



CRANIAL ANATOMY, TAXONOMIC IMPLICATIONS AND PALAEOPATHOLOGY OF AN UPPER JURASSIC PLIOSAUR (REPTILIA: SAUROPTERYGIA) FROM WESTBURY, WILTSHIRE, UK

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Abstract: Complete skulls of giant marine reptiles of the Late Jurassic are rare, and so the discovery of the 1.8-m-long skull of a pliosaur from the Kimmeridge Clay Formation (Kimmeridgian) of Westbury, Wiltshire, UK, is an important find. The specimen shows most of the cranial and mandibular anatomy, as well as a series of pathological conditions. It was previously referred to *Pliosaurus brachyspondylus*, but it can be referred reliably only to the genus *Pliosaurus*, because species within the genus are currently in need of review. The new specimen, together with another from the same locality, also referred to *P. brachyspondylus*, will be crucial in that systematic revision, and it is likely that the genus *Pliosaurus* will be found to include several

genera. The two Westbury *Pliosaurus* specimens share many features, including the form of the teeth, but marked differences in the snout and parietal crest suggest sexual dimorphism; the present specimen is probably female. The large size of the animal, the extent of sutural fusion and the pathologies suggest this is an ageing individual. An erosive arthrotic condition of the articular glenoids led to prolonged jaw misalignment, generating a suite of associated bone and dental pathologies. Further damage to the jaw joint may have been the cause of death.

Key words: Plesiosauria, Pliosauroida, Pliosauridae, *Pliosaurus*, Kimmeridge Clay, Upper Jurassic, palaeopathology.

PLIOSAURUS is an enigmatic, advanced sauropterygian, first described almost two centuries ago (Owen 1841), but which remains poorly understood. *Pliosaurus* is the basis of higher taxonomic groupings (Superfamily Pliosauroida; Family Pliosauridae), and yet its holotype lacks a modern redescription. This study describes a remarkable new specimen, a putative member of the genus *Pliosaurus* (BRSMG Cd6172) recovered from the Kimmeridge Clay at the Lafarge cement works, Wiltshire, compares it with a previously described specimen from the same locality (BRSMG Cc332) referred to *P. brachyspondylus*, and analyses and interprets a series of pathologies in the specimen.

The history of taxonomic relationships within the Plesiosauria and especially the Pliosauroida is long and complicated (reviewed by Tarlo 1960; Brown 1981; Noë 2001; Ketchum and Benson 2010). Since the time of Owen (1841), the position of pliosauromorphs, plesiosaurs with large canine teeth, large heads and short necks, within Plesiosauria, has been problematic. Williston (1907) was

one of the first to suggest that the short pliosauromorph neck might have evolved several times, an idea also discussed by other authors (White 1940; Bakker 1993; Carpenter 1997). Pliosauromorph polyphyly was subsequently recovered in some phylogenetic analyses (Bardet and Godfroit 1998; Druckenmiller 1999; O'Keefe 2001, 2004), but pliosauromorphs formed a clade in others (Druckenmiller and Russell 2008; Smith and Dyke 2008). For example, O'Keefe (2001, 2004) found that Pliosauroida contained only Pliosauridae and Rhomaleosauridae, whereas another short-necked clade, Polycotyliidae, was included in Plesiosauroida. Druckenmiller and Russell (2008), on the other hand, recovered the clade Pliosauroida as traditionally defined and a new group, Leptocleidia, and they found that O'Keefe's (2004) Rhomaleosauridae was not a clade, but rather *Rhomaleosaurus megacephalus*, *R. victor* and *Macroplata tenuiceps* formed three successive basal taxa within Pliosauroida. Finally, Ketchum and Benson (2010) found that the 'pliosauromorph' taxa Leptocleididae and Polycotyliidae were

sister taxa within Plesiosauroidea, while Rhomaleosauridae was a clade within Pliosauroidae, as a sister group to Pliosauridae.

These contrasting hypotheses demonstrate deep uncertainty concerning the interrelationships of major clades within Plesiosauria. The pliosaurian body plan includes not only a large head and short neck, but also relatively long coracoids and ischia, and low-aspect-ratio limbs (O'Keefe 2002), so multiple origins of the pliosauromorph bauplan would imply striking convergences (O'Keefe and Carrano 2005). A full cladistic analysis of Pliosauroidae is in preparation (M. Gómez-Pérez and L. F. Noè, pers. comm. 2011). In this study, we contribute to the systematic revision of Pliosauroidae, as well as to understanding of pliosaurian palaeobiology, by: (1) providing a description of the cranium and mandible of an Upper Jurassic pliosaur (BRSMG Cd6172) from Westbury in Wiltshire; (2) comparing BRSMG Cd6172 with a previously described pliosaur, BRSMG Cc332 (Taylor and Cruickshank 1993), from the same locality; (3) questioning the original criteria used to classify BRSMG Cc332 as *Pliosaurus brachyspondylus*; and (4) describing and interpreting a set of pathologies in BRSMG Cd6172, not previously recognised in a pliosauroid.

MATERIALS AND METHODS

Material. BRSMG Cd6172 was found partially disarticulated in a calcareous clay matrix, with a thick to thin indurated calcitic layer on bone surfaces. Both dorsal and ventral surfaces were also variably encrusted with invertebrate epibionts. On preparation, the mineralised bone surfaces were pale or dark brown and variably crushed. The cranium and mandible were preserved as complete elements, while postcranial elements were mostly extracted from nodules. Preparation of the material has continued since 1994, and the following elements have been exposed: cranium, mandible, ribs (seven large elements and numerous fragments), vertebrae (at least 17 complete) some with associated neural processes, propodials, epipodials, paddle and phalangeal elements, gastralia, part of the right scapula, part of the left coracoid, part of the left scapula and possible pelvic elements.

Locality and horizon. BRSMG Cd6172 was found in the Kimmeridge Clay of the new quarry at the Lafarge cement works, Westbury, Wiltshire, UK (NGR ST 8817 5267), on 12 May 1994 and collected by a large team in the subsequent summer. The stratigraphic section at Westbury (Fig. 1; Birkelund *et al.* 1983) shows that BRSMG Cd6172 was found 7 m below the *Crussoliceras* limestone horizon in the *eudoxus* biozone E4, the fourth of five biozones comprising the lower Kimmeridgian substage. BRSMG Cc332 (Taylor

and Cruickshank 1993) was discovered in the old quarry on 2 July 1980, 1 m below the *Crussoliceras* limestone horizon, in *eudoxus* biozone E5. More details of the locality, stratigraphy, discovery and excavation of the Westbury pliosaurs are given by Taylor and Cruickshank (1993), Taylor *et al.* (1995), Grange *et al.* (1996) and Sassoon *et al.* (2010).

Methods. Preparation of the material followed conventional manual mechanical techniques. Loose limestone and shell-bed matrix was removed using a scalpel, while more stubborn encrustations were removed with a compressed air-driven HD-type pneumatic engraving chisel (Ken Mannion Fossils, Barton, Lincolnshire) or with a stream of aluminium oxide abrasive powder (Powder No. 1, 29 microns; Production Equipment Sales, Uckfield, East Sussex, UK) from an Airbrasive jet tool (model AJ-1; Texas Airsonics Inc., Corpus Christi, TX, USA). Following initial preparation work, the skull and other bony elements were consolidated and reassembled. A solution of Paraloid B72 dissolved in acetone was used for both surface consolidation (10 per cent w.b.v. Paraloid in acetone) and as an adhesive (60 per cent w.b.v. Paraloid in acetone). Further details of the preparation and conservation of BRSMG Cd6172 are outlined by Sassoon *et al.* (2010).

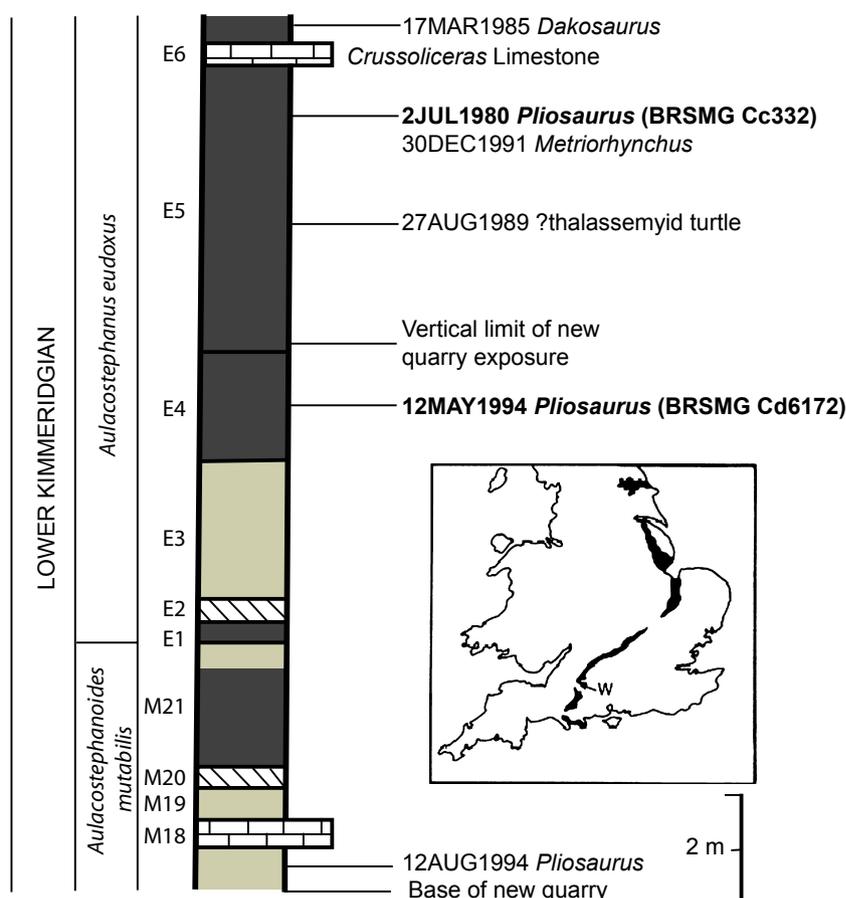
Cranial reconstructions of BRSMG Cd6172 are presented in three standard views: dorsal, ventral and left lateral (Fig. 2A–C). As the mandible is substantially complete, only interpretive drawings in dorsal and ventral views are presented. Diagrammatic reconstructions of cranium and mandible were produced by scaling photographs and referring to measured proportions, while making allowance for crushing. The positions and orientations of the teeth were inferred from the size and orientation of the functional alveoli.

X-radiographs of pathological elements were obtained using a Dragon mobile DR (digital radiography) system, with a 4-kW generator and a Canon CXDI-50G 400 speed portable DR detector. Specimens were placed on the detector, at 720 mm from the X-ray generator, and photographed.

Institutional abbreviations. BHN, Musée de Boulogne-sur-Mer (collections held now at Muséum d'Histoire Naturelle, Lille); BRSMG, Geology Collections, Bristol City Museum and Art Gallery; CAMSM, Sedgwick Museum of Earth Sciences; MNHN, Muséum National d'Histoire Naturelle de Paris; NHMUK, Palaeontology Department, Natural History Museum, London; OXFUM, Oxford University Museum of Natural History; PETMG, Peterborough City Museum and Art Gallery.

Anatomical abbreviations used in figures and tables. ?, probable or questionable element; –, alveolus absent; a, angular; acr, anterior transverse crest; adg, anteriorly directed grooves; addfo, adductor fossa; aiv, anterior interpterygoid vacuity complex; afgf, anterior flange under glenoids; alv, alveolus; ant, anterior;

FIG. 1. Stratigraphy of the Lower Kimmeridge Clay, Lafarge cement works, Westbury, Wiltshire, UK. M18–M21, *Aulacostephanoides mutabilis* biozones; and E1–E6, *Aulacostephanus eudoxus* biozones. Horizons of the two Westbury pliosaurs (BRSMG Cd6172 and BRSMG Cc332) are shown in bold, and other marine reptiles from the section are also indicated. Ornament represents major rock types: dark grey, oil shale; light grey, laminated shale; cross-hatched, shelly horizon; brick pattern, limestone. The sketch map shows the distribution of Kimmeridgian rocks across England, and ‘W’ marks Westbury, site of discovery of the pliosaur (modified from Birkelund *et al.* 1983; for further details see Sassoon *et al.* 2010).



apt, anterior ramus of the pterygoid; ar, articular; arg, articular glenoid; bo, basioccipital; b, attached bone; boc, base of crown; brk, break; C, caniniform tooth; c, coronoid; car, carina; cav, cavity; ce, coronoid eminence; cons, constriction; cr, crown; d, dentary; dam, damage; dav, dentary alveolar channel; dc, dentary constriction; dep, depression; dia, diastema; dmo, depressions from misaligned overbite; drt, dentary raised triangle; e, estimated length; ec, ectopterygoid; emb, embayment between tooth sockets; eo, exoccipital-opisthotic; ep, epipterygoid; er, enamel ridge; f, frontal; fa, functional alveolus (with number); fac, facet; for, foramen or foramina; falv, alveolus filled with bone; fra, fracture; frag, tooth fragmented; ft, functional tooth (with number); H, hooked posterior tooth; hsd, heart-shaped depression; in, internal naris; ips, inter-parietal suture; j, jugal; L, left; l, lacrimal; lat exp, lateral expansion; le, lesion; lfa, left functional alveolus (with number); lfgf, lateral flange under glenoids; lft, left functional tooth (with number); lpt, lateral ramus of the pterygoid; lra, left replacement alveolus; lrt, left replacement tooth (with number); max, maximum; mf, Meckel's foramen; mfgf, medial flange under glenoids; min, minimum; mis, missing; ms, mandibular symphysis; mus, muscle scars; mx, maxilla; mxa, maxilla alveolar channel; n, nasal; obs, alveolus obscured; orb, orbit; p, parietal; path, pathology; pc, parietal crest; pcp, parietal crest peak; pcr, posterior transverse crest; pf, parietal foramen; phal, phalangeal; piv, posterior interpterygoid vacuity; pl, palatine; plf, palatine foramen; plp,

pulp cavity; pma, premaxilla alveolar channel; pmfp, premaxillary facial process; pmx, premaxilla; po, postorbital; pof, post-frontal; post, posterior; ppt, posterior ramus of the pterygoid; prf, prefrontal; ps, parasphenoid; pt, pterygoid; ptf, pterygoid flange; q, quadrate; qcl, lateral quadrate condyle; qcm, medial quadrate condyle; qpt, quadrate ramus of the pterygoid; qs, quadrate sulcus; R, right; r, roughened area; ra, replacement alveolus (with number); rap, retroarticular process; rdg, ridge; rfa, right functional alveolus (with number); rft, right functional tooth (with number); rng, enamel ring; rra, right replacement alveolus (with number); rrt, right replacement tooth (with number); rt, base ('root') of tooth; sa, surangular; saf, surangular facet; sed, sediment infill; sf, smooth face of tooth; sof, suborbital fenestra; sp, splenial; sq, squamosal; sut, suture; tf, temporal fenestra; v, vomer; vb, vomerine boss; vert, vertebra; vk, ventral keel; X, tooth absent.

SYSTEMATIC PALAEOLOGY

Class REPTILIA Laurenti, 1768

Superorder SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Suborder NEOPLESIOSAURIA Ketchum and Benson, 2010

Superfamily PLIOSAUROIDEA (Seeley, 1874) Welles, 1943

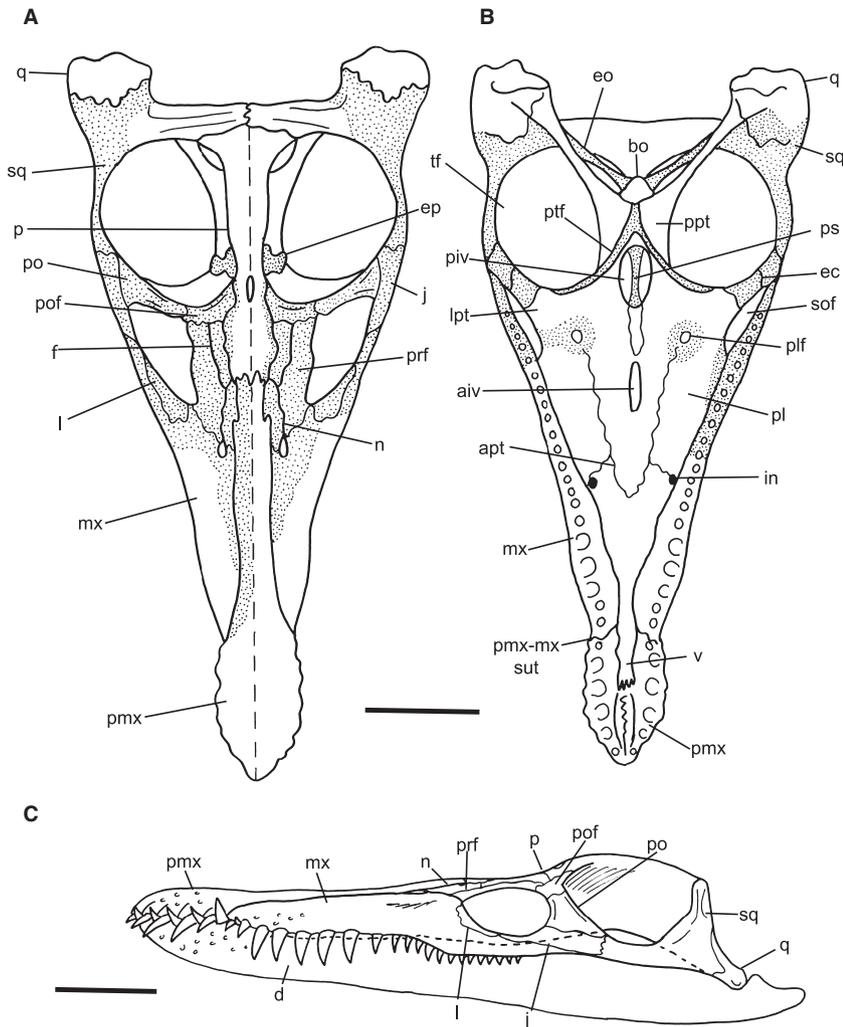


FIG. 2. Skull reconstruction of *Pliosaurus* sp. (BRSMG Cd6172), in A, dorsal; B, ventral; and C, lateral views. Areas not preserved on the specimen and wholly reconstructed in A and B are shown stippled. Scale bars represent 400 mm.

