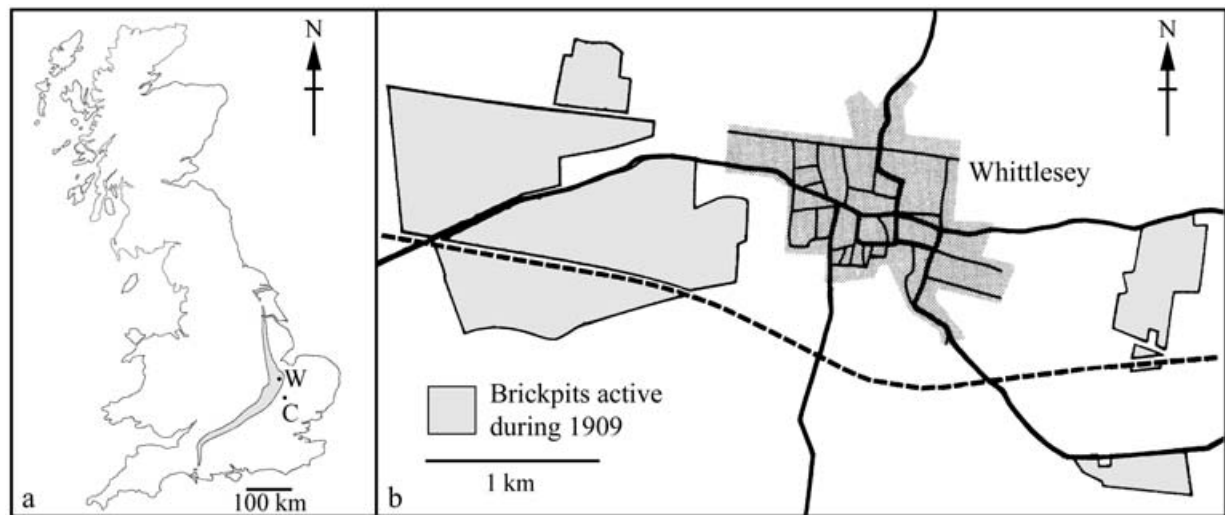


Figure 1. Locality maps. (a) Mainland Britain showing the outcrop of the Oxford Clay Formation in England (after Martill & Hudson, 1991), Abbreviations: C – Cambridge, W – Whittlesey, Cambridgeshire, the location from which CAMSM J.27424 was recovered. (b) Modern extent of the brick pits active in the Whittlesey area and working the Peterborough Member, Oxford Clay Formation during 1909 (modified from Hillier, 1981).

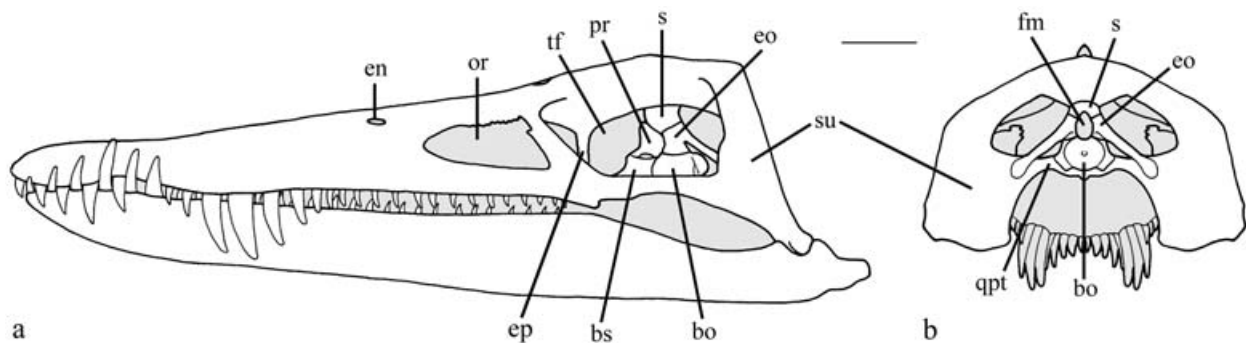


Figure 2. Outline cranial reconstructions of the Callovian pliosaur *Liopleurodon ferox* Sauvage, 1873 to indicate gross morphology and location of dorsal braincase elements in (a) left lateral, and (b) posterior views. Scale bar 100 mm. Abbreviations: bo – basioccipital, bs – basisphenoid, en – external nares, eo – exoccipital-opisthotic, ep – epipterygoid, fm – foramen magnum, or – orbit, pr – prootic, qpt – quadrate ramus of pterygoid, s – supraoccipital, su – suspensorium, tf – temporal fenestra.

