Cranial Anatomy and Functional Morphology of Pliosaurus brachyspondylus (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire

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Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire

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SUMMARY

An exceptionally complete skull, mandible and other bones of *Pliosaurus brachyspondylus* were collected from the Kimmeridge Clay of Westbury, Wiltshire, in 1980. The recovery and preparation of this large specimen required special techniques. The specimen is apparently part of a more complete skeleton, mostly destroyed before discovery. The decayed carcass was apparently disrupted so that the skull finally lay upside down over many of the teeth, which had fallen out, while the mandible lay several metres away. The reasons for this are unclear.

The skull does not differ markedly from the usual pliosauroid pattern, being long and low, with a wide gape, narrow snout, and high temporal region. There are no nasals. The mandible cannot be satisfactorily reconstructed due to crushing but does not appear to deviate from the usual pliosauroid pattern.

The dentition is robust and caniniform anteriorly, presumably to penetrate, hold and kill large prey. The posterior teeth are hook-shaped posteriorly to act as ratchets, helping to move large prey items back into the gullet.

The jaw musculature is reconstructed as a dual-function system, the pterygoideus musculature being specialized to close the open jaws rapidly against inertia and drag, and the main adductor mass being specialized to clamp the jaws tightly onto prey. The cranial skeleton is well adapted to resist bending stresses induced when the animal bit onto prey. However, there is no evidence for any adaptation to torsional resistance, such as a pterygoid flange-mandible contact, as would be useful in twist-feeding to dismember large prey.

Pliosaurus, at about 10 m overall length, may have been large enough to swallow most potential prey without being particularly specialized to dismember it. Its wide gape would help it swallow large prey. However, the comparatively narrow anterior snout, and evidence from gut contents in other specimens,

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suggest that it was an opportunistic feeder on a wide variety of prey of different sizes, including cephalopods and presumably fish and other reptiles. Large orbits and the lack of acoustically isolated ears indicate that it was primarily a visual hunter. The nares seem too small to be used in respiration, and may instead have been used in underwater olfaction.

1. INTRODUCTION

On 2 July 1980 the almost complete skull and some other bones of a large pliosauroid plesiosaur were discovered in a quarry in the Kimmeridge Clay near Westbury, Wiltshire, England (figure 1), and eventually donated to Bristol City Museums and Art Gallery by the quarry owners, the Blue Circle Cement Company. This specimen, informally named the 'Westbury pliosaur', was immediately excavated by Museum staff, briefly displayed in September 1980, and reported by Crane (1980). It became available for permanent exhibition and study in 1989 with the completion of preparation and mounting work (Taylor 1989*a*). An associated popular booklet (Swansborough 1989) identified it, following L. B. Halstead and M.A.T., as *Liopleurodon*. We reidentify it here as *Pliosaurus brachyspondylus*. Few comparable specimens of Kimmeridgian pliosauroid heads have been discovered and none is so complete. This study aims to describe the provenance, taxonomy, and taphonomy of this specimen, and the functional anatomy of its head, to extend our understanding of pliosauroid diversity. A.R.I.C. prepared the reconstruction drawings, and M.A.T. wrote the description and functional analysis.

The assemblage is registered as BRSMG Cc332 with individual elements designated by alphabetical suffixes (e.g. Cc332ab). Full lists of bones, associated specimens, and excavation and preparation records are deposited at BRSMG (Geology Files 198 and 301–310; Geology MS. 95), and are henceforth cited as 'BRSMG Archives'. Repository abbreviations are: BMNH: Natural History Museum, Cromwell Road, London SW7 5BD, U.K.; BRSMG, Bristol City Museums and Art Gallery, Queen's Road, Bristol BS8 1RL, U.K.

Figure 1. The Kimmeridgian outcrop in England. W, Westbury, findspot of BRSMG Cc332 *Pliosaurus brachyspondylus*.