Family PLIOSAURIDAE Seeley, 1874

Genus PLIOSAURUS Owen, 1842

Type species. *Pliosaurus brachydeirus* Owen, 1841 (OXFUM J.10454).

Pliosaurus sp. indet.

Figures 2–11

Diagnosis. BRSMG Cd6172 is a pliosaurian plesiosaur presenting the following cranio-dental features: a large subtriangular skull, maximum length 1.8 m, with a snout bearing a rosette of six pairs of premaxillary teeth. Ratio of skull length: maximum width, 7:3. Parietal crest smooth and shallowly raised with maximum elevation of 85 mm at more than three-quarters distance along its length; ratio of total crest length: position of parietal foramen, 2.5:1. Long mandibular symphysis extending to midway between the eighth and ninth pair of functional

alveoli; anterior tip of dentary dips slightly; dentary bears 24 (left) and 27 (right) functional alveoli. Functional alveoli regularly spaced. Teeth trihedral in cross-section with two finely crenulated carinae dividing the crown into a smooth, unornamented outer portion and a peaked, two-faced inner axial portion; the two crown faces forming the peaked axial portion ornamented with prismatic ridges.

Remarks. The focus of this analysis is a description of the cranio-dental material from BRSMG Cd6172, the ‘second Westbury pliosaur’. However, comparison is made with BRSMG Cc332, the ‘first Westbury pliosaur’, because the two specimens were found at the same locality, although at slightly different stratigraphic horizons (Fig. 1). Although no formal description of BRSMG Cd6172 exists to date, the specimen has been referred to as ‘in all likelihood’ a specimen of *Pliosaurus brachyspondylus* on the basis of the ‘elongated mandibular symphysis’ (Grange *et al.* 1996, p. 112). Earlier, BRSMG Cc332 was also clas-

sified as *P. brachyspondylus* (Taylor and Cruickshank 1993). These taxonomic assignments were made using criteria that are considered contentious, as discussed below.

DESCRIPTION

Cranium

The skull is triangular, with a long snout expanded anteriorly into a slight rosette. The cranium is preserved dorsoventrally crushed, with a maximum height of 150 mm, excluding the separate parietal crest. The *in vivo* height of the skull is difficult to estimate, but was probably low, with the height less than the width at the quadrate condyles.

The bone surface is generally well preserved, although crushing and fusion prevent tracing of sutures in some areas. A significant proportion of the dorsal roofing elements are missing, revealing the dorsal surface of the palate for much of its length. The temporal bars are absent, but proportions of the preserved material suggest the presence of large temporal fenestrae as in other pliosaurians (Romer 1956), and a maximum width of the skull was estimated for the reconstruction (Fig. 2A–B; Table S1). Much of the suspensorium is dorsoventrally crushed, and the squamosals are folded onto the dorsal surface of the palate. The

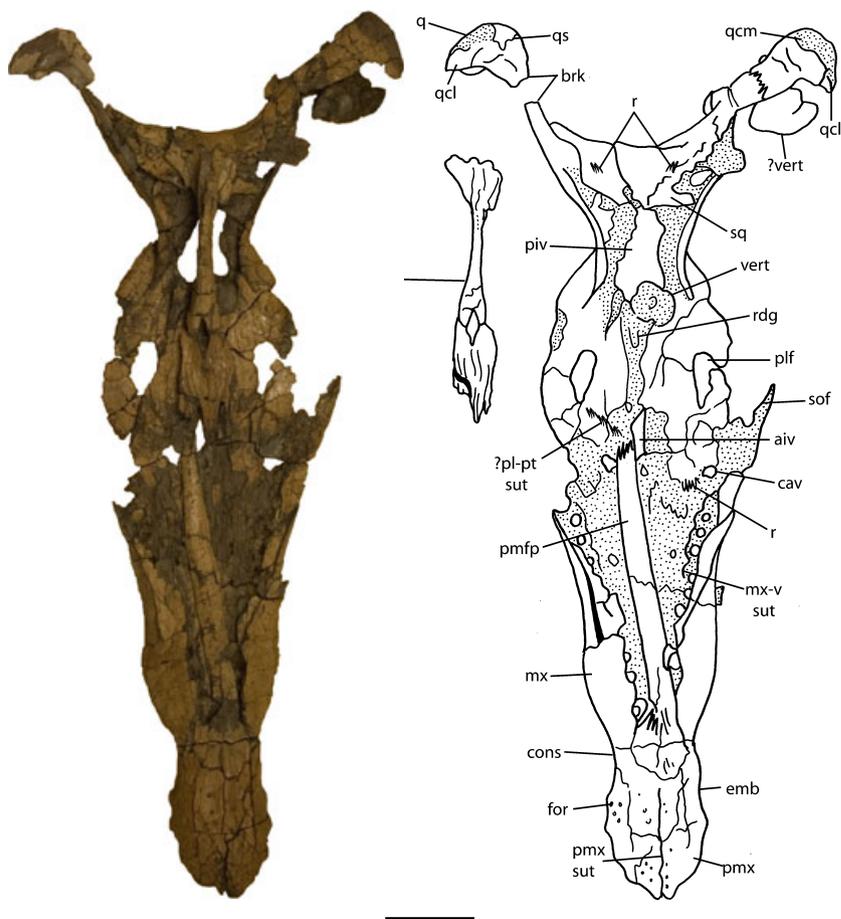
quadrate is preserved in contact with the posterior rami of the pterygoids. The braincase is almost entirely absent, but the basioccipital is preserved as a separate element.

The parietal crest was recovered, separated from the skull, broken in two. The parietals align with the heavily interdigitating premaxilla–parietal suture on the posterior margin of the premaxilla facial process. When aligned on the skull, the parietal foramen lies just behind the level of the orbits (Fig. 3).

Ventrally, the palate is better preserved than the dorsal roofing elements (Fig. 4). The palate is essentially complete, apart from the missing lateral margins beneath and beyond the orbital region. The functional alveoli are symmetrically aligned and are used as landmarks in the description below.

Premaxilla. The premaxilla is a long element forming the anterior part of the snout and dorsally extending posteromedially to approximately the level of the orbits. Anteriorly, the premaxillae join in a midline suture, expand laterally and arch convexly dorsally. Both premaxillae and maxillae are heavily pitted with foramina on their dorsal surfaces; 193 foramina are present on the premaxillae (Fig. 5A, C). Many of the large foramina are associated with grooves directed anteriorly, which were formerly channels for blood vessels or branches of the ethmoidal or olfactory (I) nerves (Sues 1987; Rieppel 1995). Pressure has separated the premaxillae along the median suture anteriorly (Fig. 5A),

FIG. 3. Photograph and interpretive drawing of the cranium of *Pliosaurus* sp. (BRSMG Cd6172), in dorsal view. Parietal crest placed to one side in the interpretive drawing to reveal posterior palate in dorsal view. Scale bar represents 200 mm.



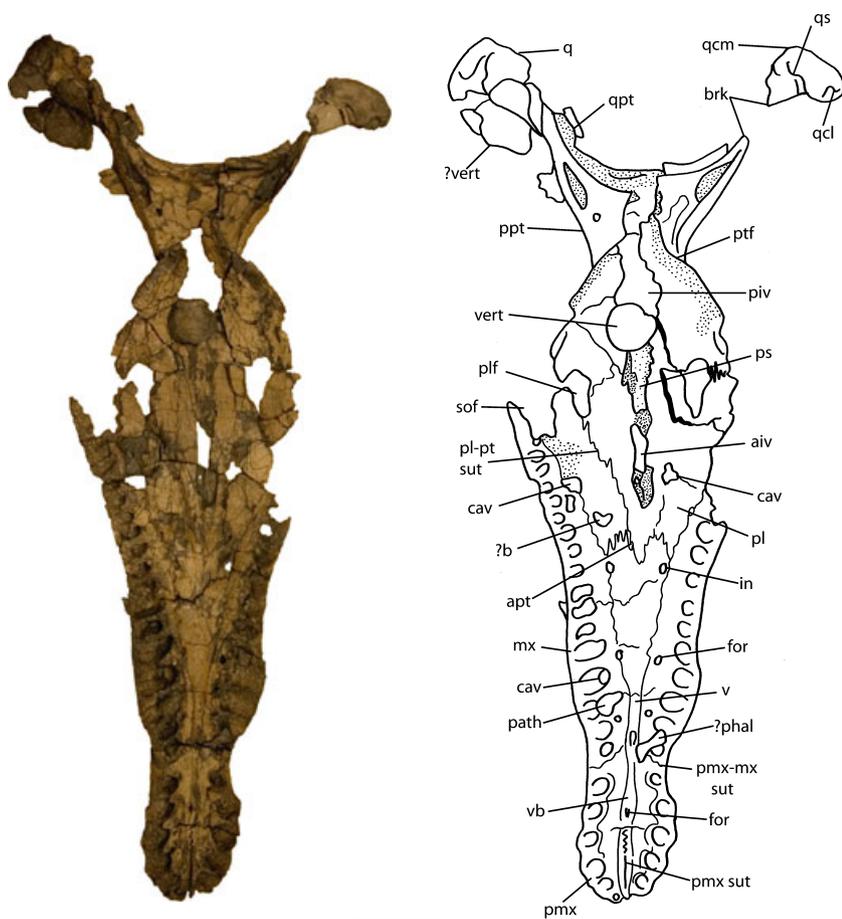


FIG. 4. Photograph and interpretive drawing of the cranium of *Pliosaurus* sp. (BRSMG Cd6172), in ventral view. Scale bar represents 200 mm.

and the dorsal surfaces of both premaxillae and maxillae bear gentle raised bumps caused by crushing of the intermediate areas into the underlying alveoli. The expanded snout flares laterally, expanding around the functional alveoli to produce a sinuous margin with embayments between the alveoli (Fig. 5) that accommodated teeth from the lower jaw when the jaws were closed. A mediolateral constriction occurs at the site of the premaxilla–maxilla suture. Posteriorly, the left premaxilla forms a narrow, dorsally projecting premaxillary facial process, crushed onto the palate and displaced to the right; only a small portion of the right premaxillary facial process is preserved, displaced to cover the left premaxilla anteriorly (Fig. 3).

On the palatal surface, the premaxilla bears the anterior functional alveoli and forms the anterior margin of a diastema, completed posteriorly by the maxilla. The premaxilla contacts the maxilla midway along the diastema in a crenulated suture, which is diagonally oriented at a shallow angle. Laterally, the premaxilla overlies the maxilla with a slight marginal notch (Fig. 5C).

Maxilla. The maxilla is a large elongate element forming the lateral margins of the snout. On the dorsal surface, the maxilla contacts the premaxilla anteriorly and the base of the premaxilla facial processes medially. Maxilla contacts on the dorsal surface vary among pliosaurian species (Ketchum and Benson 2010) but

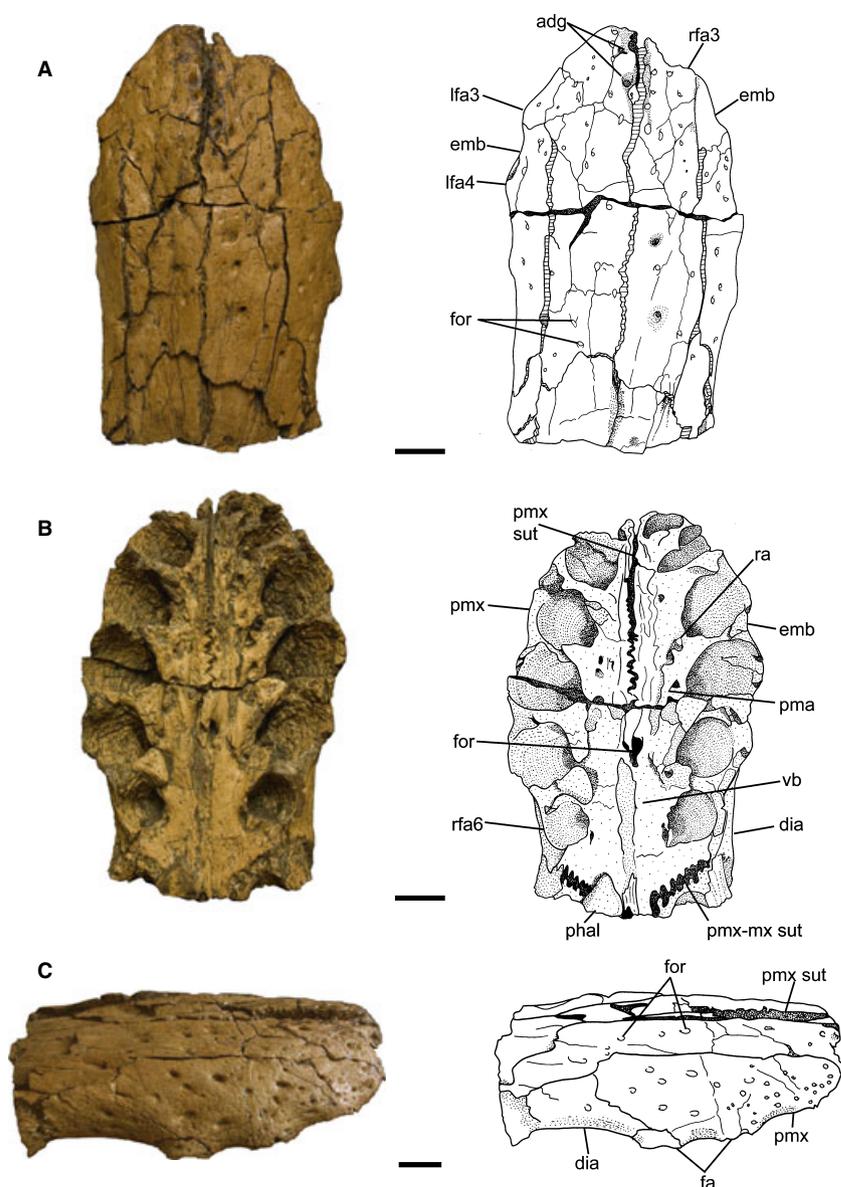
are not preserved in BRSMG Cd6172. Both maxillae are fragmented medially (Fig. 6A) and narrow posteriorly (Fig. 3).

On the ventral surface, the maxillae bear the posterior functional alveoli and anteromedially converge to almost meet along the ventral midline (Fig. 4). Medially, the maxillae meet and overlie the vomers. Posteriorly, the maxilla contacts the palatine in a butt-jointed suture, which runs parallel to the tooth row. The maxillary tooth rows are both incomplete posteriorly and terminate ventrolaterally in elongate trailing edges, with the terminal functional alveoli missing.

Parietal. The parietal is an elongate bone forming the cranial midline, posterior to the premaxillary facial processes and extending to the cranial vertex. The tightly conjoined parietals expand anteriorly to contact the premaxillary facial processes and then narrow medially, before widening again posteriorly. The posterior contact with the squamosal is obscured by crushing.

The conjoined parietals form a well-preserved parietal ('sagittal' of Andrews 1913) crest medially. The median parietal suture is visible anterior to the parietal ('pineal' of Andrews 1897) foramen, but posteriorly, the suture is completely fused (Fig. 7A). Posterior to the parietal foramen, the parietal crest rises at a shallow angle to a maximum height of 85 mm three-quarters along its length and then descends smoothly (Fig. 7C). No embayments are present along the length of the crest, and there are

FIG. 5. Photographs and interpretive drawings of the anterior snout of *Pliosaurus* sp. (BRSMG Cd6172), in A, dorsal; B, ventral; and C, oblique right lateral views. Scale bars represent 50 mm.



no signs of a roughened parietal knob, as observed in both *P. brachyspondylus* (Taylor and Cruickshank 1993) and *Simolestes* (Noè 2001). However, slight roughening occurs 40 mm behind the parietal foramen, and again at the parietal peak, 270 mm behind the foramen.

Vomer. The conjoined vomers form stout bars supporting the snout ventrally. The vomers emerge anteromedially from between the premaxillae, level with the fifth functional alveoli, and extend to slightly beyond the internal nares posteriorly (Figs 4 and 5B). The vomers are narrow anteriorly, their emergence from beneath the premaxillae marked by a medially placed foramen (Fig. 5B). Immediately behind the foramen, the vomers form a vomerine boss, beyond which the midline suture runs anteroposteriorly in a straight line, but behind the seventh functional alveolus, the vomers fuse. At the premaxilla–maxilla junction, the vomers form a slight depression, and behind the tenth

maxillary functional alveolus, the vomers expand (Fig. 6B). At the level of functional alveoli 9–11, the vomers flatten to contact the palatines and pterygoids posteriorly.

The vomer–palatine suture is heavily crenulated, partly fused and incompletely visible (Fig. 4). The suture trends posterolaterally but disappears into an undefined roughened area medially. The pterygoids meet medially and overlie the back of the vomers as a bony projection; contact between vomers and pterygoids has been reported in *Simolestes* (Noè 2001), while in other genera (e.g. *Liopleurodon*), there is probably no vomer–pterygoid contact (Andrews 1897, 1913; Linder 1913). On the dorsal surface of the palate, the sutures are fused into unclear roughened areas and partly obscured by the premaxillary facial process (Fig. 3).