basisphenoid contacts the basioccipital posteriorly, and these two bones are under-plated by the sheet-like parasphenoid. Anterolaterally, the epipterygoids (ep) form a pair of pillars extending from the dorsal surface of the pterygoid ventrally, and contact the parietal dorsally. Ventrally, the braincase is underlain by the posterior rami of the pterygoids.

In pliosaurs, as in some other marine reptiles, the exoccipital and opisthotic are fused to form a single bony unit (Williston, 1925; Romer, 1956). Fusion occurs in all members of the Plesiosauria (Brown, 1981), although the line of suture between the two elements may remain visible even in the adult (Andrews, 1897, 1913; Brown, 1981, fig. 36d). The exoccipital-opisthotic consists of a stout, pillar-like body, and a

very elongate paroccipital process (the opisthotic was formerly known as the ‘paroccipital bone’: Williston, 1925). The body of the exoccipital-opisthotic forms the lateral margin of the foramen magnum (fm, Fig. 2b), and is pierced by foramina for the passage of cranial nerves, blood vessels, the perilymphatic duct, and the semicircular canal system of the inner ear (Romer, 1956). The slender paroccipital process provides vital mechanical bracing between the suspensorium and the rear of the braincase.

4. Description

CAMSM J.27424 is the left exoccipital-opisthotic of a pliosaur. The exoccipital and opisthotic elements are

Figure 3. Photographs of CAMSM J.27424 in (a) dorsal, (b) medial, (c) ventral, (d) lateral, (e) anterior, and (f) posterior views; for interpretive drawings see Figure 4. Arrows give anatomical orientations, scale bar = 100 mm. Abbreviations: ant – anterior, dor – dorsal, med – medial.