2. MATERIALS AND METHODS

(*a*) *Locality and horizon*

The Westbury claypit was opened in 1962 to win Kimmeridge Clay for mixing with Chalk in the manufacture of Portland Cement (Hudson 1984). The pliosaur was found in one side of the quarry (Crane 1980, BRSMG Archives), at National Grid Reference ST 88175267. The locality has now been quarried away. The sequence then exposed in the pit extended from the *Rasenia cymodoce* to the *Aulacostephanus eudoxus* ammonite Zones of the Lower Kimmeridge Clay, Kimmeridgian Stage, Upper Jurassic (Crane 1980; Birkelund *et al.* 1983). Birkelund *et al.* (1983) found the pliosaur within the *A. eudoxus* Zone, in and 1 m below the top of their Subdivision E5, thus about 4.2 m below the top of the section then exposed, and 1 m below their E6 Marker or Crussoliceras Limestone. E6 is the '*Propectinatites*' Band of Gallois & Cox (1976), a lithologically persistent horizon throughout the English Kimmeridge Clay from Dorset to north Yorkshire. Both the pliosaur horizon and the '*Propectinatites*' Band fall within 'Bed 30' of Gallois and Cox (1976).

There is no one review of the stratigraphic distribution of marine reptiles in the British Kimmeridgian. The Upper Kimmeridgian is briefly reviewed by Taylor & Benton (1986), and other Kimmeridgian reptiles are reported by Lydekker (1889), Delair (1958, 1959, 1960, 1974, 1982), Tarlo (1960 and references therein), Taylor (1989*b*), and Oates (1991). Little is known of the depositional and preservational factors affecting these reptiles but R. W. Gallois (personal communication 1991, 1992) notes that recent finds of associated skeletons have tended to occur in or near the more calcareous beds of the Kimmeridge Clay, notably Beds 18, 30 and 44 of Gallois & Cox (1976) and Cox & Gallois (1981), at least in those cases where the precise locality has been recorded. This correlation is consistent with, but cannot be regarded as being proven by, the relatively poor data available from the few known finds. BRSMG Cc332 came from Bed 30 at Westbury. A specimen of the pliosauroid *Liopleurodon macromerus* was recovered from Stretham borrow pit, about 8 km south of Ely, Cambridgeshire (Tarlo 1959*b*), which was mostly in Bed 18. Bed 30 occupies much of the exposed sequence at Roslyn Hole, Ely, Cambridgeshire (Gallois 1988), which yielded a partial skeleton of *Pliosaurus brachyspondylus* (Tarlo 1959*a*). Bed 44 is included in the section at Downham Market flood relief channel, Norfolk, which yielded the genotype specimen of the ichthyosaur *Grendelius mordax* McGowan, 1976. The second, and more complete, specimen of *G. mordax* (BRSMG Ce16696) came from 'about 20 feet' below the White Stone Band at the eastern end of the Kimmeridge Ledges, Dorset, thus

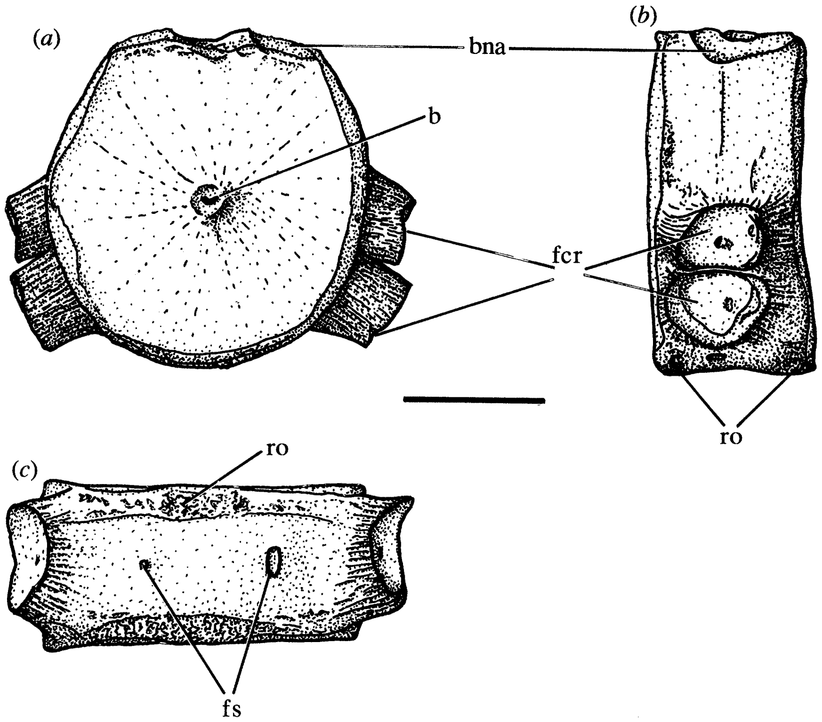

Figure 2. BRSMG Cc332 *Pliosaurus brachyspondylus*. BRSMG Cc332cd, anterior cervical centrum. (*a*) posterior face; (*b*) left view, front to left; (*c*) ventral view, front to top. Scale bar, 5 cm. For abbreviations in this and other figures, see p. 417

within Bed 45 or perhaps the topmost part of Bed 44 (Cox & Gallois 1981). However, Oates (1991) noted that marine reptile bones, including associated and articulated skeletons, are most numerous in that part of the Kimmeridge Clay section at Aylesbury, Buckinghamshire, which may represent Beds 36 to 42. The localization of large, well-articulated skeletons to certain horizons is well seen in the Oxford Clay (Callovian) of England (Martill 1985).