Palatine. Each palatine is a long strip of bone running from the vomers anteriorly, contacting the maxilla laterally in a butt-jointed suture, meeting the pterygoid dorsomedially and

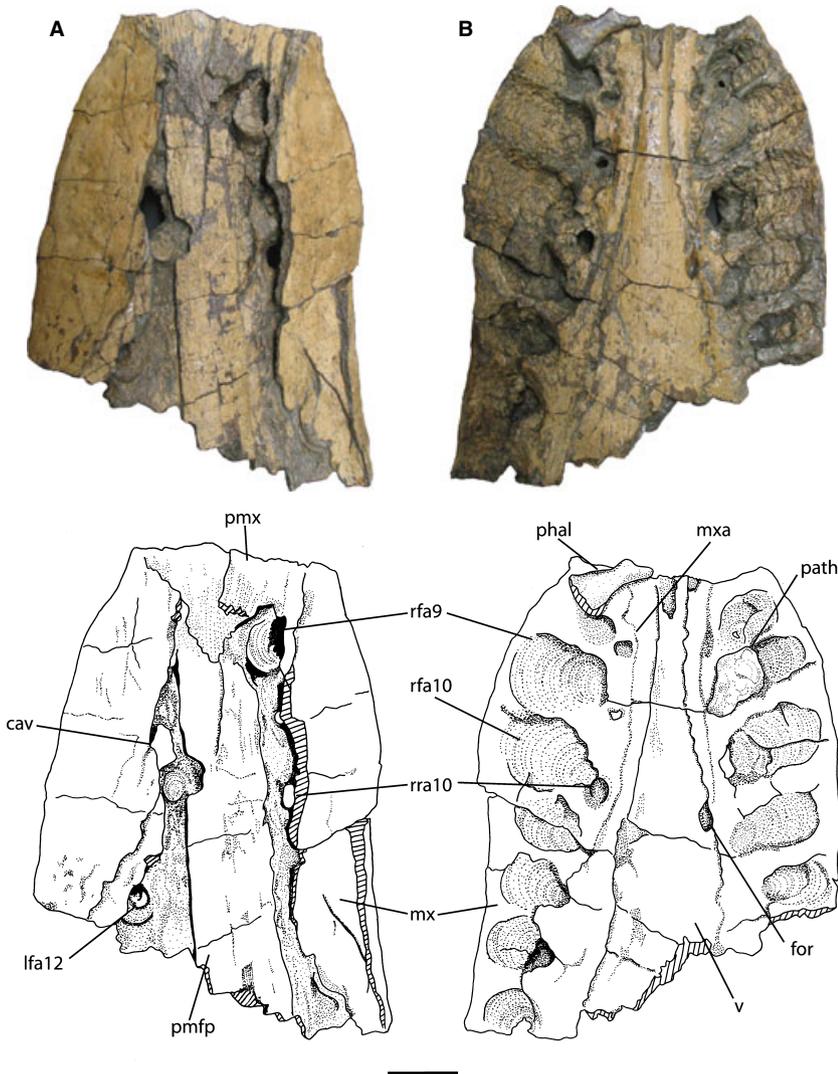


FIG. 6. Photographs and interpretive drawings of the rostrum between functional alveoli 8 and 14 of *Pliosaurus* sp. (BRSMG Cd6172), in A, dorsal; and B, ventral views. Depth of penetration of right functional alveolus nine (rfa9) is visible on the dorsal surface. Scale bar represents 50 mm.

probably the (unpreserved) ectopterygoid posteriorly. A section of the palatine–pterygoid suture is visible on the left of the palate (Fig. 4), although the equivalent suture on the right is unclear. Palatine foramina are partially preserved along the palatine–pterygoid suture; these are elongate openings, unevenly cracked along much of their margins, making their original size difficult to determine, although they were probably quite small. Elements lateral to the palatine foramina are mostly missing. Suborbital fenestrae in pliosaurians normally lie lateral to the palatine foramina (Romer 1956), and a small portion of the medial margin of the left suborbital fenestra may be preserved as a short section of smooth bone.

Level with right functional alveolus 17, a bone (possibly a small paddle element) 45 mm across and with a maximum width of 20 mm at its centre, is welded into the surface of the left palatine (?b, Fig. 4). At an equivalent position on the dorsal surface, there is a raised ridge, resulting from *post-mortem* plastic deformation of the bone.

Pterygoid. The pterygoid is a large, flat, triradiate element contacting the vomer anteriorly and extending to the jaw articula-

tion posteriorly. It consists of anterior, lateral, posterior and quadrate rami. The pterygoids have extensive medial contact for much of their length, and the interpterygoid suture is fused and mostly indistinguishable. The lateral rami normally extend to the cheek region (Romer 1956), but this contact is not preserved.

Medially, the anterior pterygoid rami part to form the anterior interpterygoid vacuity (Fig. 4). The anterior interpterygoid vacuity is preserved as a large opening with a smooth edge on the left, but bounded by broken bone on the right. Noè (2001) observed in *Liopleurodon* that the anterior interpterygoid vacuity is a collection of foramina rather than a single opening and the number of foramina is variable between individuals. In BRSMG Cd6172, the size of the opening in life cannot be estimated, but it is possible that the smooth margin marks the edge of a single anterior interpterygoid vacuity.

Each lateral pterygoid ramus bounds the anterior margin of the subtemporal fenestra and normally contacts the ectopterygoid. The thickened posterior margins of the lateral pterygoid rami form a ventral pterygoid flange, a low elevation on the ventral surface of each lateral ramus (Fig. 4). Each flange curves posteromedially, with the two flanges converging, and probably

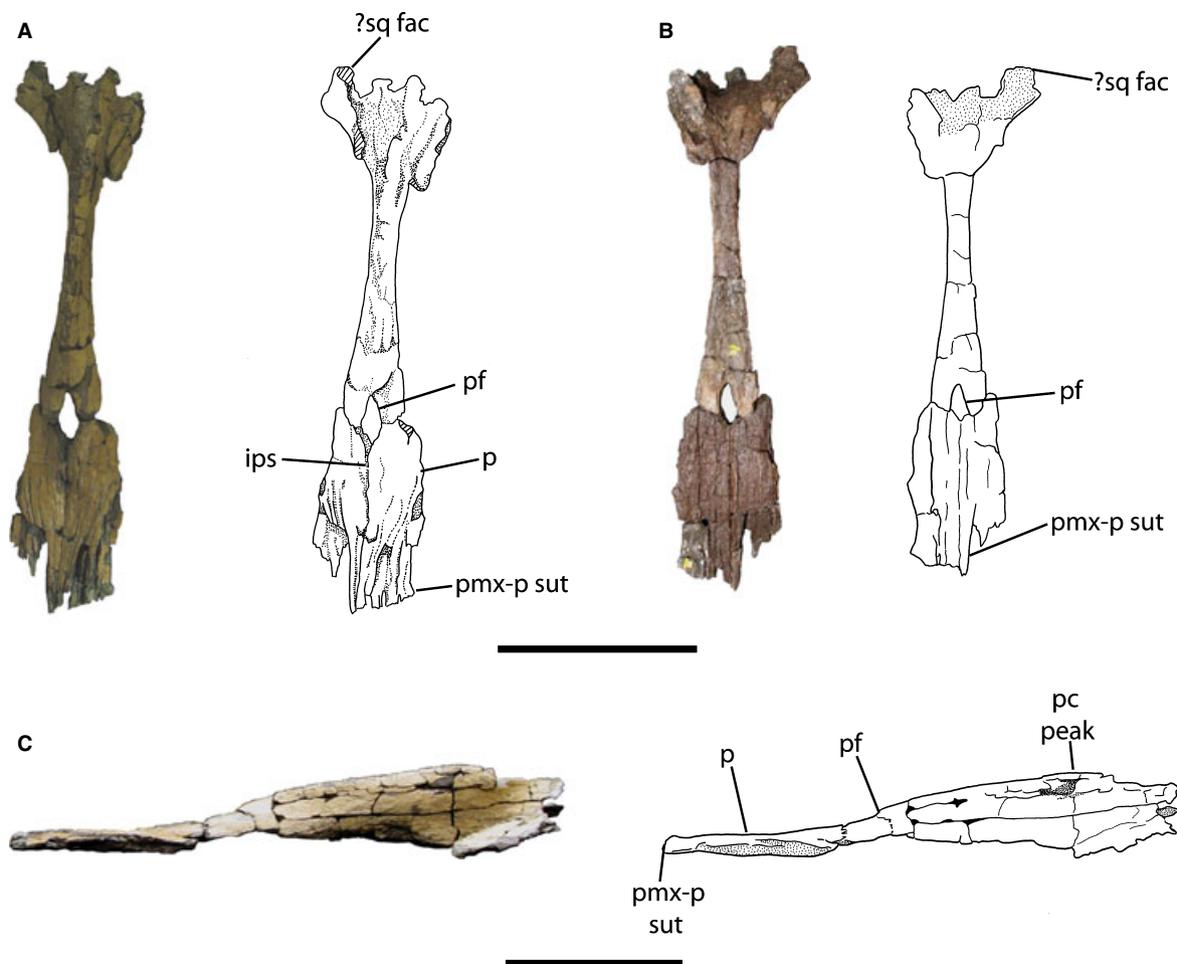


FIG. 7. Photographs and interpretive drawings of the parietal crest of *Pliosaurus* sp. (BRSMG Cd6172), in A, dorsal; B, ventral; and C, left lateral views. Scale bars represent 200 mm.

meeting posteriorly along the midline as a ridge (also seen in *Liopleurodon*; Andrews 1897). However, this convergence cannot be observed as the pterygoid behind the posterior interpterygoid vacuity is not fully preserved (compare Fig. 4 with reconstruction Fig. 2B). In some pliosaur genera, for example, *Simolestes*, the ventral pterygoid flanges do not coalesce (Noè 2001). The construction of the ventral pterygoid flange is controversial and varies among plesiosaurian species (Carpenter 1997; Ketchum and Benson 2010). Storrs (1997) and O'Keefe (2001) stated that the flange anteriorly was composed mostly of the ectopterygoid. However, Druckenmiller (2002a) showed that the pterygoid flange was formed by both the pterygoid and ectopterygoid. In BRSMG Cd6172, the ectopterygoid is not preserved but evidently lies far laterally, so the pterygoids probably contributed to most of the ventral pterygoid flange.

Medially, the lateral pterygoid rami open out to form the lateral edges of the posterior interpterygoid vacuity (Fig. 4). The lateral border of the vacuity is broken and poorly preserved. In other pliosaurian specimens, the posterior interpterygoid vacuity is divided by the parasphenoid (Romer 1956), but this opening is not preserved in BRSMG Cd6172. The posterior rami of the pterygoids meet again posteriorly, behind the posterior inter-

pterygoid vacuity. The posterior rami lie beneath the braincase (Romer 1956), but of this only the basioccipital was recovered, separated from the skull. On the ventral surface, the posterior rami of the pterygoids diverge to form the quadrate rami, which project posterolaterally as two massive bones, deeper than wide, and thicker ventrally than dorsally. The left pterygoid ramus contacts the quadrate posterolaterally, but the suture between the two elements cannot be distinguished; the contact between the right pterygoid ramus and quadrate is incompletely preserved (Figs 3 and 4). On both sides, the skull is distorted, flattening the original three-dimensional arrangement of the pterygoid–quadrate contacts.

Parasphenoid. The parasphenoid is a small, elongate bone normally extending from the braincase along the midline of the cranium, but the section dividing the posterior interpterygoid vacuities is not preserved. Anteriorly, the parasphenoid extends towards the anterior interpterygoid vacuity. On the dorsal surface of the palate, the parasphenoid forms a thick, roughened ridge running anteroposteriorly between the interpterygoid vacuities (Fig. 3). On the palatal surface, the parasphenoid forms a strong interdigitating suture with the pterygoids laterally.

Posteriorly, it is partly obscured by a vertebra (Fig. 4) closely apposed to the surface of the pterygoid anterior to the posterior interpterygoid vacuity.

Suspensorium. The suspensorium, consisting of the squamosals and quadrates in life, would have formed a massive posterior arch to the skull (Romer 1956; Fig. 2C). However, as a result of crushing and missing elements, its height and curvature can only be estimated. The jaw articulations project laterally beyond the sides of the skull, and the suspensorium has an overall triradiate shape.

The squamosals have broken and folded forward, and the left squamosal has sheared laterally to the right, so the medial squamosal suture is no longer visible. Two symmetrical muscle scars (Fig. 3) are present on the remains of the two squamosals and probably represent the dorsal connections of the *M. depressor mandibulae* (Taylor 1992). The anterior squamosal rami, which contact the jugal to form the temporal bars, are not preserved.

On the posterior cranial surface, the squamosal rami normally contact the quadrates posteroventrally in a three-way junction with the quadrate rami of the pterygoids (Andrews 1897). However, the squamosal elements are broken, and the quadrates only contact the pterygoid rami as preserved. The remains of a squamosal–quadrate suture are visible on the left as a large crenulated suture.

The quadrates are stout bones forming the articulations with the lower jaw ventrally; both are well preserved. The quadrate is mediolaterally convex in posterior view, with the curvature continuing onto the anterior surface as a concavity. Anteriorly, a deeply incised quadrate sulcus (Fig. 4) lies immediately above the quadrate condyle, and this may represent the insertion of cartilage sheathing the mandibular joint. The quadrate is thickest at the quadrate condyle, which is divided by an oblique, antero-posteriorly trending depression. This creates the classic plesiosaurian double condyle on the ventral surface, with a shallow lateral condyle and a deeper medial condyle (Romer 1956; Fig. 3).

Mandible

The mandible is essentially complete although, in common with many other specimens, the prearticulars are missing (Romer 1956). The mandible retains excellently preserved details of tooth replacement and pathologies including (1) an arthrotic condition of the jaw articulation, not previously described in pliosaurids, (2) evidence of a prolonged dental malocclusion associated with the articular pathologies and (3) a transverse fracture across the right articular.

The mandible is crushed dorsoventrally, and the two rami are differentially preserved (Table S1B), although the heights of the rami vary between genera (Godefroit 1994; Noè 2001). The right ramus is crushed and foreshortened, but retains its original orientation. The left ramus maintains its original height but has been twisted to the left, so the medial surface faces dorsally (Fig. 8).

Anteriorly, the mandibular rami meet in a deep, akinetic symphysis, laterally expanded and on the ventral surface developed into a keel (Fig. 9B). Posterior to the symphysis, the rami divide at an acute angle. The right ramus is less crushed, becoming more vertically oriented posteriorly, especially in the region of

the coronoid eminence. Both rami turn medially at the surangular–coronoid suture, producing a wishbone shape, closely matching the ventral margins of the cranium above. The anterior lateral expansion of the dentary level with functional alveoli 4–6 and the subsequent dentary constriction level with functional alveoli 8–10 approximately correspond to the inverse of the shape of the cranial margins, which have an anterior medial constriction at the premaxilla–maxilla suture followed by a lateral expansion of the maxillae over alveoli 9–11. These features allow occlusion of the large, anterior caniniform teeth both dorsally and ventrally (Fig. 2C).

Posteriorly, each ramus terminates in an expanded region, the glenoid of the articular, which accommodates the quadrate. The articulation forms an orthal hinge joint with a double condyle. The jaw articulation is placed well back, behind the level of the occipital condyle (Fig. 2B–C).

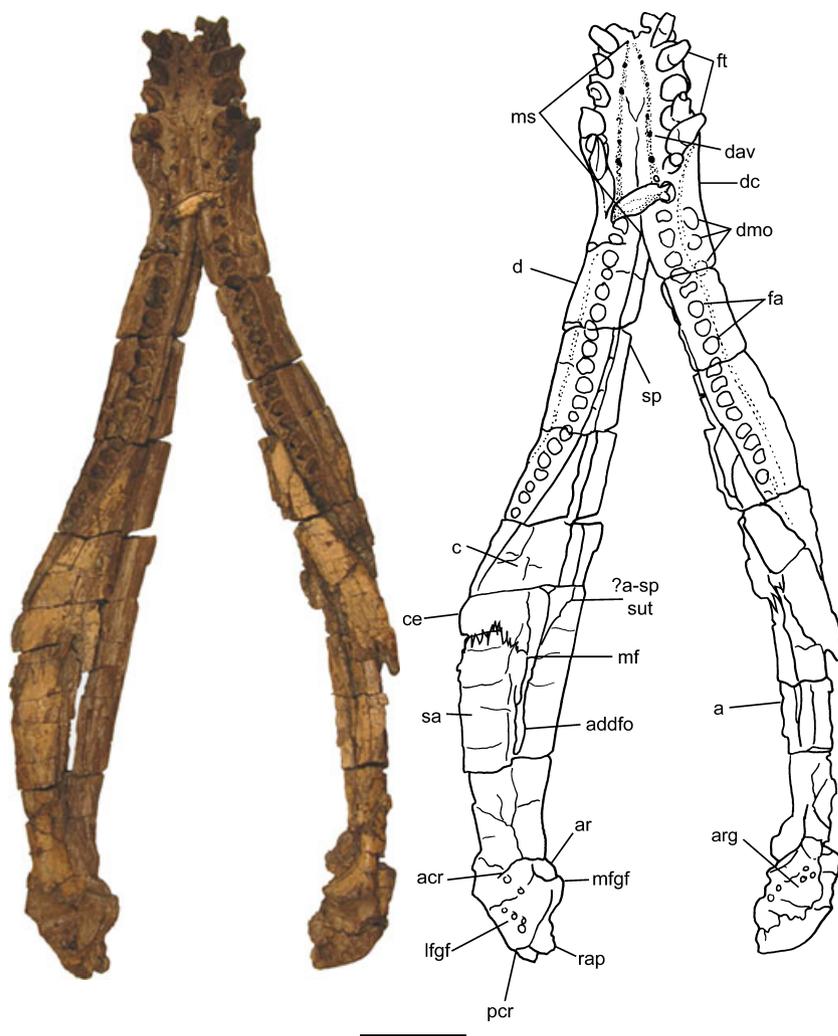
Dentary. The dentary forms approximately three-quarters of each ramus anterior to the coronoid eminence. The two dentaries suture anteromedially on the dorsal and ventral mandibular surfaces of the mandible and contact the splenials ventromedially. The dentary–splenial contact continues postero-medially but is separated by the angular posteriorly. Each dentary contacts, and is overlain by, the coronoid on the medial surface posterior to the mandibular symphysis and dorsal to the splenial. The dentary–coronoid contact extends posteriorly to the coronoid eminence. Posteriorly, the dentary contacts the surangular (Fig. 8).