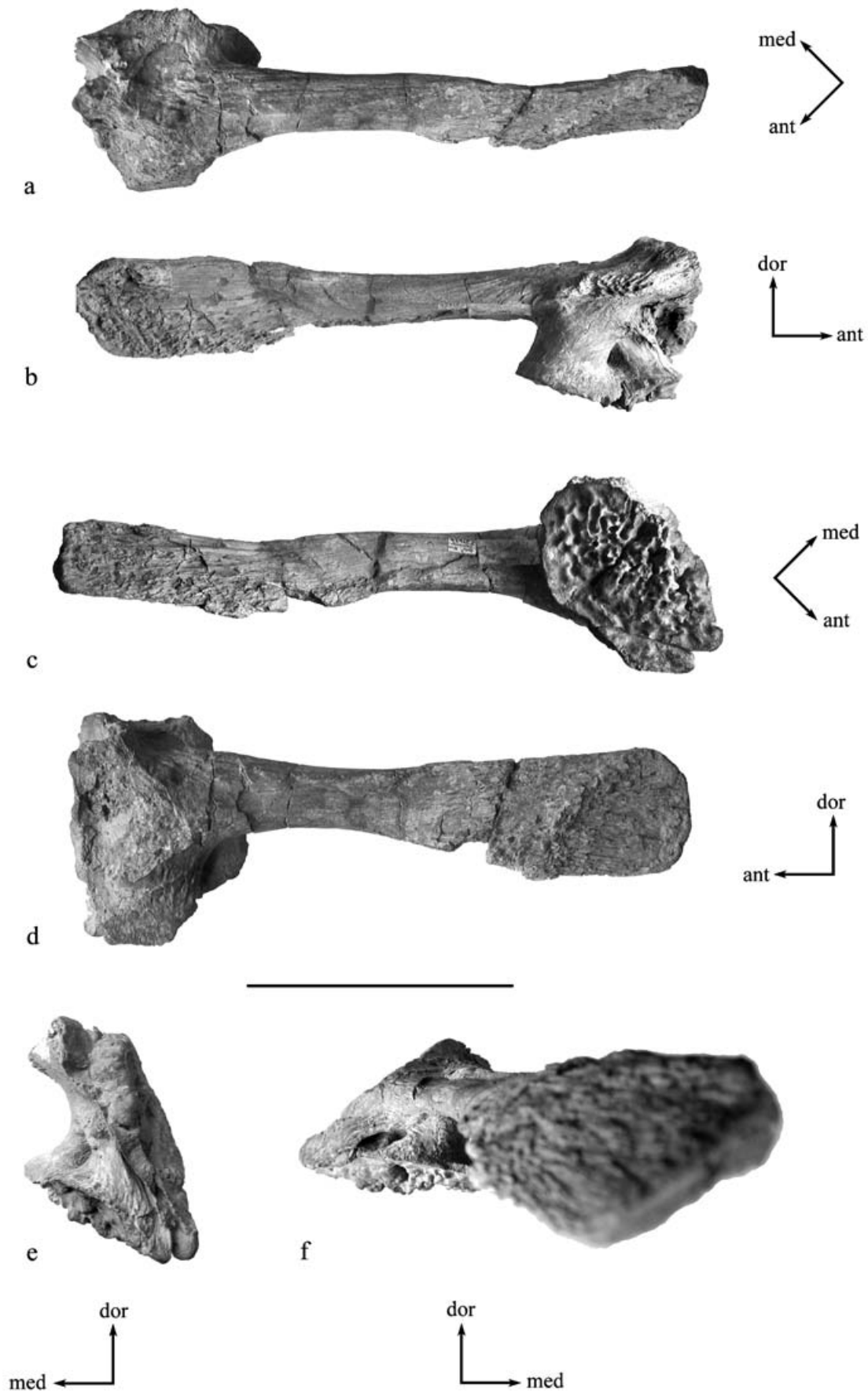


Figure 3. For legend see facing page.

fused, but the suture between them is clearly defined in most places. The exoccipital forms the majority of the medial and ventral surfaces of the body, and the opisthotic forms the lateral surface of the body and the whole of the paroccipital process. The opisthotic is incomplete anteriorly, the damaged area revealing the internal surface of the exoccipital (Figs 3a–f, 4a–f).

In dorsal view (Figs 3a, 4a) CAMSM J.27424 preserves the supraoccipital facet (s fac, Fig. 4a, d, e) anteriorly. The medial surface of the supraoccipital facet is formed by the exoccipital, and the lateral surface by the opisthotic; slight crushing has folded the exoccipital and opisthotic elements together along the line of the suture (sut, Fig. 4a). Posterior to the supraoccipital facet, the line of division between the exoccipital and opisthotic is unclear except immediately anteromedial to the paroccipital process, where it is a fine but well-defined sutural line. Dorsolaterally, the surface of the opisthotic is damaged, resulting in loss of the lateral surface of the supraoccipital facet, and the total loss of the prootic facet (by comparison to *Peloneustes* (Andrews, 1913) and *Kimmerosaurus* (Brown, 1981)). Posteriorly, the opisthotic forms the whole of the long, stout and posterolaterally directed paroccipital process (pp, Fig. 4a–d, f). Proximally, the paroccipital process is oval in cross-section and slightly dorsolaterally to ventromedially flattened for approximately half its length. Distally, the paroccipital process is flattened, and its lateral surface is crossed by a curved, anteroventrally to posterodorsally trending ridge of bone that delineates the roughened posterior distal facet (pdf, Fig. 4a, d, f) for contact with the suspensorium (Andrews, 1913). The posterior terminal end of the paroccipital process (pte, Fig. 4a, c, f) is heavily pitted, strongly suggestive of a cartilage cap or dense fibrous connection to the quadrate–squamosal–pterygoid complex in life.

The medial surface of CAMSM J.27424 (Figs 3b, 4b) is formed by the exoccipital anteriorly and the opisthotic posteriorly. The body is deeply embayed to form the lateral wall of the foramen magnum (fm, Fig. 4b, e). Posterodorsal to the foramen magnum, the exoccipital is roughened into an atlas-axis articulating facet (aaf, Fig. 4a–e), equivalent to the ‘facet like a zygapophysis’ of *Peloneustes* (Andrews, 1913, p. 36). The ventral edge of the exoccipital gives no indication that it contacted its counterpart beneath the foramen magnum or formed any part of the occipital condyle. This lack of junction between the two exoccipital–opisthotics ventrally appears to be normal for pliosaurs.