(*b*) *Taxonomy*

Class: Reptilia
Subclass: Sauropterygia Owen, 1860
Order: Plesiosauria de Blainville, 1835
Superfamily: Pliosauroidea (Seeley, 1874) Welles, 1943
Family: Pliosauridae Seeley, 1874
Genus: *Pliosaurus* Owen, 1842
Pliosaurus brachyspondylus (Owen, 1840)

Tarlo (1960; now better known as L. B. Halstead) revised the taxonomy of the Upper Jurassic pliosauroids and Brown (1981) discussed plesiosaur taxonomy in general. Only two valid genera, *Liopleurodon* Sauvage, 1873, and *Pliosaurus* Owen, 1842, are known from the Kimmeridgian, and even these are poorly known. *Stretosaurus* Tarlo, 1959*b* is a junior synonym of *Liopleurodon* (Halstead 1989). Initially the Westbury Pliosaur was tentatively assigned to *Liopleurodon* by L. B. Halstead and M.A.T. (in Swansborough 1989). However, reconstruction of the missing mandibular symphysis by comparison with the skull (§ 3*b*) shows that the symphysis bore approximately 11 pairs of teeth, as in *Pliosaurus*, not the 5–6 pairs diagnostic of *Liopleurodon*.

Tarlo (1960) listed two valid Kimmeridgian species of *Pliosaurus*: *P. brachydeirus* (Owen, 1842) and *P. brachyspondylus* (Owen, 1840). They are poorly known from a few incomplete skeletons and Tarlo was only able to make a brief differential diagnosis (1960, pp. 152, 157): *P. brachydeirus*, ‘Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae with well-marked ventral keel; posterior cervical vertebrae with boss in centre of articular surface. Epipodials short’; *P. brachyspondylus*, ‘Teeth trihedral in cross-section, outer surface smooth and flat. Cervical vertebrae with finely sculptured double rugosity on ventral surface and no ventral keel: posterior cervical vertebrae with no boss in centre of articular surfaces’.

The characters of the teeth are clearly non-diagnostic and the specific identity therefore depends on the characters of the cervical vertebrae. The four cervicals in BRSMG Cc332 (figure 2) bear ventral rugosities, but no ventral keel. Two (Cc332cc,de) have only very low bosses around the notochordal pit in the anterior articular surface, so match the definition given for *P. brachyspondylus*. However, the other two (Cc332cd, dd) bear ill-defined swellings around the pit on both articular surfaces. More recently, the presence or absence of rugosity on plesiosaur vertebrae has been interpreted as an ontogenetic feature of little taxonomic significance (Brown 1981) and we suspect that the presence and size of the central swelling of the articular surface is also in part ontogenetic. If so, then the specific distinction depends solely on the presence of ventral keels on the cervical centra. Although we do not consider this to be at all conclusive evidence, we assign BRSMG Cc332, for now, to *Pliosaurus brachyspondylus* (Owen, 1840).