As a fused unit, the dentaries comprise almost all the symphyseal region (Fig. 9A). Dorsally, the dentary suture is fused anteriorly, rising gently to the level of the third functional alveolus, after which it dips to form a shallow concavity, which then rises again at the level of the fifth alveolus to form the dentary raised triangle (Noè 2001). Behind this, the interdental suture becomes serrated and then fades beyond the seventh functional alveolus. There is a medial heart-shaped depression level with functional alveoli four and five, separating the anterior, smooth part of the symphysis from the posterior, raised and crenulated part. The smooth anterior section suggests soft tissue, a tongue, in life. Ventrally, the dentaries fuse anteriorly and the suture curves posterodorsally, beneath the splenials (Fig. 9B).

The dentaries, and hence the mandibular symphysis, divide between functional alveoli 8 and 9. The dentary alveolar channel (containing the replacement alveoli) runs dorsolaterally around each dentary, medial to the functional alveoli. These channels converge to meet and form the heart-shaped depression, then separate and continue dorsally. Beyond the level of the eighth functional alveoli, the dentary alveolar channel runs closer to the functional alveoli with the replacement alveoli almost in contact.

Medially, each dentary forms the roof and lateral surface of Meckel's canal, which exits at Meckel's foramen on the medial surface of the mandible (Fig. 8). Meckel's canal is completed by the splenial ventromedially, the coronoid medially and the angular posteroventrally; it accommodates the mandibular cartilage, the mandibular ramus of the trigeminal (V) nerve and the mandibular artery and veins (Romer 1956). The external surfaces of the dentaries are heavily ornamented with foramina (Fig. 9B),

FIG. 8. Photograph and interpretive drawing of the mandible of *Pliosaurus* sp. (BRSMG Cd6172), in dorsal view. Scale bar represents 200 mm.



frequently associated with anteriorly directed grooves. Some grooves may be continuous with Meckel's canal and hence may be branches of the trigeminal nerve and blood vessels (Noë 2001).

Coronoid. The coronoid is long, transversely compressed and slightly twisted out of position on the left ramus. The coronoid extends from close to the mandibular symphysis anteriorly to the coronoid eminence posteriorly. It overlies the dentary in a prominent suture (Fig. 8). Distinguishing sutures between the coronoid and dentary has been a problem in pliosaurids and led Fraas (1910) to describe the coronoid of *Rhomaleosaurus victor* as part of the dentary. Beneath the coronoid eminence, there is a clear three-way meeting of dentary, coronoid and surangular. Posteriorly, the coronoid deepens over Meckel's canal. At Meckel's foramen, there is a concavity forming the anterior part of the adductor fossa (Fig. 8); crushing has caused a large opening on the left ramus at the position of the adductor fossa.

Splenial. The splenial is a long, narrow bone forming the ventral surface of each mandibular ramus. The splenial overlies the

coronoid dorsally and contacts the dentary anteriorly, anterodorsally and anterolaterally. Anteroventrally, the splenials are conjoined and participate in the ventral symphyseal suture where they lie superficial to the surface of the dentaries (Fig. 9B). Sediment remains behind the mandibular symphysis, so a postsymphyseal vacuity, as reported in a Colombian pliosaur (Gómez-Pérez 2008, p. 29, fig. 2.9), cannot be ascertained. Posteriorly, the splenials are closely apposed to the medial face of the angular and continue to at least the level of the coronoid eminence (Fig. 8).

Surangular. The surangular is a stout bone exposed on the dorsal, lateral and medial surfaces of each mandibular ramus. The surangular forms most of the dorsal surface of the mandibular ramus between the coronoid eminence and glenoid fossa. The surangular contacts the dentary anterolaterally and anterodorsally, the coronoid anteromedially and anterodorsally, and the angular ventrally. Each surangular forms much of the dorsal margin of Meckel's foramen. Sutural contacts between surangular and articular are not preserved on either ramus, so it is not clear whether the surangulars contact the articulars posterolaterally and posteromedially as in *Liopleurodon* (Andrews 1913).

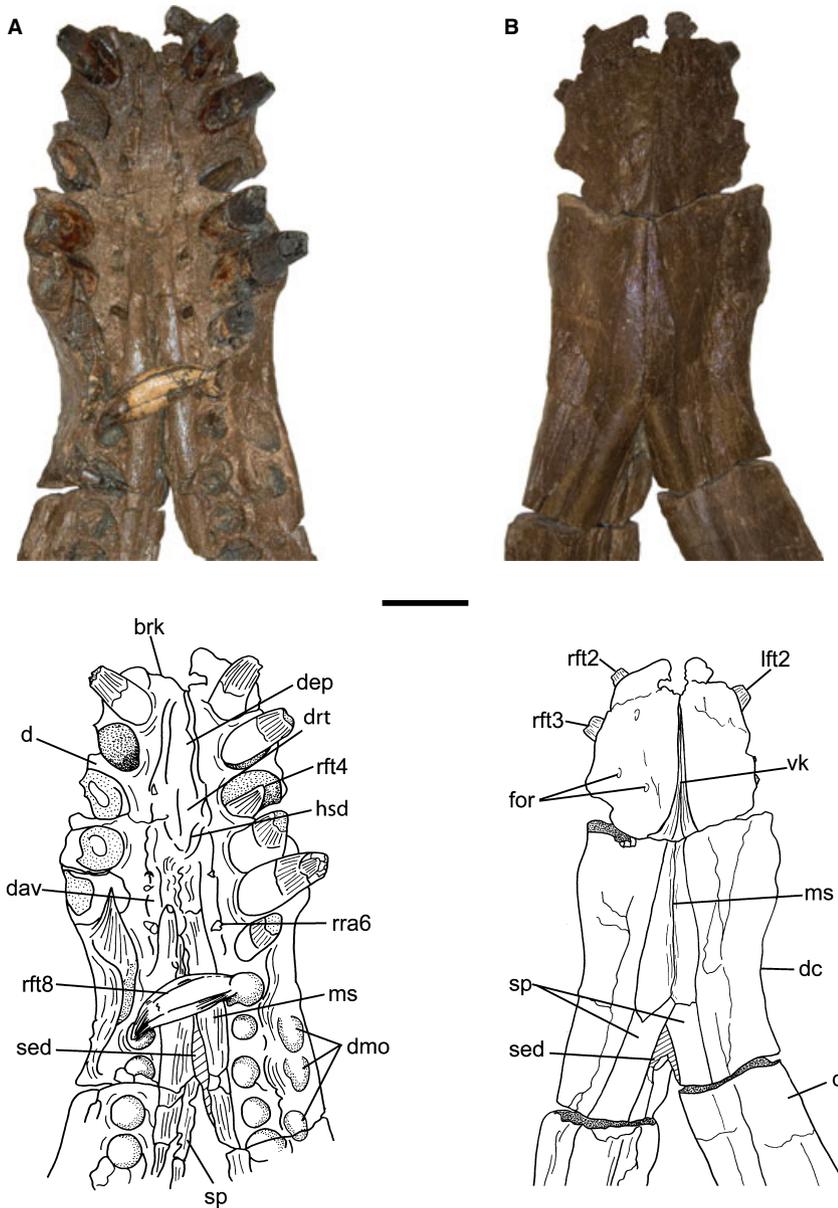


FIG. 9. Photographs and interpretive drawings of the anterior mandible showing mandibular symphysis of *Pliosaurus* sp. (BRSMG Cd6172), in A, dorsal; and B, ventral views. Scale bar represents 50 mm.

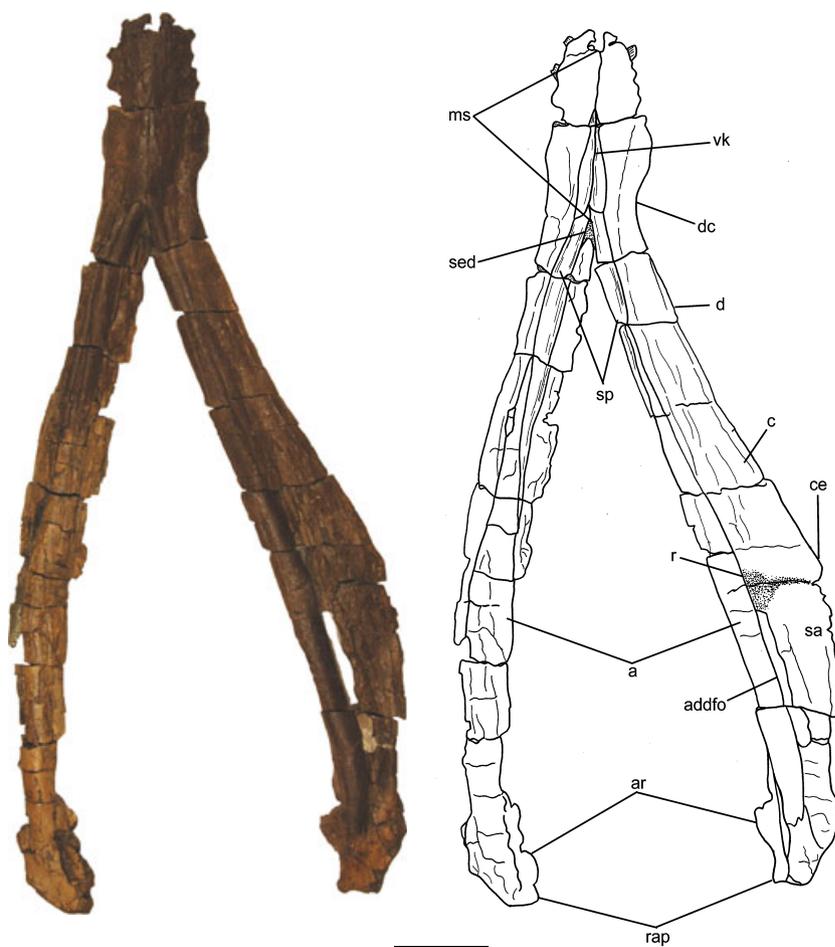
Angular. The angular is a spearhead-shaped bone forming most of the ventral surface of the mandible and extending from level with functional alveolus 14 to the retroarticular process (Fig. 10). The angular contacts the dentary anterolaterally and laterally and is overlain by the splenial anteromedially. The tapered anterior of the angular appears to be wedged between dentary and splenial.

On the lateral and medial surfaces of the mandible, the angular contacts and underlies the surangular for the posterior one-third of the jaw. The lateral angular–surangular suture extends antero-posteriorly, from the dentary–angular junction to the articular glenoid. The medial angular–surangular suture lies deep within Meckel’s foramen, extending posteriorly from a point level with the splenial–coronoid suture. The angular forms the ventral border of Meckel’s canal and Meckel’s foramen on each ramus.

Posteriorly, each angular flares medially, underlying and supporting the articular. Posteriorly, the angular forms the ventral surface of the retroarticular process, which is completed dorsally by the articular (Fig. 11B). The angular forms a complex suture with the articular, much of which is fused, although sections are visible, extending from behind the surangulars on the medial surface, around the superior margin of the retroarticular processes, and contacting the surangulars laterally (Fig. 11A–B).

Articular. Each articular is a robust bone exposed mainly dorsally. The articular contacts the angular ventrally, the surangular anterodorsally and ventrolaterally and the prearticular antero-ventrally, although the articular–prearticular contact is not preserved. The articular also forms most of the dorsal portion of the retroarticular process (Figs 8 and 11).

FIG. 10. Photograph and interpretive drawing of the mandible of *Pliosaurus* sp. (BRSMG Cd6172), in ventral view. Scale bar represents 200 mm.



The broad glenoid fossa is borne on the anterior, lateral and medial flanges of the articular (Fig. 11), demarcated anteriorly and posteriorly by a transverse crest, although both articulators have been subject to severe pathological deterioration. The transverse crests of the left glenoid fossa have been worn down, and heavy pitting is visible on the dorsal articular surface (Fig. 11A, C). The right articular has been more severely eroded and has a deep crack running transversely across the glenoid fossa, through a mixture of pathological and taphonomic deterioration (Fig. 11C). On both rami, the retroarticular processes have been eroded to two small stumps.

Teeth and dentition

The dentition of BRSMG Cd6172 is fully thecodont, with the functional alveoli forming a single row along the margins of the premaxilla, maxilla and dentary (Owen 1841). Each functional alveolus is associated distolingually with a replacement alveolus, located within a groove (Figs 9A and 12A). There are 23 functional alveoli on the right upper jaw and 17 on the left (Fig. 4), and the mandible bears a complement of 24 functional alveoli on the right ramus, and 27 on the left (Fig. 8; Table S2). A total of 59 tooth crowns were preserved with the specimen, including many functional teeth found loose in the sediment.

Tooth structure. The teeth are typically pliosaurian (Tarlo 1960), with a curved, tapering, conical crown and a bulbous, hollow base that anchors the tooth into the supporting bone, the analogue of the mammalian root (Fig. 13). Each tooth is recurved, the crown more so than the base. The dentition is anisodont, and the teeth fall broadly into two categories: large, deeply rooted caniniforms with the crown triangular in cross-section, and smaller, more sharply recurved or hooked teeth with a more rounded crown cross-section (Fig. 13A–H). Individual teeth vary in size and proportion according to their position along the jaws, and their stage in the developmental cycle (Tables S2A–C and S3). The bases of the caniniforms lay deep within the supporting bone and almost met along the midline, as seen in a cross-sectional break through the dentary (Fig. 14D). The hooked teeth are associated with the smaller, shallower, more posteriorly placed alveoli.

General descriptions of pliosaurian teeth are available elsewhere (Tarlo 1960; Taylor 1992; Taylor and Cruickshank 1993; Cruickshank 1994; Noè 2001), and here, the following descriptive terms are used here to describe the asymmetry of the teeth and their spatial orientation: ‘convex’ – the surface on the outside of the main tooth curvature; ‘concave’ – the surface on the inside of the main tooth curvature (Noè 2001); ‘flat’ – the flattened tooth surface bounded by two carinae; and ‘axial’ – the two faces opposite to the flat surface and ornamented with

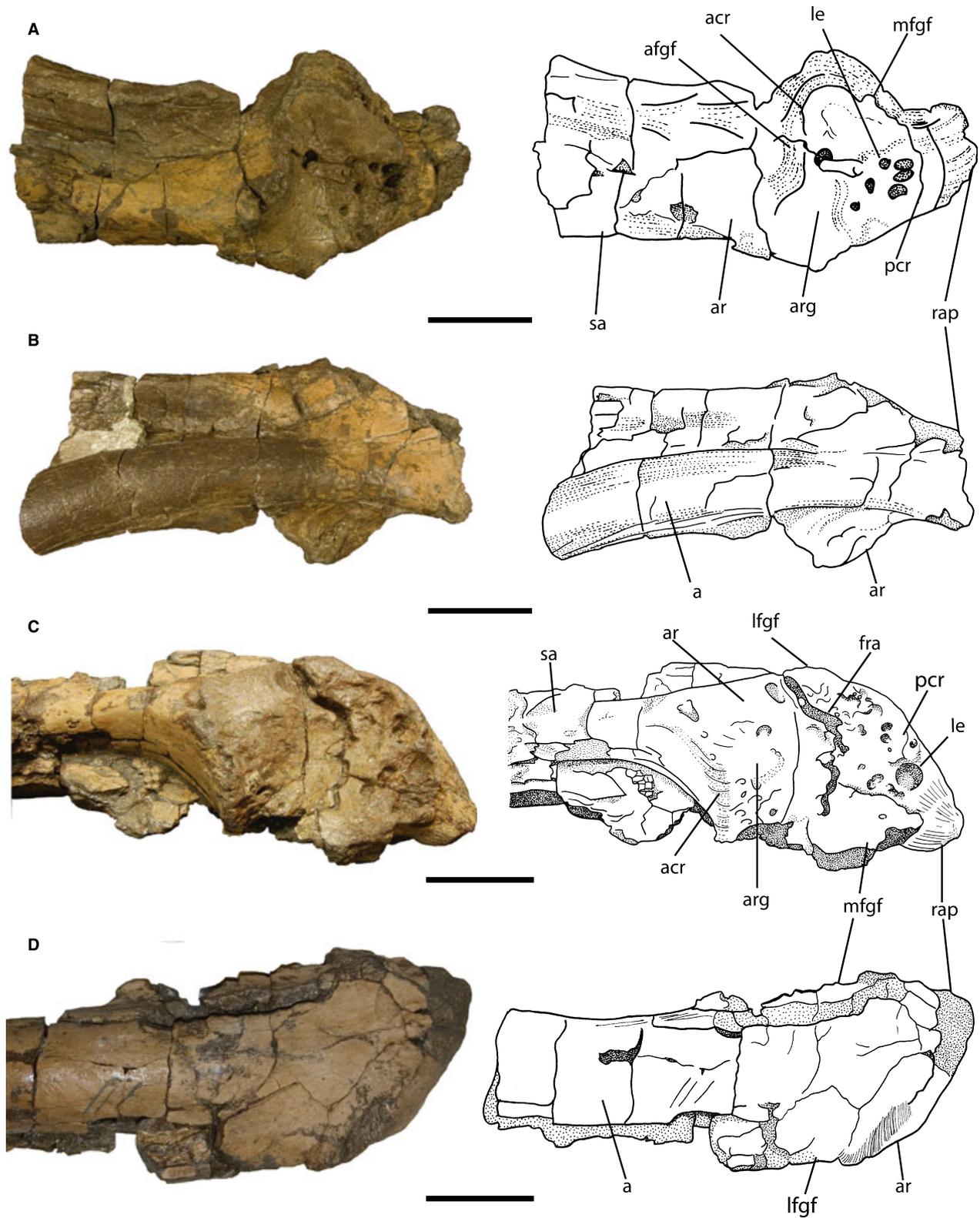


FIG. 11. Photographs and interpretive drawings of the articular regions of *Pliosaurus* sp. (BRSMG Cd6172). A, B, left articular in dorsal (A) and ventral (B) views; C–D, right articular in dorsal (C) and ventral (D) views, showing pathological lesions and symptoms of erosive arthrosis. Scale bars represent 100 mm.