The exoccipital–opisthotic suture (sut, Fig. 4b, f) is a fine ridge, closely following the ventromedial edge of the paroccipital process. Immediately posterior of the suture, the anteromedial surface of the paroccipital process is coarsely ornamented.

The ventral surface of the body of CAMSM J.27424 (Figs 3c, 4c) is gently convex and considerably roughened anteriorly for cartilaginous union with the basioccipital (bo fac, Fig. 4b–f). The majority of the basioccipital facet is formed by the exoccipital, the anteromedial edge of which is angled dorsally. A small part of the basioccipital facet is formed by the opisthotic laterally, with the exoccipital and opisthotic separated by a deep incisure (sut, Fig. 4c).

The lateral surface of CAMSM J.27424 (Figs 3d, 4d) is formed by the opisthotic, with a small area of the lateral surface of the exoccipital revealed anteriorly by bone breakage. The damaged area, formed by loss of the anterolateral surface of the opisthotic, reveals two smooth areas of the internal osseous auditory labyrinth (Baird, 1970), separated by a roughened area of bone. The ventral smooth area is large, oval shaped, and formed by the lateral surface of the exoccipital (au, Fig. 4a, d, e). In other members of the Plesiosauria, this opening has been interpreted as containing the ampulla for the posterior vertical semicircular canal (in *Peloneustes*: Andrews, 1913) or the utriculus (in plesiosaurs: Brown, 1981), but it probably housed both (Maisch, 1998). Anterodorsal to the ventral smooth area is a roughened and pitted area of bone that is interpreted as the internal exoccipital–opisthotic suture (sut, Fig. 4c). Anterodorsal of this roughened sutural surface is a smaller, but incomplete area of smooth bone formed by the lateral surface of the opisthotic. This smooth area of bone is interpreted as the medial surface of the posterior vertical semicircular canal (pvs, Fig. 4d, e). The posterior of the fenestra ovalis, if originally present, is not preserved due to loss of the anterolateral margin of the opisthotic.

In anterior view, the majority of CAMSM J.27424 is formed by the exoccipital, because the anterior of the opisthotic is missing laterally (Figs 3e, 4e). The exoccipital–opisthotic suture (sut, Fig. 4e) passes from the supraoccipital facet dorsally, extends around the ampullary–utricular recess, and passes onto the anterior of the bone in a deep groove, before crossing onto the ventral surface. Ventromedial to the suture, the anterior of the exoccipital is pierced by an elongate, dorsomedial to ventrolateral oriented cleft (ajf, Fig. 4e). This cleft is interpreted as the anterior jugular (or

Figure 4. Interpretive drawings of CAMSM J.27424 in (a) dorsal, (b) medial, (c) ventral, (d) lateral, (e) anterior, and (f) posterolateral views; for matching photographs see Figure 3, scale bar = 100 mm; for anatomical orientation bars see Figure 3. Abbreviations: aaf – atlas-axis articulating facet, ajf – anterior jugular foramen, au – ampulla–utriculus recess, bo fac – basioccipital facet, ef – eustation foramen, fm – foramen magnum, pcf – posterior common foramen, pdf – posterior distal facet, pjf – posterior jugular foramen, pp – paroccipital process, pte – posterior terminal end, pvs – recess for posterior vertical semicircular canal, s fac – supraoccipital facet, sut – exoccipital–opisthotic suture, XII – hypoglossal foramen.