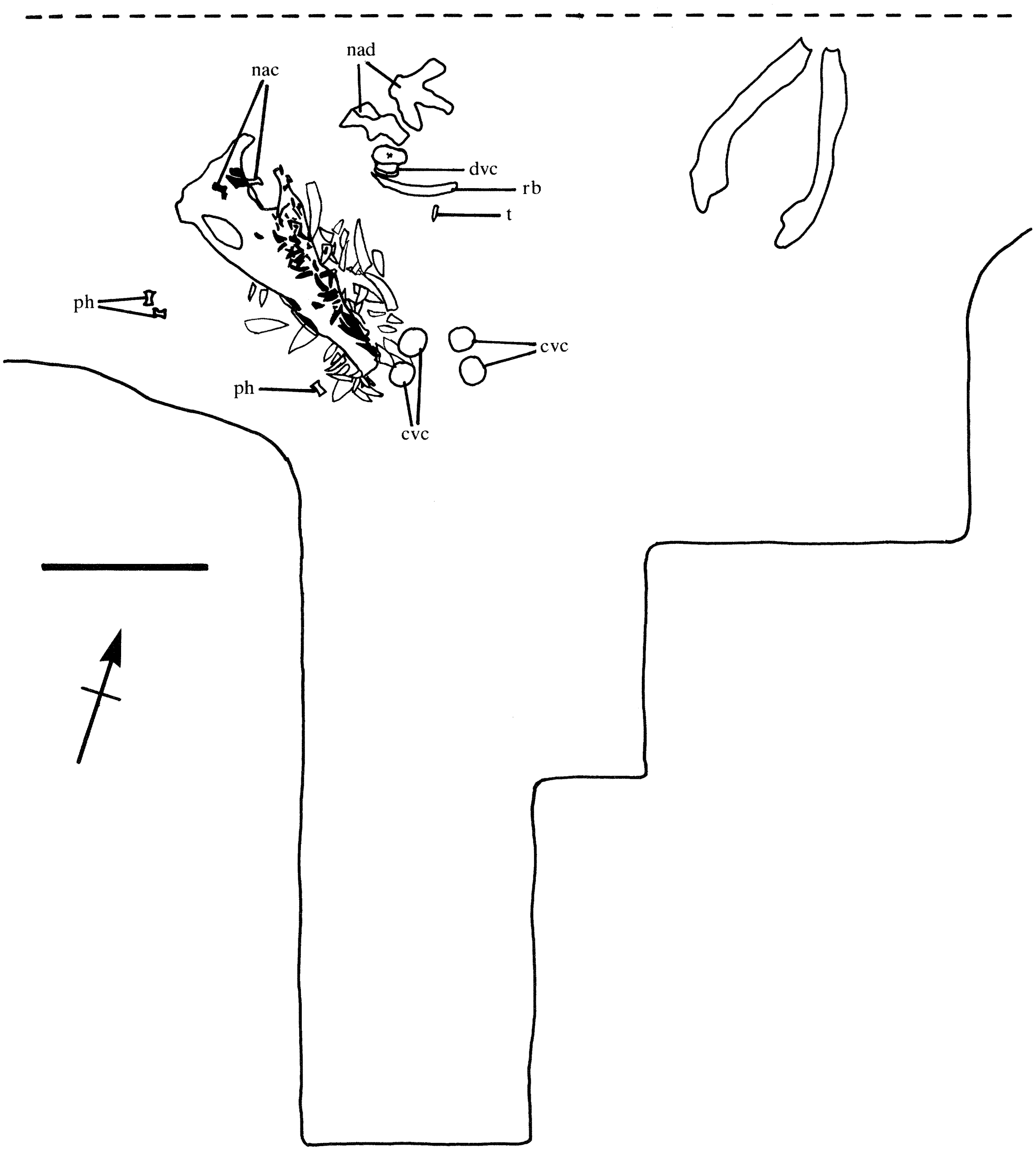

Figure 3. Sketch plan of excavation for BRSMG Cc332 *Pliosaurus brachyspondylus*, showing scatter of bones around skull and mandible, both of which were lying inverted. Note loss of mandibular symphysis and presumably other items at edge of bedding plane (dashed line) removed by excavating machinery before the specimen was discovered. Not all elements were recorded during excavation, and others which were apparently disturbed have been omitted, so that this is only a partial record of the taphonomy of the site. The teeth and bones around the skull are shown in outline (not covered by the skull) or solid (covered by the skull). Scale bar, 1 m.

(*c*) ***Excavation and preparation***

The excavation and preparation of the specimen are recorded in photographs, notes and videotape in BRSMG archives (§ 1). They are worth describing as solutions to the technical problems posed by the collection of large, delicate vertebrate skeletons from soft, unstable matrices (cf. Rixon 1976; Crowther & Collins 1987).

Excavation was directed by Dr M. L. K. Curtis (then Curator of Geology, BRSMG). The original excavation was done by hand around the mandible and skull. A number of bones and teeth had been removed without their position being recorded, but the location of most items was recorded. The mandibular symphysis had been destroyed by machinery; fragments of it and other bones were found amongst the scattered bone on the slope. Several other bones had also been disturbed by machinery. For these reasons the bone scatter map is incomplete (figure 3).