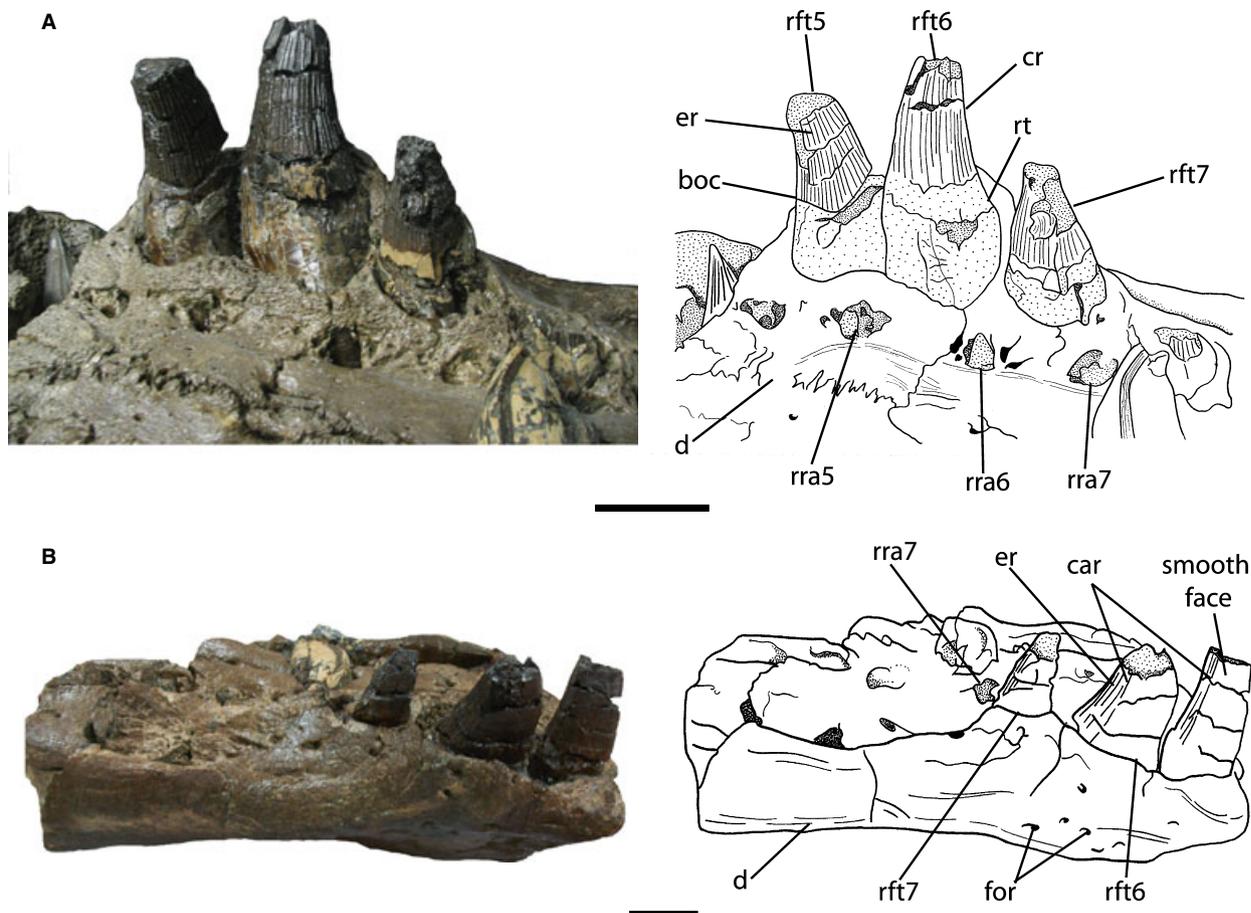


FIG. 12. Photographs and interpretive drawings showing details of the dorsal surface of the mandible of *Pliosaurus* sp. (BRSMG Cd6172); A, oblique left lateral view showing functional and replacement teeth in lingual view; B, oblique, right lateral view showing functional teeth in labial view. Scale bar represents 50 mm.

enamel ridges (Fig. 13). When these terms are used in the special senses defined here, they are enclosed in inverted commas. A minor curvature also occurs normal to the main 'concave'-'convex' curve, giving the tooth directionality when viewed from the 'axial' surfaces, either right or left. This directionality relates to the anatomical placement of the tooth (Noè 2001); right-handed teeth belong either on the right cranial margin or on the left mandibular ramus; conversely, left-handed teeth reside in the left cranial margin or in the right mandibular ramus.

Twelve complete but detached teeth were prepared, while other loose teeth were incomplete or fragmented. The hooked posterior teeth are stouter and more curved than the caniniforms. The length, crown curvature and stoutness of a selection of teeth are shown in Table S3. The range of crown curvature and stoutness for the caniniform teeth is 0.94–1.26 and 0.53–0.74 ($n = 10$), and for the hooked teeth, 1.20–1.50 and 0.42–0.50 ($n = 5$), respectively.

Tooth ornamentation. The teeth have a characteristic ornamentation of longitudinal enamel ridges on the two 'axial' surfaces, and these run for varying distances from the base of the crown towards the apex, but few reach the apex. The enamel ridges

are 1–2 mm wide on the largest caniniforms and triangular in cross-section (Fig. 13A, B). The 'flat' surface is smooth and remains largely free of ornamentation, but is bounded by two finely crenulated carinae. The function of the enamel ridges and carinae was to enlarge wounds during prey capture and dismemberment (Massare 1987). The ridges may also have helped the tooth penetrate and withdraw from the prey by breaking suction, acting like the 'blood gutter' groove on a military bayonet.

Both large and small teeth have well-developed bands, possibly resulting from tooth growth, that encircle the teeth, oriented perpendicular to the long axis (Fig. 13D); these rings extend the full length of the tooth, from base to crown. The bands are of variable thickness and on the crowns are more prominent on the 'flat' than on the 'axial' surfaces, where they are obscured by enamel ridges. The smaller teeth have fewer, more widely spaced bands, whereas on the larger caniniform teeth, the bands become more numerous and very closely spaced towards the apex.

Dentition. The anteriormost pair of alveoli, in both upper and lower jaws, are small and directed somewhat anteriorly (Fig. 14A–C). In the upper jaws, the premaxillae contain 12

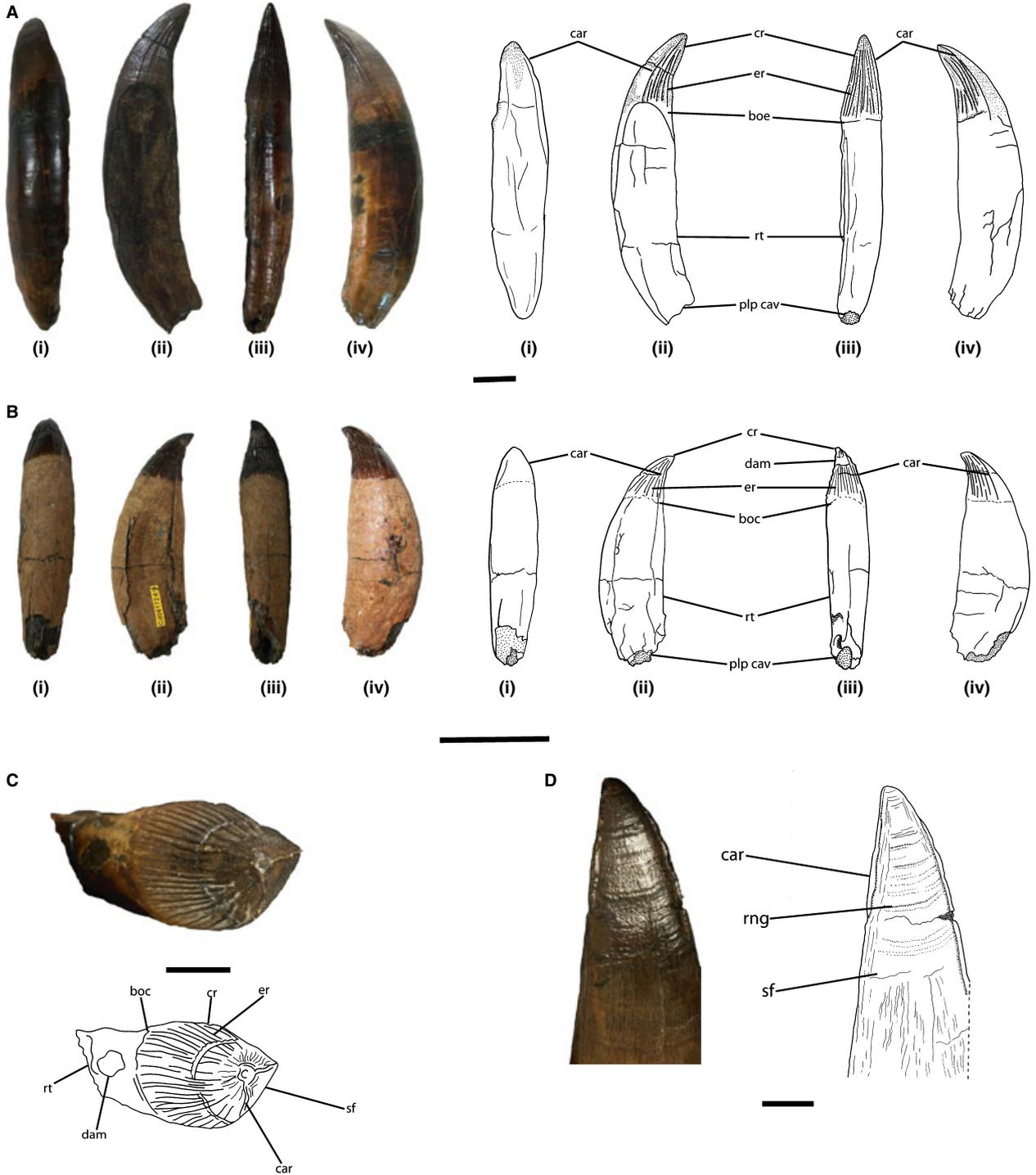


FIG. 13. Photographs and interpretive drawings of the teeth of *Pliosaurus* sp. (BRSMG Cd6172). Four orientations of a caniniform tooth (A) and a hooked posterior tooth (B) in (i) 'convex', (ii) 'flat', (iii) 'concave' and (iv) 'axial' views, as the tooth is rotated clockwise; (C) a caniniform tooth in apical view demonstrating the trihedral structure; and (D) the convex face of a caniniform tooth showing the smooth surface with lateral carinae and enamel rings. Scale bars A–C represent 50 mm; D represents 10 mm.

functional alveoli, six on each side of the snout. Functional alveoli 2–5 are large, fan laterally around the premaxillae and contained large caniniform teeth. From the sizes of the alveoli

(50–55 mm diameter), the largest premaxillary teeth were functional teeth 3–5 (Table S2A). The sixth functional alveolus is smaller and projects more vertically.

The maxillae bear the posterior upper dentition from the seventh functional alveoli. The first pair of maxillary alveoli is relatively small, and the alveoli increase in size posteriorly to house a second set of large, laterally oriented, caniniform teeth in maxillary alveoli 9–11. Based on alveolar size, the largest maxillary caniniforms were at least as large as those in the premaxilla.

The dentary accommodates the lower dentition for approximately two-thirds of its length. On the left, the first functional alveolus is crushed and incompletely preserved; the corresponding right functional alveolus houses a developing tooth (Fig. 6A). Posteriorly, the dentary alveoli enlarge to the sixth alveolus, with the mandible expanding laterally to accommodate the larger teeth, giving the mandibular symphysis a sinuous border. Beyond the symphysis, the mandible constricts medially and curves ventrally. This constriction acts as accommodation space for the maxillary caniniforms above.

Teeth are in place only in the dentary (Fig. 8), with 17 functional teeth either *in situ* or broken but closely associated with their alveoli. Several of these teeth have missing crowns so their length can only be estimated from the diameter of the surviving portion. However, the right dentary anterior caniniform teeth 2–7 are preserved *in situ* (Fig. 12), showing their orientation and elevation. The ‘flat’ surfaces of the teeth (Fig. 13) are oriented labially, while the ‘axial’ surfaces project lingually. The enamelled crowns are elevated 30–40 mm above the mandibular surface.

From functional alveolus 12 in the upper jaw, and seven in the mandible, there is a gradual reduction in tooth size. The posterior alveoli housed the smaller, more hooked teeth, with functional and replacement alveoli lying closer together. The more posterior alveoli become progressively smaller, more vertically oriented and more shallowly placed, with fewer replacement teeth preserved.

RECONSTRUCTIONS

The size and position of the orbits in BRSMG Cd6172 were inferred by comparison with BRSMG Cc332 (Fig. 2). The margins of the cranium would have extended laterally to accommodate the large orbits, which in life lay far from the snout tip. In other specimens of *Pliosaurus*, the orbits were large and anterodorsally oriented, suggesting that BRSMG Cd6172 exhibited limited stereoscopic vision but with a wide lateral sweep (Taylor and Cruickshank 1993). The size, shape and position of the temporal fenestrae were inferred from the relative position of the quadrates. The temporal fenestrae accommodated heavy musculature, typical of an aquatic top predator (Massare 1987; Taylor 1992; Taylor and Cruickshank 1993).

Missing elements. Skull roofing elements (nasals, prefrontals, frontals, lacrimals, postfrontals, postorbitals and epipterygoids) are not preserved in BRSMG Cd6172, and these are reconstructed from other pliosaurian species (Andrews 1897; Taylor and Cruickshank 1993; Fig. 2A–B). The absence of nasals in Plesiosauria was received wisdom for some time (Storrs 1991; Taylor and Cruickshank

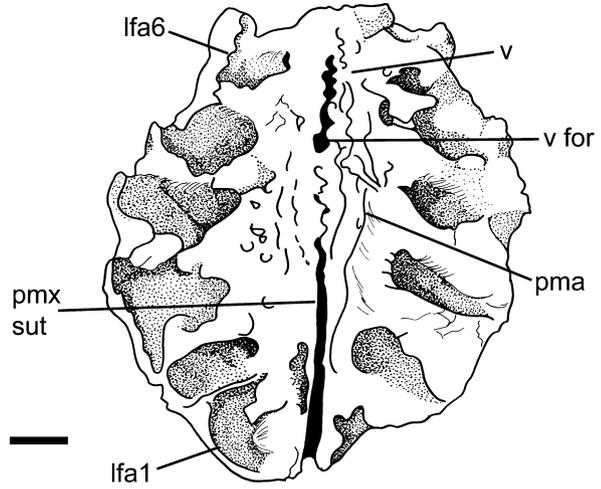
1993; Carpenter 1997; see also Ketchum and Benson 2010), and lacrimals were also thought to be missing in Sauropterygia (Storrs 1991; Carpenter 1996; Rieppel 1998). Basal sauropterygians, such as *Nothosaurus* (Rieppel and Wild 1994, 1996) and *Pistosaurus* (Sues 1987), have reduced nasals, and it was suggested that these were either lost or fused with the frontals (Romer 1956) in derived sauropterygians. However, two of us (LFN, JS) have observed that BRSMG Cc332 does possess nasals (*contra* Taylor and Cruickshank 1993), which are also undoubtedly present in the Callovian *Liopleurodon* (Noè 2001). Further, lacrimals also appear in both species (Druckenmiller and Russell 2008; Ketchum and Benson 2010). Therefore, the reconstructions of BRSMG Cd6172 (Fig. 2A–C) show both nasals and lacrimals. The presence of nasals and lacrimals, however, should not be surprising as pliosaurids retain a number of plesiomorphic characters (Ketchum and Benson 2010), also present in BRSMG Cd6172, such as coronoids and suborbital fenestrae; the latter are not present in plesiosauroids or other sauropterygians (Druckenmiller 2002b).

Dentition. Although incompletely preserved, the original arrangement and sizes of the teeth can be inferred from the size, position and orientation of the dental alveoli (Fig. 14). Occlusion of the anterior dentition could be reconstructed with confidence, but less certainly for the posterior teeth. The position of the mandibular functional tooth row suggests that, in life, it lay medial to the upper tooth row (Fig. 2C). The relative position of alveoli in upper and lower jaws (Fig. 14) suggests that the mandible bit inside the premaxillae as in other reptiles (Edmund 1969). Posteriorly, the premaxilla and dentary caniniform teeth were oriented somewhat laterally, so they passed around the opposing jaw, with the curvature of the teeth ensuring the crown apex remained approximately vertical (Fig. 14).