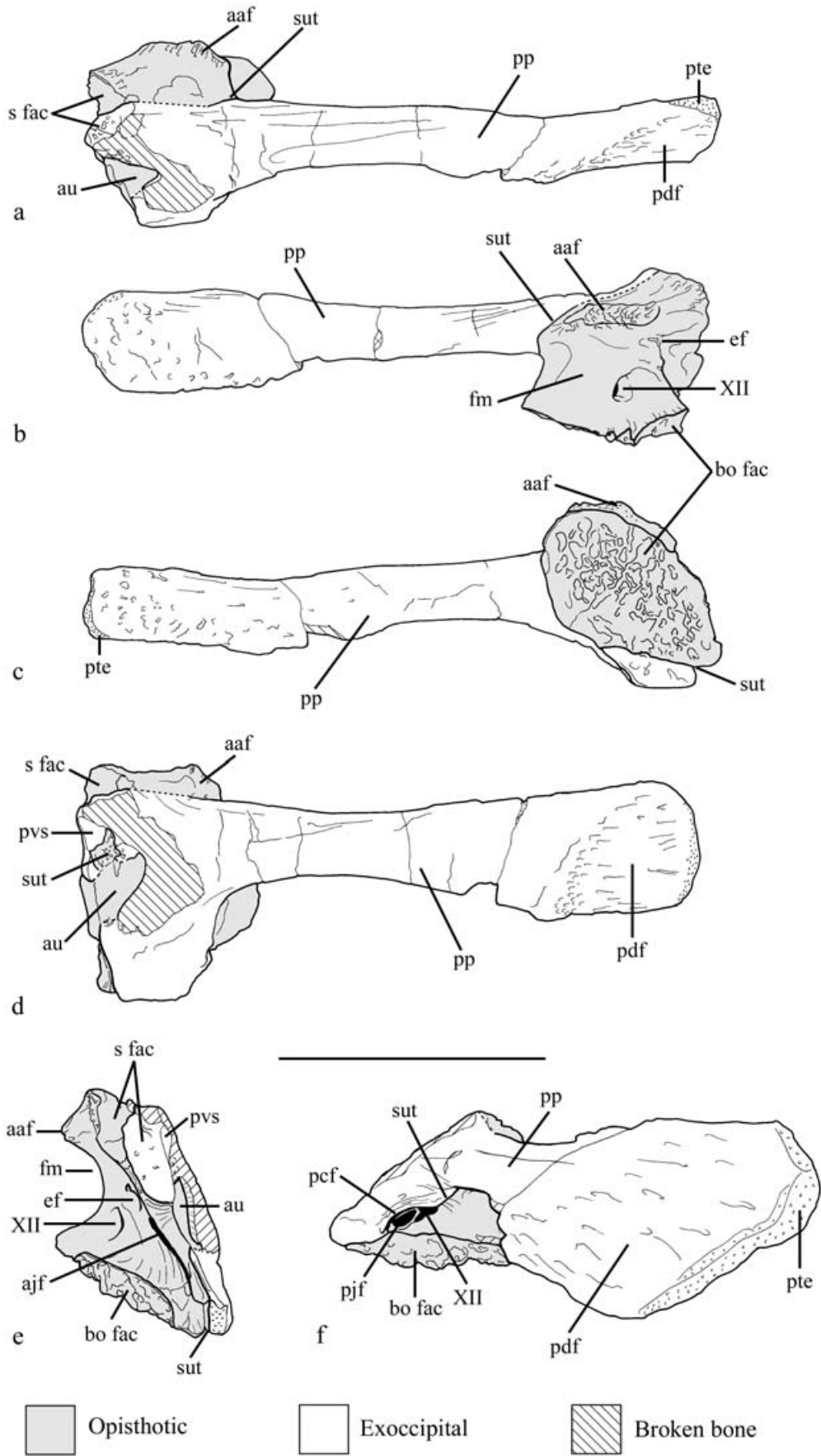


Figure 4. For legend see facing page.

vagus) foramen, for passage of the vagus (X) and accessorius (XI) nerves, and the posterior cerebral vein (Romer, 1956; Brown, 1981). The glossopharyngeal (IX) nerve, one branch of the hypoglossal (XII) nerve, and an extension of the perilymphatic duct from the inner ear may also have passed through the anterior jugular foramen (Romer, 1956). Medial to the anterior jugular foramen, the exoccipital is pierced by two foramina. The first is sub-circular, relatively large and lies anteroventral to the foramen magnum. This foramen lies at the level of the floor of the braincase (XII, Fig. 4b, e), and is interpreted as the exit for two or three branches of the hypoglossal (XII) nerve (Romer, 1956). A second, smaller foramen lies dorsal to the first and close to the upper edge of the anterior jugular foramen. This upper foramen may represent the endolymphatic foramen (ef, Fig. 4b, e) for the exit of the endolymphatic duct from the inner ear into the cranial cavity (Romer, 1956). This foramen was considered the exit for a blood vessel in *Peloneustes* (Andrews, 1913).

The posterior surface of CAMSM J.27424 is formed by the exoccipital medially, and the opisthotic laterally (Figs 3f, 4f). The exoccipital-opisthotic suture passes from beneath the base of the paroccipital process into an elongate, dorsomedially to ventrolaterally oriented groove. Within the groove lie two subequally sized foramina. The rounded dorsomedial foramen is interpreted as the posterior expression of the hypoglossal (XII) foramen (XII, Fig. 4f) and the elongate ventrolateral foramen as the posterior jugular foramen (pjf, Fig. 4f). Thus, the anterior jugular and hypoglossal foramina combine within the exoccipital-opisthotic to form a posterior common foramen (pcf, Fig. 4f).

5. Interpretation and discussion

5.a. Comparison and identification

Five species of pliosaur, all belonging to monospecific genera, are known from the Callovian Oxford Clay Formation (L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001): *Liopleurodon ferox* Sauvage, 1873; *Pachycostasaurus dawni* Cruickshank, Martill & Noè, 1996; *Peloneustes philarchus* (Seeley, 1869) Lydekker, 1889; *Pliosaurus andrewsi* Tarlo, 1960; and *Simolestes vorax* Andrews, 1909. Cranial material is known for all five genera (L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001, *contra* Tarlo, 1958; see also Andrews, 1913; Linder, 1913; Dawn, 1991; Martill, 1992). The braincase is most completely known in *Peloneustes philarchus*, including a complete and uncrushed pair of exoccipital-opisthotics (NHM R3803; Andrews, 1913, fig. 11). The braincase is partially known in *Liopleurodon ferox* (NHM R2446 and NHM R2680; Andrews, 1897, 1913) and *Simolestes vorax* (NHM R3319; Andrews, 1909, 1913), both species preserving incomplete exoccipital-opisthotic elements (L. F. Noè,

unpub. Ph.D. thesis, Univ. Derby, 2001). The braincase is not preserved in *Pliosaurus andrewsi* or *Pachycostasaurus dawni*, so comparison cannot be made to these taxa.

The left exoccipital-opisthotic of *Peloneustes philarchus* NHM R3803 (Andrews, 1913) is considerably smaller than that of CAMSM J.27424. The length of the exoccipital-opisthotic from the top of the supraoccipital facet to the posterior distal facet is 78 mm in NHM R3803, but is 208 mm long in CAMSM J.27424. The anterior jugular foramen in NHM R3803 is aligned along the exoccipital-opisthotic suture (Andrews, 1913; fig. 12D), but in CAMSM J.27424 the anterior jugular foramen is situated wholly within the exoccipital, and ventral to the exoccipital-opisthotic suture (Fig. 4e). In both taxa, the posterior jugular and hypoglossal (XII) foramina exit into a posterior common foramen along the line of the exoccipital-opisthotic suture. In *Peloneustes* the basioccipital facet is sub-quadrangle, but anteroposteriorly elongated in CAMSM J.27424. The paroccipital process in *Peloneustes* is relatively shorter, and the distal end thicker and more rounded than in CAMSM J.27424 (Andrews, 1913, pp. 36–7, figs 11, 12). Thus, CAMSM J.27424 differs substantially in size and morphology from NHM R3803, so the exoccipital-opisthotic described here cannot be referred to *Peloneustes*.

Comparison between CAMSM J.27424 and *Simolestes vorax* is problematic, as the surviving left exoccipital-opisthotic in the holotype (NHM R3319) is considerably crushed and broken. However, the skull of *Simolestes* is relatively short and wide (Noè, 1999; L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001), and the paroccipital process was probably proportionally shorter and more laterally oriented than in CAMSM J.27424. However, confirmation of this inference will have to await the recovery of better-preserved cranial material of *Simolestes*.

CAMSM J.27424 can be compared to two individuals of *Liopleurodon ferox*, NHM R2446 and NHM R2680 (Andrews, 1913). NHM R2446 (previously assigned to *Liopleurodon pachydeirus*; for taxonomic revision see L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001) preserves an incomplete anterior columnar body of a left exoccipital-opisthotic complex. The bone is badly damaged but of similar size to CAMSM J.27424. The exoccipital-opisthotic body of NHM R2446 is broken along the jugular foramen, and preserves both the anterior and posterior hypoglossal (XII) foramina in the same relative positions as CAMSM J.27424. However, the line of the exoccipital-opisthotic suture cannot be traced in NHM R2446, so comparison cannot be made to the position of the hypoglossal (XII) foramen in relation to the suture. The anterior of the paroccipital process of NHM R2446 is orientated with the flattened surfaces more or less vertically aligned, in contrast to the medially tilted dorsal surface of the paroccipital process in CAMSM J.27424. This

difference in orientation of the proximal end of the paroccipital process may be the result of compaction in CAMSM J.27424.