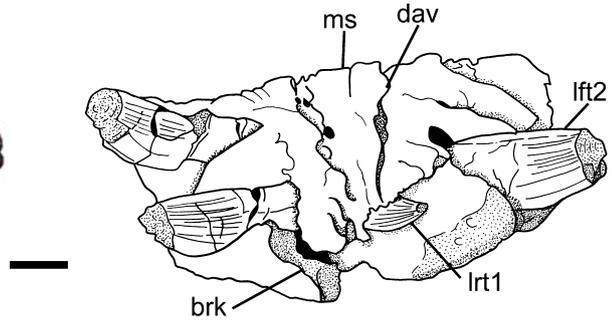
The largest mandibular teeth, numbers 4–6, coincide with the constriction at the premaxilla–maxilla suture. More posteriorly, the maxillae flare laterally so maxillary teeth 9–11 overlapped the dentaries at the dentary constriction. The posterior alveoli in both maxillae and dentaries were more vertically oriented, and, judging by the relative position of the alveoli, the teeth in both jaws alternated without touching, with the mandibular teeth lying slightly medially (Fig. 2C).

Tooth orientation and position. The orientation of the large anterior alveoli in both cranium and mandible suggests that the caniniform teeth did not emerge from the jaws horizontally as in *Nothosaurus* (Noè 2001; Rieppel 2001), or vertically as in Mosasauridae (Caldwell 2007). The bases of the caniniform teeth were recumbent, emerging at approximately 45 degrees (Fig. 14A, B), but

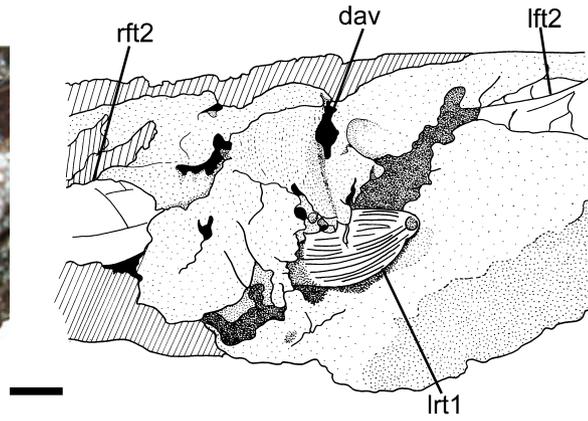
A



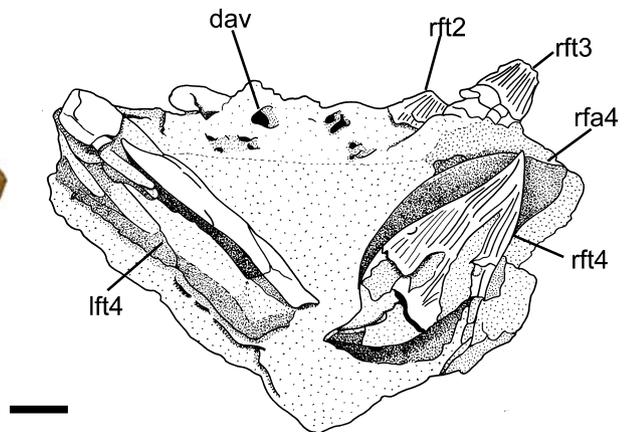
B



C



D



this angle was compensated for by the curvature of the teeth, which protruded outwards before turning towards the opposing jaw. Thus, the crown was placed more vertically than the alveoli suggest (Fig. 12), with the tooth recumbence not as extreme as in *Cryptoclidus* (Andrews 1910) or the extant gharial, *Gavialis* (Taylor 1992).

Individual caniniform teeth were implanted with the base much elevated above the jaw margin (Fig. 12A). This suggests considerable amounts of oral soft ('gum') tissue (Noè 2001). The teeth also have deep bases, as shown in dentary cross-section (Fig. 14D), where the bases almost meet along the ventral midline. The deep bases functioned to anchor the teeth against both longitudinal and transverse stresses (Taylor 1992) and to reinforce the dermal bones against the forces generated during prey capture (Massare 1987).

A model of tooth orientation in Callovian pliosaurs has been proposed in which tooth implantation varies slightly along the length of the jaw, correlating with a change in orientation as the jaws widen for prey capture (Noè 2001). This arrangement is thought to optimise the positions of the teeth for directing food into the gullet. However, in BRSMG Cd6172, the more posterior teeth were not preserved *in situ*, so subtle changes in orientation could not be established. The current view of tooth arrangement in *Pliosaurus* (Andrews 1913; Taylor and Cruickshank 1993) is that the crowns of anterior caniniform teeth pierced flesh, while the recurved tips of the smaller, posterior teeth acted as ratchets to secure and move large food items from mouth to gullet, aided by the tongue and hyoid musculature (Taylor 1987). A complete functional model of this mechanism, taking into account variation in tooth orientation as the jaws move, is required.

PALAEOPATHOLOGIES

There are three, and possibly four, pathological conditions in the skull of BRSMG Cd6172. (1) Dorsomedial to left maxillary functional alveolus 9, on the palatal surface, is a mass of callosal tissue 30 mm wide and 50 mm long, forming a lump. This callus rests over the whole of left replacement alveolus 9 and covers 20 mm of the functional alveolus (Fig. 15). (2) Lateral and slightly dorsal to right dentary functional alveoli 9–11 are three cavities with a maximum length of 30 mm, which resemble shallow, slightly oblique and distorted functional alveoli (Fig. 16A–B). (3) The glenoid surfaces of the articulars

are severely pockmarked with cavities of various sizes, ranging from 5 to 25 mm in diameter. (4) Both retroarticular processes have been eroded down to stumps, although some of this damage undoubtedly arose from taphonomic processes.

Articular pathology. The glenoid surfaces of both articulars show multifocal destruction of the articular surfaces exposing subchondral bone (Fig. 11A, C), but there does not seem to be any sign of florid osteophyte deposition typical of osteoarthritis (Rothschild and Tanke 1991), so that condition can be excluded. Most of the bone alterations described here appear to be periosteal (i.e. on the outer layer of the cortex), and X-radiographs indicate they do not reach far down into the bone mass (Fig. 17A–B). The lip of the glenoid on the left articular is severely eroded, and marginal osteophyte development surrounds the whole of the jaw joint, suggesting that the damage arose from a pathological condition in life rather than *post-mortem* taphonomic damage. In spite of the evident pathology, the left articular is preserved intact and fairly complete (Figs 11A and 17B).

The right articular has more bone mass missing than the left and was more fragmentary and needed more consolidation and reconstruction during preparation. Some of this damage is probably taphonomic. However, the distribution of bone deterioration on the right articular is similar to the left side, with extensive cavitation and marginal osteophyte development. In addition to cracks, there is also a clear fracture running mediolaterally across the glenoid (Fig. 11C). X-radiographs show that the fracture extends deep into the bone (Fig. 17A), but does not penetrate to the ventral side (Fig. 11C–D).

Interpretation. These pathologies suggest a sequence of mishaps in the life of an ageing pliosaur. First, a progressive disease of the jaw joint caused prolonged jaw misalignment, and this may have eventually led to jaw fracture and contributed to the creature's death.

The symptoms can be ascribed to the natural ageing process, aggravated by a systemic erosive arthrosis affecting the jaw joint (Rothschild and Martin 1993). The joint surfaces are normally capped with articular cartilage, and a synovial membrane lines the enclosed articular cavity, secreting the lubricating synovial fluid. Cartilage degeneration is a natural part of the ageing process, and the synovial joint becomes worn. As cartilage lacks its own blood supply in adults, once damaged it cannot be repaired.

FIG. 14. Photographs and interpretive drawings of details of the snout and mandible of *Pliosaurus* sp. (BRSMG Cd6172); A, premaxillae in anterioventral view showing distribution and angles of tooth sockets; B, dentaries in anterodorsal view, showing preserved angles of teeth *in situ*; C, magnified view of B showing emerging left replacement tooth one; D, posterior view of section through dentary at the level of fourth functional tooth sockets (rfa4) showing depth of insertion of caniniform tooth bases. Scale bars represent 50 mm.

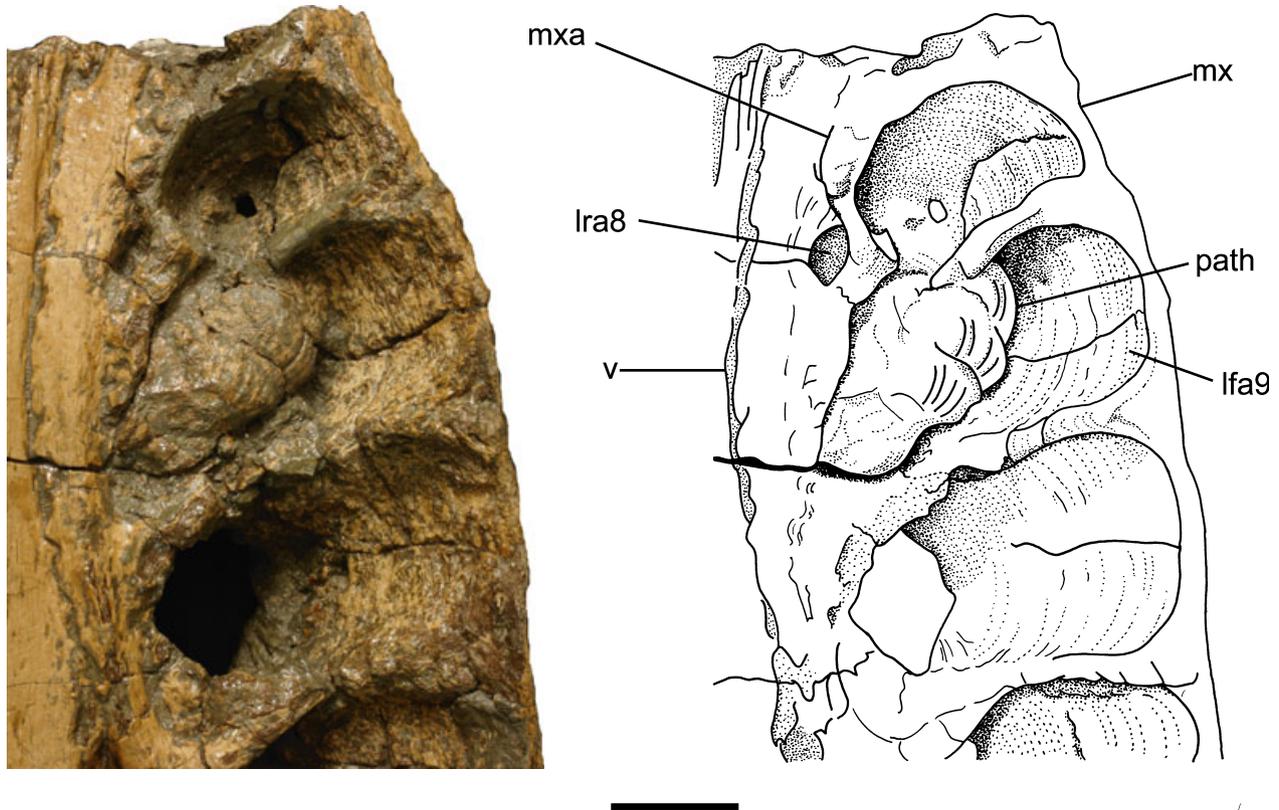


FIG. 15. Photograph and interpretive drawing of the pathology (path) at left functional alveolus nine (lfa9) on the ventral surface of the maxilla of *Pliosaurus* sp. (BRSMG Cd6172), in ventral view. Scale bar represents 30 mm.

Rothschild (2009) observed similar symptoms in other fossil material and diagnosed the arthrotic condition as spondyloarthropathy (Rothschild and Tanke 1991; Rothschild and Martin 1993; Rothschild *et al.* 2002). This condition is often recognised by fusion in axial and peripheral postcranial elements. A typical, but not exclusive, symptom is ankylosing spondylitis, and fusion of phalangeal joints is frequently observed (Rothschild 2005, 2009). Preliminary study of the postcranial material of BRSMG Cd6172 shows at least one example of phalangeal ankylosis, but as yet no vertebral fusion. Thus, the condition in BRSMG Cd6172 could be a combination of senescence with spondyloarthropathy, but an accurate diagnosis requires further work.

The consequences of the pathologies in BRSMG Cd6172 can be hypothesised. In a healthy pliosaur, the skull and mandible were akinetic, and the arrangement of the bones would not permit lateral movement at the quadrate–articular junction, but only vertical hinge action. The skull is stabilised by bony structures acting with muscles to resist the powerful forces generated by struggling prey (Noè 2001): the glenoid sulcus butts against the condyle to stabilise the joint against transverse forces, and the anterior and posterior transverse ridges of the glenoid fossa resist anteriorly and posteriorly directed

forces. However, in BRSMG Cd6172, the ridges of the glenoid have been eroded and damaged by arthrosis, permitting lateral displacement of the jaw (Fig. 18A–D).

Further pieces of evidence for lateral jaw displacement in BRSMG Cd6172 are the dorsolateral cavities on the right dentary that occur at the dentary constriction (Fig. 16A–B). Here, the right mandibular ramus has been slightly flattened, giving the impression that the cavities faced dorsally, but during life they were oriented more laterally on the outer side of the dentary, slightly below the functional tooth row. The lateral displacement of the arthrotic right jaw joint caused permanent tooth malocclusion, and the large caniniform teeth 9–11 of the right maxilla, normally occluding outside the mandibular constriction, cut into the mandible side. The greatest erosion was from teeth 9 and 10, while tooth 11 formed a shallower cavity (Fig. 16A–B).

Jaw displacement also caused other damage. An osseous mass at left maxillary functional alveolus 9 (Fig. 15) is a reaction to peri-apical infection caused by abnormal tooth replacement, a fractured tooth or most likely persistent trauma from an impacting tooth from the lower jaw. Any of these factors could encourage callus formation during bone healing (Lingham-Soliar 2004), but the infec-

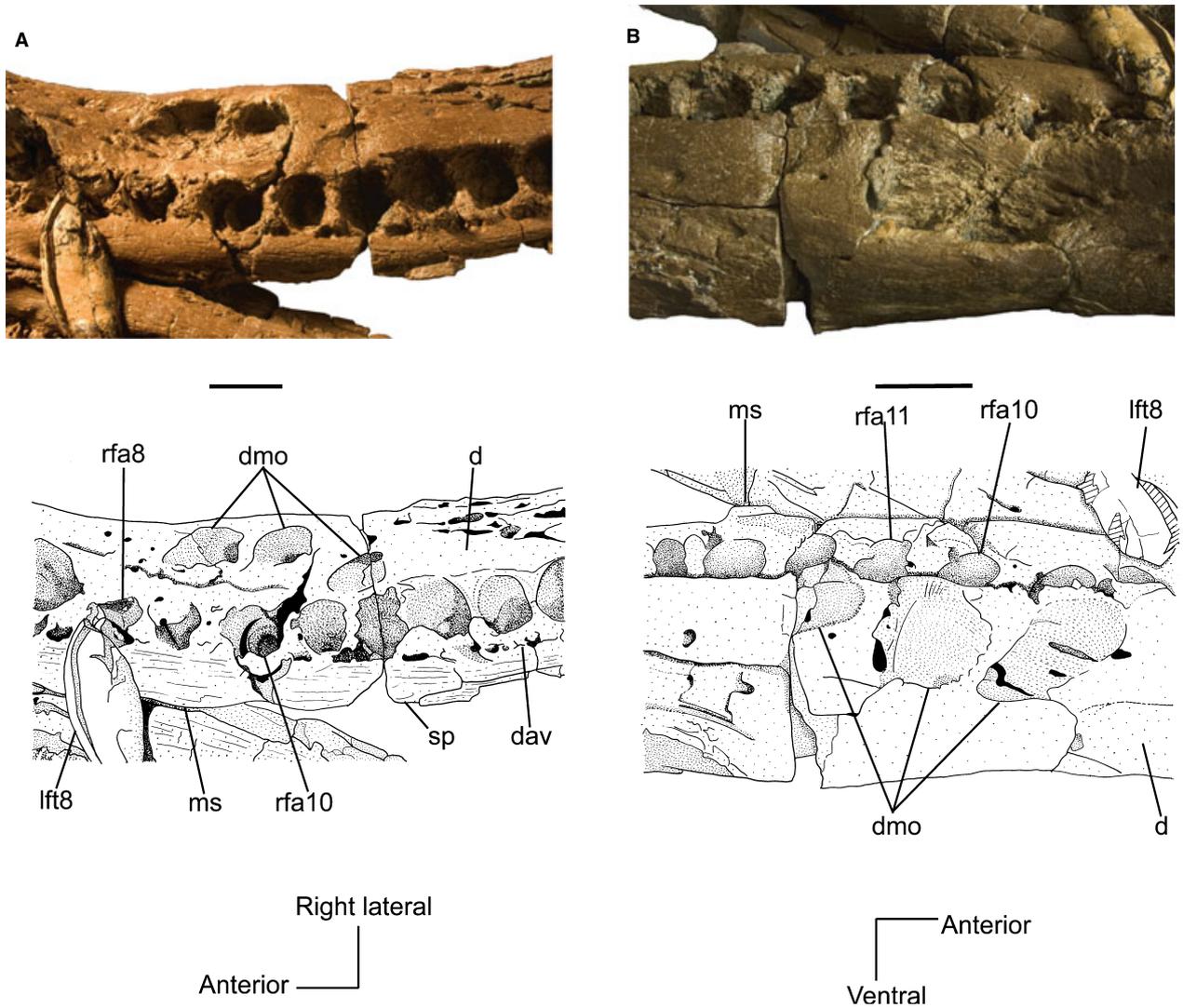
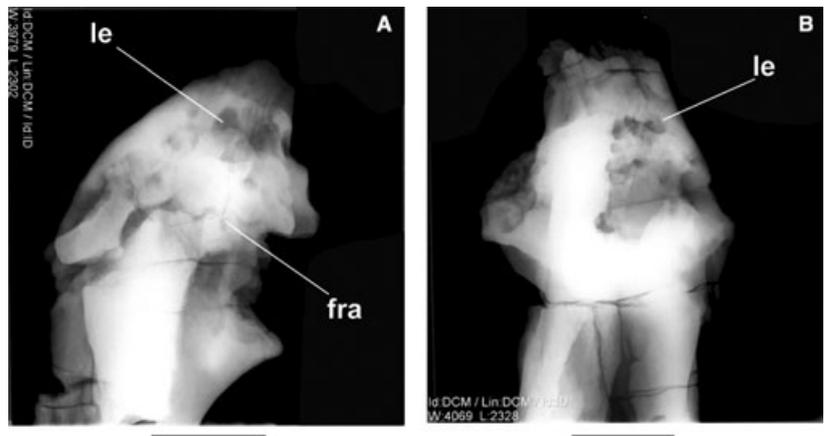


FIG. 16. Photographs and interpretive drawings of the right dentary showing depressions owing to misaligned overbite (dmo) of *Pliosaurus* sp. (BRSMG Cd6172), in A, dorsal; and B, oblique, right lateral views; orientation of photographs and interpretive drawings indicated by directional arrows. Scale bars represent 50 mm.