NHM R2680 is a complete, but isolated and somewhat crushed cranium of *Liopleurodon ferox*. NHM R2680 preserves a left exoccipital-opisthotic, complete with paroccipital process, which is only slightly smaller than that in CAMSM J.27424. The body is compressed between the cranial roof and palate (Andrews, 1897, 1913), and the location of the exoccipital-opisthotic suture and the various foramina cannot be determined. However, the gross morphology and relative proportions of the exoccipital-opisthotic in NHM R2680 match that of CAMSM J.27424. The distal end of the paroccipital process is somewhat thicker and more rounded in NHM R2680, although this may be a result of distortion in CAMSM J.27424. Thus, comparison of CAMSM J.27424 with the available Callovian pliosaur braincase material indicates that the morphology of CAMSM J.27424 is closest to NHM R2446 and NHM R2680. CAMSM J.27424 is therefore tentatively ascribed to *Liopleurodon ferox*. This is the first recorded occurrence of a substantially complete, three-dimensionally preserved exoccipital-opisthotic attributable to *Liopleurodon*.

5.b. The size of the animal

The size of the cranium from which CAMSM J.27424 was derived can be estimated by comparison with NHM R2680. The isolated cranium of NHM R2680 has a snout to occipital condyle length of 1120 mm (Andrews, 1913, p. 21) and a paroccipital length of 150 mm (Andrews, 1897, p. 178). CAMSM J.27424 has a paroccipital process length of 165 mm. Assuming a 1:1 growth ratio between the cranium and paroccipital process beyond the 1.12 m cranial length of NHM R2680, the length of skull from which CAMSM J.27424 came can be estimated at approximately 1.23 m. This length estimate is slightly shorter than an 'old adult' (*sensu* Brown, 1981) individual of *Liopleurodon ferox* (NHM R3536), estimated at 1265 mm from snout tip to occipital condyle (Andrews, 1913, p. 22).

The overall length of the animal from which CAMSM J.27424 came can be estimated by comparison to a skeleton of *Liopleurodon ferox* (GPIT 1754/2). GPIT 1754/2 has a skull:total body length ratio of approximately 1:5.19 (skull length 0.94 m, overall body length including skull 4.88 m). This would indicate a calculated overall body length for the CAMSM J.27424 animal of approximately 6.39 metres.

5.c. Developmental stage

A number of features of CAMSM J.27424 give an indication of the ontogenetic stage of the animal from which this element came. The exoccipital and opisthotic are fused, but this occurs early in the onto-

geny of the Callovian Sauropterygia (Maisch, 1998). However, there is no indication of fusion between the exoccipital-opisthotic and the supraoccipital or basioccipital elements of the braincase. In fully adult Callovian pliosaurs, it is common for remnants of the exoccipital-opisthotic to be firmly sutured to the basioccipital (L. F. Noè, unpub. Ph.D. thesis, Univ. Derby, 2001), but the ventral surface of CAMSM J.27424 is entire and free of attached or detached bone. This precludes the individual from being an 'old adult'. However, the exoccipital-opisthotic is fully formed, with no indication of a substantial cartilaginous component. The size of CAMSM J.27424 compared to 'old adult' (*sensu* Brown, 1981) individual of *Liopleurodon ferox* (NHM R3536) also suggests CAMSM J.27424 was relatively mature. Thus, from the available evidence, the animal from which the CAMSM J.27424 was derived is inferred to have been an 'adult' individual (*sensu* Brown, 1981) at the time of death.

6. Conclusions

CAMSM J.27424 is an isolated left exoccipital-opisthotic from the braincase of a Callovian pliosaur. This exoccipital-opisthotic was recovered from the Peterborough Member or bottom of the Stewartby Member of the Oxford Clay Formation, and is attributed to *Liopleurodon ferox*. CAMSM J.27424 is interpreted as having come from an 'adult' individual (*sensu* Brown, 1981) of *Liopleurodon* with a cranial length of approximately 1.23 metres and an estimated overall body length of approximately 6.39 metres.

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