FIG. 17. X-radiographs of the articulars showing penetration of pathological lesions (le) of *Pliosaurus* sp. (BRSMG Cd6172); A, right articular; and B, left articular in dorsal views. The transverse fracture (fra) across the right articular is indicated. Compare with Figure 11. Scale bars represent 100 mm.



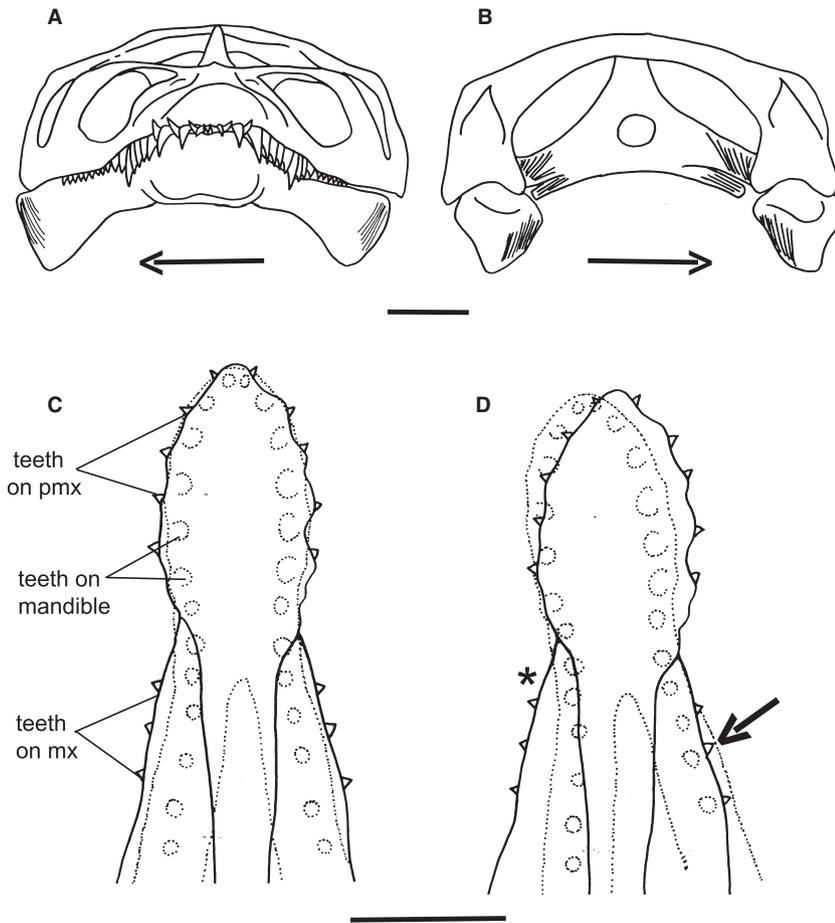


FIG. 18. Illustrations to show proposed right lateral displacement of mandible in *Pliosaurus* sp. (BRSMG Cd6172); A, anterior; and B, posterior views of skull, arrows indicate direction of displacement of mandible relative to cranium. C–D, dorsal views of rostrum (solid lines) and mandible (dotted lines, showing positions of functional alveoli); C, normal alignment; D, misaligned mandible in BRSMG Cd6172 with arrow to indicate upper jaw overbite eroding depressions in mandible lateral to right dentary tooth positions 9–11, and asterisk to indicate position of tooth pathology on rostrum at left maxillary tooth position nine. A–B, Scale bar represents 100 mm; C–D, scale bar represents 200 mm.

tion is here linked to persistent impact of left tooth 9 from the lower jaw in the region of left maxilla tooth position 9 (Fig. 18).

The pliosaur lived for some time with its displaced jaw and must have been able to feed. However, progressive arthrosis would have weakened the jaw joint over time. Normal jaw muscle contraction during prey capture rotates the mandible upward against the upper jaw, generating a powerful bite force and a strong downward reaction force at the jaw joint (Taylor 1992; Taylor and Cruickshank 1993). A diseased and weakened jaw joint would not tolerate such feeding forces, and eventually, the jaw might have reached its stress limit and fractured. There is no observable healing reaction at the fracture site, suggesting that, if indeed damage occurred during life, the animal did not survive long afterwards. Healing reactions in bones are usually observable within 3 weeks of damage (McKibbin 1978) so it is likely that the animal died within that interval following the fracture. Equally, of course the jaw might have been fractured after death, perhaps through violent disturbance of the carcass, and there is no way to distinguish the two hypotheses.

PLIOSAUR SYSTEMATICS

Comparison between Westbury pliosaurs 1 and 2

The two Westbury pliosaurs BRSMG Cc332 (Taylor and Cruickshank 1993) and BRSMG Cd6172 (described here) were found close together (Fig. 1), and they are tantalisingly similar. Dorsally, the cranium of BRSMG Cc332 is much more complete than BRSMG Cd6172, although cranial proportions of BRSMG Cd6172 could be extrapolated from the shape of preserved elements and ratios calculated, normalised for length (Table S1): differences range from 0 to >30 per cent. Similar or identical ratios in both specimens include the following: distance from tip of premaxilla to premaxilla–maxilla suture, distance from tip of premaxilla to premaxilla–parietal suture, distance from premaxilla to internal nares and distance from premaxilla to palatal foramen. Differences between the two specimens include overall morphology of the premaxillae (Fig. 19) and overall shape, although not relative position, of the parietal crest. The articular glenoids (Fig. 19B, E) also differ because of pathological degeneration in BRSMG Cd6172.

There are differences in snout shape. The snout of BRSMG Cc332 is narrower and the spaces between functional alveoli larger (Table S4; Fig. 19A, D). BRSMG Cd6172 shows a widening of the snout at the level of alveoli 4–5 (Table S4), and the vomerine boss and sharp anterior fusion between the premaxillae in palatal view are more robust in BRSMG Cd6172. This shows two, large, elongate, medially placed foramina just anterior to the vomerine boss, whereas in BRSMG Cc332, there is only a trace of a small foramen (Fig. 19A, D).

Tooth counts are difficult to assess because both specimens are incomplete: in BRSMG Cc332, the tips of the premaxillae and the whole of the mandibular symphysis are missing, and in BRSMG Cd6172, the posterior tooth-bearing sections of the maxillae are missing. For BRSMG Cc332, Taylor and Cruickshank (1993) estimated a total of 10 premaxillary, 49 maxillary and 63 mandibular functional alveoli, giving a total of 122 tooth positions in all. In BRSMG Cd6172, there are 12 premaxillary, 28 maxillary and 51 mandibular alveoli, and the missing portions of the maxillae would have held a further *c.* 20 functional alveoli on the right and *c.* 12 on the left, estimated by counting the number of small alveoli in the last 100 mm of the maxilla, and extrapolating to its presumed termination level with the mid-point of the posterior interpterygoid vacuity (Taylor and Cruickshank 1993). Thus, the estimated number of maxillary alveoli is 60, giving a total tooth count of 123 for BRSMG Cd6172.

Teeth from the two Westbury pliosaurs are essentially identical in stoutness and crown curvature (Table S3). For the caniniform teeth, the mean crown curvature in BRSMG Cd6172 is 1.16 ± 0.09 SD (range = 0.94–1.26, $n = 10$) and stoutness 0.68 ± 0.07 SD (range = 0.53–0.74, $n = 10$) compared with BRSMG Cc332, where mean crown curvature is 1.20 ± 0.08 SD (range = 1.10–1.31, $n = 6$) and stoutness 0.67 ± 0.10 SD (range = 0.56–0.79, $n = 6$). For the hooked posterior teeth, in BRSMG Cd6172, the mean crown curvature is 1.35 ± 0.12 SD (range = 1.20–1.50, $n = 5$) and stoutness 0.47 ± 0.03 (range = 0.42–0.50, $n = 5$), whereas for BRSMG Cc332, mean crown curvature is 1.49 ± 0.09 SD (range = 1.38–1.60, $n = 4$) and stoutness 0.48 ± 0.04 SD (range = 0.45–0.53, $n = 4$). Unpaired Student's *t*-tests, comparing crown curvature and stoutness in caniniform and hooked teeth from the two specimens, showed no significant difference (at 95 per cent confidence; Appendix S1).

Taxonomy

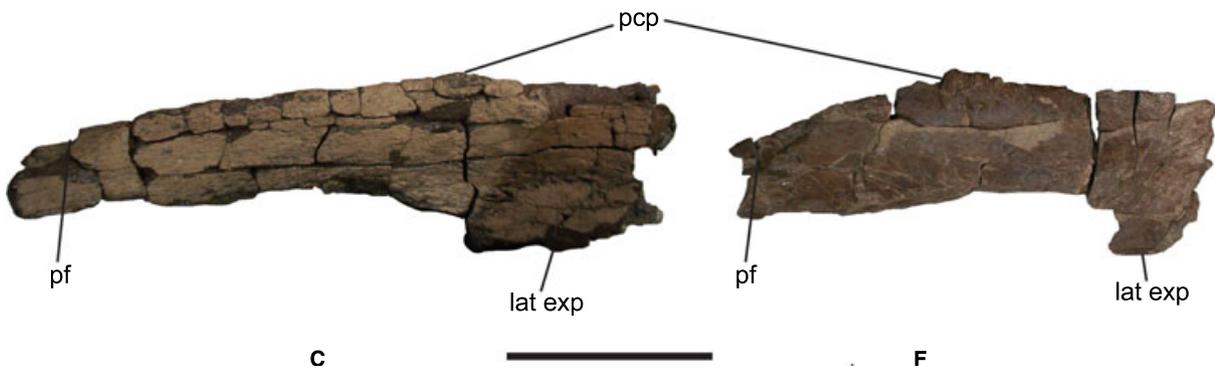
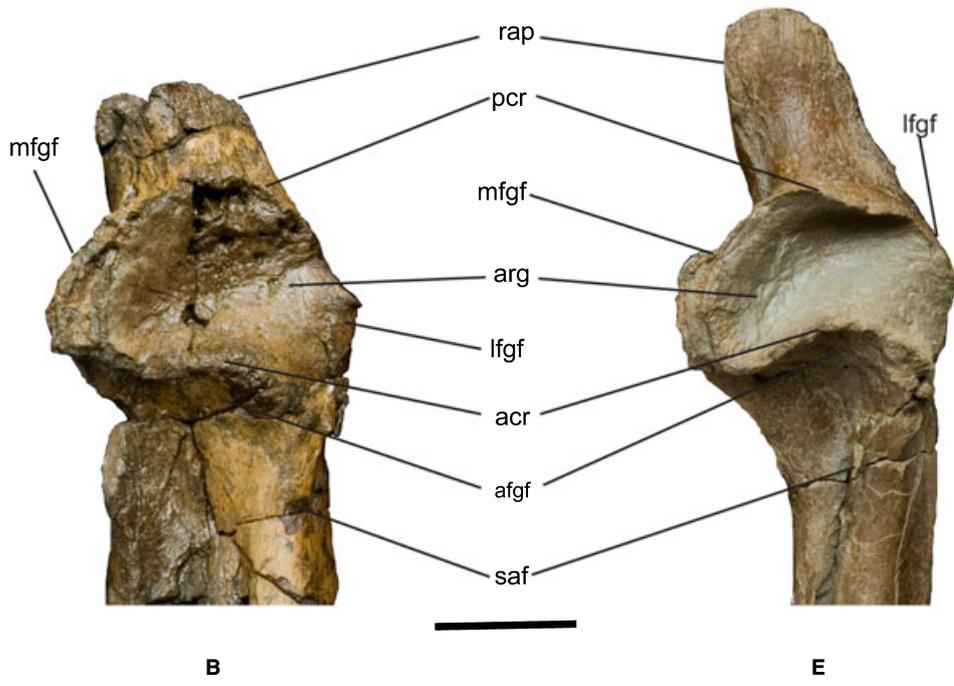
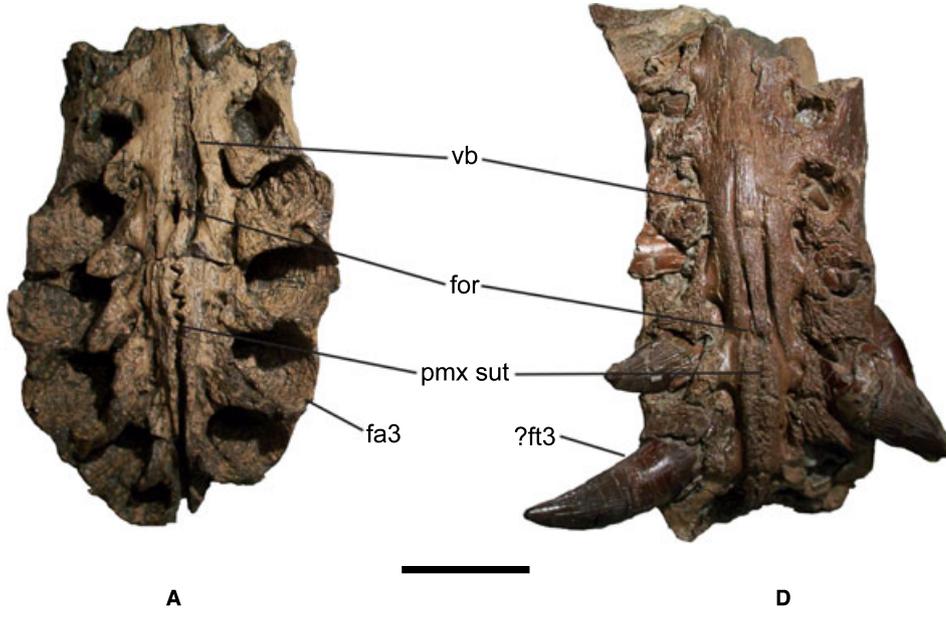
In a precladistic phylogeny of pliosaurians (Tarlo 1960), genera and species were differentiated on features of the teeth, mandibles, cervical vertebrae, scapulae (although this character proved problematic as some were later shown to be ilia; Halstead 1989) and epipodials. Length

of the mandibular symphysis, in conjunction with the number of caniniform teeth, was considered diagnostic of the various pliosaur genera (Tarlo 1960).

In a subsequent noncladistic study, fifteen anatomical characters were considered taxonomically important for Pliosauroida (Brown 1981). Diagnostic cranial characters were as follows: skull size, tooth form and ornamentation, length of mandibular symphysis, number of symphyseal alveoli containing caniniform teeth, number of pairs of dentary teeth, regularity of dentition and form of occipital condyle. Brown (1981) suggested that the number of pairs of premaxillary teeth was not diagnostic because the apparently primitive number of five was retained in pliosaurs, but this is not so (Andrews 1913; Tarlo 1960). The total number of teeth in the jaws is also not a reliable character because it can vary ontogenetically, with younger individuals having fewer teeth than adults (Brown 1981). The structures of the pterygoid, paraoccipital process and parietal crest have been considered taxonomically significant, but these features can also be ontogenetically or sexually variable (Brown 1981).

Some authors have suggested that cranial characters are more taxonomically robust than postcranial characters because the latter are more likely to converge as adaptations to an aquatic lifestyle (Bakker 1993; Carpenter 1997; Storrs 1999; Noè 2001). However, Ketchum and Benson (2010) have argued that cranial and postcranial characters are equally homoplastic, based on the comparison of character partitions in their cladistic analysis.

Taxonomic controversies and assignment of the Westbury pliosaurs. The criteria used to classify BRSMG Cc332, the first Westbury pliosaur, as *Pliosaurus brachyspondylus* (Taylor and Cruickshank 1993) were based on the Tarlo–Halstead (the same author) classification (Tarlo 1960; Halstead 1989) that recognised two genera and three species of Kimmeridgian pliosaurs. The criteria were as follows: (1) all Kimmeridgian pliosaurs had trihedral teeth and could therefore easily be distinguished from Oxford Clay pliosaurs, all with subcircular teeth. The teeth of BRSMG Cc332 are trihedral (Taylor and Cruickshank 1993). (2) Two genera of Kimmeridgian pliosaurs, *Liopleurodon* Sauvage, 1873 (represented by the single species *L. macromerus*, formerly *Pliosaurus macromerus* Phillips, 1871) and *Pliosaurus* Owen, 1842 were recognised, distinguished on the basis of the length of their mandibular symphyses. *Pliosaurus* species had 10 or more pairs of symphyseal caniniform teeth, while *Liopleurodon* had 5–6. The mandibular symphysis of BRSMG Cc332 is missing, but based on reconstruction, 11 pairs of symphyseal teeth were estimated (Taylor and Cruickshank 1993). (3) Two species of Kimmeridgian *Pliosaurus* were considered valid (Tarlo 1960), differentiated by the presence (*P. brachydeirus* Owen, 1842) or absence (*P. brachyspondylus* Owen,



1840) of a ventral keel on the cervical vertebrae. Taylor and Cruickshank (1993) stated that these vertebral features could vary ontogenetically (Brown 1981) and were therefore cautious in assigning BRSMG Cc332, with no ventral keel, to *P. brachyspondylus*.

Recently, Noè *et al.* (2004) challenged the use of mandibular symphyseal length for classifying just two species of Kimmeridgian pliosaurs, providing two reasons: first, there was no convincing representative specimen of *L. macromerus* with a lower jaw associated with postcranial material, and second, the new taxon, *Pliosaurus portentificus* Noè *et al.*, 2004 from the Kimmeridge Clay of Ely, showed a mandibular symphyseal morphology intermediate between the two. Thus, all material assigned to *Liopleurodon macromerus* has provisionally reverted back to *Pliosaurus macromerus* (see also Hampe 1992), pending a full review of Kimmeridge Clay pliosaurs.

The second Westbury pliosaur, BRSMG Cd6172, is indeed a pliosauroid based on 13 cranial and mandibular synapomorphies (Ketchum and Benson 2010, characters 4, 10, 48, 49, 60, 63, 87, 90, 91, 98, 99, 102 and 107), and a pliosaurid based on a further five (Ketchum and Benson 2010, characters 14, 37, 55, 67, 97; Table S5). The specimen can be assigned to *Pliosaurus* based on various characters (Tarlo 1960; Brown 1981; Noè *et al.* 2004). However, the assignment of the first Westbury pliosaur to *P. brachyspondylus* by Taylor and Cruickshank (1993), and the identification of the second specimen, cannot be confirmed until work in progress on pliosaurid taxonomy (Gómez-Pérez and Noè, in prep.) is completed.

New Kimmeridgian pliosaur genera? The mandible of *Pliosaurus* was diagnosed as having a mandibular symphysis with 10–12 pairs of teeth (Tarlo 1960), and indeed, the two species within the genus, *P. brachydeirus* and *P. brachyspondylus*, were reported to have 10–11 pairs (Owen 1841; Phillips 1871; Tarlo 1960). However, the tooth count for *P. brachyspondylus* was based on a referred specimen, CAMSM J.35991 (Tarlo 1959, 1960). There have now been reports of a wider range of variability in the number of symphyseal teeth in specimens currently recognised as *P. brachyspondylus*: three show nine pairs of symphyseal alveoli (BHN2R.370; MNHN cat. 24.1; uncatalogued specimen in the Institut Catholique de Lyon; Bardet *et al.* 1993, 1994; Noè *et al.* 2004). BRSMG Cd6172 has at most nine pairs of teeth around the symphysis, which appears to terminate between alveoli 8 and 9. The mandibular symphysis of BRSMG Cc332 is absent, but Taylor and Cruickshank (1993) estimated 10–11 pairs of symphyseal teeth, although this may be erroneous, as argued below.

The variation in symphyseal tooth count in specimens reported as *P. brachyspondylus* requires further investigation, especially as the new species, *P. portentificus*, was identified on the possession of eight symphyseal teeth (Noè *et al.* 2004). Hence, there are currently three recognised symphyseal morphologies within *Pliosaurus*: ‘long’ (10–11 tooth pairs e.g. in *P. brachydeirus*), ‘intermediate’ (8 tooth pairs in *P. portentificus*) and ‘short’ (5–6 tooth pairs in *P. macromerus*). If the length of the mandibular symphysis is a robust generic character in *Pliosaurus*, as it appears to be in the Callovian pliosaurs (Noè 2001), the variation in symphyseal length in specimens of ‘*P. brachyspondylus*’ requires reassessment and suggests the presence of several genera of Kimmeridgian pliosaurians.

Differences between BRSMG Cd6172 and BRSMG Cc332

The uncertainties in pliosaurian taxonomy, and in particular that of *Pliosaurus*, make a detailed comparison of the two Westbury pliosaurs necessary. Although BRSMG Cd6172 is larger than BRSMG 332, the two Westbury pliosaurs resemble each other in relative cranial and mandibular dimensions, the position of landmark features (Table S1A, B) and tooth morphology (Table S3), all of which strongly suggest specific identity. Most features do not vary by more than 10 per cent, and the greatest differences are found in features where estimation was required in BRSMG Cd6172 because of missing elements (Table S1). Other small differences, such as the distances from the premaxilla to the anterior and posterior interpterygoid vacuities, are comparable, and small percentage variations can be explained by taphonomic enlargement of the vacuities in BRSMG Cd6172. Although there are numerous similarities in gross morphology, certain details are strikingly different between the two specimens, most obviously: (1) features of the premaxillary snout, (2) size and shape of the parietal crest (Fig. 19A–F) and (3) number of postsymphyseal tooth positions in the mandible. However, these apparent differences must be assessed for possible ontogenetic variation, sexual dimorphism and taphonomic distortion. The position of the internal nares also requires discussion.

Snout. Differences in snout shape can be explained partly by greater taphonomic crushing and spreading in BRSMG Cd6172 and also evidenced by the reduced lateral snout height which gives exaggerated lateral flare (Tables S4 and S6). However, the snout of BRSMG Cc332 is narrower, more gracile and the teeth more widely spaced around the premaxillae (Fig. 19A, D). Also, the length of the

FIG. 19. Photographs comparing elements from the two Westbury pliosaurs, *Pliosaurus* sp. (BRSMG Cd6172; A–C) and *Pliosaurus brachyspondylus* (BRSMG Cc332; D–F); A, D, anterior of snout in ventral view; B, E, left articular glenoid in dorsal view; and C, F, parietal crest in left lateral view. Scale bars represent 100 mm.

vomerine boss differs proportionally by more than 25 per cent (Fig. 19A, D). The number of teeth in the premaxillae of BRSMG Cc332 was estimated as five on each side (Taylor and Cruickshank 1993), but because the tips of the premaxillae are broken off, an uncounted pair of small anterior teeth might also exist. An anterior pair of premaxillary teeth is present in BRSMG Cd6172 (Fig. 14A), giving a total of six tooth positions on each premaxilla, and the same could be true in BRSMG Cc332 (pers. obs.), so giving the same premaxillary tooth count.

In BRSMG Cd6172, level with the fifth premaxillary alveoli, there are two, large, medially placed foramina, which appear to form a canal between the alveoli (Figs 5B and 19A). In BRSMG Cc332, there is a dip representing a much smaller, apparently single, foramen at the same position (Fig. 19D). The purpose of these foramina is not known, but they could represent an accessory olfactory organ, such as Jacobson's organ found in extant reptiles (Carpenter 1997; Miller and Gutzke 1999).

Parietal crest. The posterior midline extension of the premaxillary facial process meets the parietal at proportionally the same point in the two Westbury pliosaurs, which is a diagnostic feature in Pliosauridae (Ketchum and Benson 2010). However, the general shapes and proportions of the two parietal crests are different; the pineal foramen and the highest point of the crest are set further back in BRSMG Cd6172 (Fig. 19C, F). The crest is proportionally taller in BRSMG Cc332, at its highest point creating a clear parietal eminence (referred to as a 'parietal knob' by Noè 2001). In BRSMG Cc332, this feature was dismissed as pathological (Taylor and Cruickshank 1993), but similar structures are seen in other pliosaurians, for example, three specimens of *Simolestes* (PETMG R296, PETMG R188 and NHMUK R3170; Noè 2001). However, the holotype of *Simolestes vorax* (NHMUK R3319) does not possess this structure, but instead has a slightly roughened area posterior to the parietal foramen. The variable presence of the parietal eminence in the same species suggests sexual dimorphism.

Tooth count. The estimated total tooth count of 123 for BRSMG Cd6172 is close to the 122 functional alveoli estimated in BRSMG Cc332 (Taylor and Cruickshank 1993). However, the distributions of the functional alveoli in the two specimens are different, with more tooth positions in the upper jaws (12 premaxillary and an estimated 60 maxillary in BRSMG Cd6172, compared to 10 and 49 in BRSMG Cc332) and fewer in the lower jaws (51 dentary in BRSMG Cd6172, against an estimated 63 in BRSMG Cc332). As already indicated, the number of premaxillary teeth was likely the same in both.

Taylor and Cruickshank (1993) estimated 10 or 11 pairs of teeth around the missing mandibular symphysis

of BRSMG Cc332, by comparing reconstructed mandibular proportions with measurements of the skull. In BRSMG Cd6172, there are nine pairs of symphyseal teeth, and even if the number is overestimated in BRSMG Cc332 by one or two pairs (Taylor and Cruickshank 1993), this would reduce the estimated total number of mandibular teeth from 63 to 61 or 59, still considerably more than the 51 preserved in BRSMG Cd6172.

Thus, the difference in tooth count between the two Westbury pliosaur specimens seems to occur posterior to the symphyseal region in both the maxillae and dentaries. However, the posterior alveoli may not have held functional teeth, as they are small and shallow (Taylor and Cruickshank 1993). If so, the number of posterior functional alveoli may be variable, even between individuals of the same species, although it would be difficult to explain the presence of toothless functional alveoli at the rear of the jaws. Therefore, the total tooth count may not be a robust character for assessing differences between pliosaurian species, as previously suggested (Brown 1981).

Internal nares. Taylor and Cruickshank (1993) presented a model for BRSMG Cc332 in which the internal nares were too small to function in respiration and were used simply for underwater olfaction (Cruickshank *et al.* 1991), and the animal breathed at the surface by gulping air through its mouth. This was, however, based on a probable misidentification of the internal nares as two small foramina, each bounded laterally by the maxilla and medially by the vomer at a position level with the 7–8th alveoli. Not only were these proposed internal nares in BRSMG Cc332 rather small, they were also placed far forward, suggesting a very long canal connecting the internal to the external nares.

In BRSMG Cd6172, the internal nares are identified as two smooth-edged foramina lying further back from the snout, level with the 15th alveoli and close to the vomer–palatine suture. These pass into canals on the dorsal surface of the palate. A small pair of foramina, level with the eighth pair of alveoli, is also present in BRSMG Cd6172, but these are not the internal nares and have no associated narial canals. BRSMG Cc332 also shows a pair of foramina further back on the palate, at approximately the same position as the internal nares of BRSMG Cd6172 (Table S1A(ii)), and these are identified here as the true internal nares in BRSMG Cc332. This would place the internal nares in both Westbury specimens in the same relative position, implying a shorter, but still inverted, narial tract with the capacity to act as a hydrodynamically driven olfaction system (Cruickshank *et al.* 1991).

Developmental stage of BRSMG Cd6172. Opportunities for studying ontogeny in the vertebrate fossil record are rare, but pliosaurs have provided examples of substantially

complete ontogenetic sequences (Andrews 1895; Wiffen *et al.* 1995; Caldwell 1997) and some juvenile material (Cruikshank 1994; Storrs 1997; Kear 2007; Bardet *et al.* 2008; Vincent 2010). Brown (1981) and Grossmann (2007) distinguished between adult and juvenile specimens using the extent of fusion of the neural arches to the vertebral centra. The lack of fusion in cranial elements is also a common trait in many juvenile pliosauroids (Andrews 1913) and plesiosauroids (Andrews 1910; Brown 1981; Carpenter 1997; Maisch 1998; Kear 2007). Early ossification of exoccipital–opisthotic and interparietal sutures has been observed (Kear 2007), but advanced ossification of sutures tends to be a sign of maturity. In general, the extent of sutural fusion is a good indicator of developmental stage (Storrs 1993; Caldwell 1997; Gasparini *et al.* 2003; Kear 2007). In BRSMG Cd6172, many sutural surfaces show signs of advanced ossification and fusion (the parietal–parietal, vomer–vomer, vomer–palatine, pterygoid–quadrate, etc., sutures), suggesting that BRSMG Cd6172 is an ‘old’ individual (Brown 1981). There are no available accounts of senescent pliosaurian specimens in the literature, but BRSMG Cd6172 appears to be such an aged individual on the basis of (1) its large size, (2) the extent of sutural fusion and (3) age-related pathologies.

Westbury I and II: same species different sex? There are strong indications that the two Westbury pliosaurs belong to the same species, but BRSMG Cc332 is smaller and has a more gracile snout and a parietal eminence on the parietal crest. These might be ontogenetic differences, but are more likely to be sexually dimorphic. In the parietals, the crest is the last part to ossify (Brown 1981), so a larger (and older) individual might be expected to possess a more developed crest, unless the size of the crest was a sexually determined feature. In this case, BRSMG Cc332, the smaller animal, has a larger, more developed parietal crest than BRSMG Cd6172. In extant mammals such as gorillas and lions, males often possess a higher parietal crest, which acts as an anchor for powerful jaw closing muscles (Glucksman 1974), and this may have been true in pliosaurs also. Unlike mammals, where males are generally larger than females, female reptiles are often the larger of the two sexes (Cox *et al.* 2007). Perhaps then, BRSMG Cd6172 was an old, female pliosaur, while BRSMG Cc 332 was a younger male.

Tooth replacement

Tooth replacement is a continual process in reptiles (Edmund 1960, 1969) and is closely coordinated between upper and lower jaws, and left and right sides. A fossilised skull preserves the teeth at various stages of replacement ‘frozen’ at the time of death. The mandible of BRSMG

Cd6172 shows 17 functional and 10 replacement teeth *in situ*, and several stages in the tooth replacement cycle can be recognised (Table S2C). Replacement between right and left sides was broadly asynchronous (Table S2C), which avoids the loss of caniniform teeth from both sides at once.

Replacement teeth formed distolingually to functional alveoli in separate, semipermanent, replacement alveoli (Fig. 9; ‘primary alveoli’ of Taylor and Cruickshank 1993). As a replacement tooth matured, it migrated upward, resorbing the intervening bone and eventually merging with the functional alveolus (Table S2C). On fusion, the base of the existing functional tooth was resorbed, and this loosened it, so it was pushed out by the replacement tooth (Edmund 1969). New replacement alveoli formed to house replacement teeth for the next cycle, and they are represented by bone-filled secondary alveoli (Table S2C). The exposed crown of the most mature replacement caniniform tooth in BRSMG Cd6172 was 25 mm long; the depth of the base and full length cannot be determined.

Sauropterygian teeth were replaced through a threefold replacement schedule (Romer 1956; Edmund 1960; Shang 2007). Such a replacement rhythm may have existed in BRSMG Cd6172 as, at least in the anterior caniniform teeth, different stages of the full cycle appear every 3–4 teeth, but further evidence cannot be determined. Replacement cycles for the caniniform and smaller hooked teeth may have been different. If the enamel rings (Fig. 14D, H) on the teeth were growth related (Brusatte *et al.* 2007; Andrade *et al.* 2010), and as there are far more on the caniniform teeth, this suggests a longer maturation and replacement cycle, with the posterior hooked teeth replaced more frequently. High-powered CT scans of the jaws could shed light on the replacement cycle by identifying replacement teeth deep within the mandible, but the specimens were too dense for standard X-radiographs.

CONCLUSIONS

1. Based on previous work (Tarlo 1960, as modified by Noè *et al.* 2004), BRSMG Cd6172, a pliosaur from the Lafarge cement works at Westbury in Wiltshire, is assigned to the genus *Pliosaurus* (Owen 1842), but not assigned to species pending full revision of the genus.
2. Mandibular symphysis length is probably not a useful character for differentiating species of *Pliosaurus*, as there appears to be greater variability than previously thought.
3. As the criteria defining members of the genus *Pliosaurus* are currently under revision (Gómez-Pérez and Noè, in prep.), the assignment of BRSMG Cc332 to *P. brachyspondylus* (Taylor and Cruickshank 1993) is questionable, especially as the mandibular symphysis of BRSMG Cd6172 is shorter than in another specimen (CAMSM J.35991) referred to the same species.

4. Comparison of landmark measurements of BRSMG Cd6172 and BRSMG Cc332 suggests that the two specimens belong to the same species. The main anatomical differences are in the regions of the snout, parietal crest and distribution of the postsymphseal teeth, which may be sexually dimorphic differences.
5. The internal nares of BRSMG Cc332, in comparison with BRSMG Cd6172, are positioned more posteriorly than previously described (Taylor and Cruickshank 1993).
6. BRSMG Cd6172 was an old, possibly female, pliosaurian, of large size, with many fused sutures and a suite of age-related pathologies, including arthrotic disease of the articulars, which caused prolonged jaw misalignment. Evidence of pathological damage from maloccluded teeth in both lower and upper jaws supports this hypothesis. Disease possibly weakened the right jaw articulation sufficiently to cause a perimortem fracture.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Comparative dimensions, ratios normalised to skull length, and percentage differences between landmark points on the crania of the two Westbury pliosaurs BRSMG Cd6172 and BRSMG Cc332.

Table S2. Summary of data describing the dentition in BRSMG Cd6172, giving diameters of functional alveoli with missing teeth, and where present, lengths of functional and replacement teeth. (A) premaxillae, (B) maxillae and (C) dentaries.

Table S3. Comparative data for teeth from the two Westbury pliosaurs, BRSMG Cd6172 and BRSMG Cc332. Tooth crown height from bottom of enamel to apex of crown. Directionality of the tooth is given by the minor curvature viewed axially (Fig. 14A(iv), B(iv)).

Table S4. Variation in the snout widths of Westbury pliosaurs BRSMG Cc 332 and BRSMG Cd6172.

Table S5. Cranial and mandibular synapomorphies preserved in BRSMG Cd6172 justifying inclusion in Pliosauroida and Pliosauridae. Synapomorphies listed with character numbers employed by Ketchum and Benson (2010).

Table S6. Dorso-ventral depth of the snouts of Westbury pliosaurs BRSMG Cc332 and BRSMG Cd6172 at three positions.

Appendix S1. Tables of measurements and statistical data..

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