The specimen was consolidated in the field with a thick 30% solution of polyvinylacetate emulsion in water. The matrix was a calcareous clay which was locally indurated. Much of the bone and teeth were covered in a fine layer of calcite, sometimes fibrous ('beef') because of pressure-solution effects (Martill 1985). Pyrite occurred in localized patches.

The top and sides of the skull were excavated and embedded in aluminium foil, a cloth and plaster jacket and then a layer of glass fibre reinforced resin. A crate was then constructed of thick blockboard with an open top and gaps between the bottom slats. It was inverted over the skull and polyurethane foam poured into the crate. The gaps allowed expansion of the foam. The hardened foam supported the specimen, which was then undercut. Planks were nailed across the bottom as the specimen was undercut. Steel strapping was used to reinforce the crate before a mobile crane turned it over. The inverted crate was transported to the museum and mounted on a trolley for initial preparation. The right mandibular ramus was fractured into pieces; each was lifted out individually. The left ramus was removed intact in a cloth and plaster jacket using aluminium foil to separate the bone from the plaster.

A further 10 m^2 of area around the original excavation were stripped of overburden by machinery and the last 25 to 50 cm depth removed by hand, but only one additional element, a tooth, was found.

Preparation was carried out in two phases, 1980–1981 and 1986–1988. Initial preparation involved removal of the field consolidant in acetone to dismantle the fractured pieces. Mechanical preparation was used to remove most of the clay, which had cracked on drying, weakening the specimen. Original cleaning was by ultrasonic treatment in a Bondent Ltd 'Periosonic' dental cleaner, using a solution of detergent (ICI 'Teepol') in water as the ultrasonic medium. Some pieces of bone were prepared by immersion in dilute acetic acid solution. The fragments were reassembled using a thick glue of polyvinylacetate resin dissolved in acetone. These methods were used to clean most of the mandibular rami and the dorsal side of the skull which was the first to be exposed after inversion. They had the apparent advantage of avoiding the dismantling and removal of the skull from the cradle. However, with hindsight, they were not successful. The ultrasonic treatment eroded the bone especially where it was friable and fractured by crushing. Delay in completing preparation allowed the specimen to dry out; the use of water had then to be abandoned as it would have caused the unstable clay matrix to swell and then shrink again on drying out, fracturing the specimen.

During the second stage of preparation it was found that the polyvinylacetate adhesive applied several years before had failed by creeping, because of its low glass transition temperature (at which it changes from a rigid solid to a creeping 'liquid' glassy material). All previously consolidated bones were wrapped in stretch fabric bandages and soaked in propan-2-ol to remove the old glues. These bones were then taken apart and each piece was consolidated in a solution of Paraloid B72 (an acrylic copolymer resin currently provided by Conservation Resources, Oxford; 5% mass to volume in acetone) and reconstructed using a 20–30% solution of Paraloid B72 in acetone as an adhesive. Some areas then underwent surface consolidation using 10% Paraloid B72 in acetone. Paraloid B72 is a useful new consolidant, resistant to yellowing, and penetrating well when dissolved in a solvent such as acetone. It is reversible, and resists creeping, remaining hard at higher temperatures than does polyvinylacetate.

During final preparation, the ventral surface of the skull and the remaining portions of the mandible were prepared using mechanical and air abrasive methods. The skull was dismantled along existing cracks and each portion was prepared using mechanical methods, removing clay and calcite crust with hand held needles or electric percussion engravers (Burgess Engravers, various models; F. J. Joel Ltd, now unavailable; Record Power Tools, Sheffield, various models) using tungsten carbide needles manufactured from rod (Taylor 1992*a*). Final cleaning was carried out to a very high standard by D. B. Hill and E. A. Milsom, using an air abrasive with glass beads (S. S. White Model K; glass bead No. 9 powder; Reg Abrasonics, Dartford, Kent) at 1–2 bar pressure for general cleaning, increasing to 2–3 bar for heavy calcite and pyrite encrustations, while the work was viewed through a stereomicroscope. A straight nozzle, internal diameter 0.46 mm, was used for most surfaces, but a right-angled nozzle of the same diameter was used for the interior of tooth sockets and other restricted areas. The last step was the construction of glassfibre reinforced plastic cradles for display and storage by D. B. Hill. The specimen remains in a number of parts which simply rest loose in the cradles and are easily accessible for study, unlike more conventional mounts embedding the specimen in a rigid matrix or fixing it on a metal armature.

(*d*) *Taphonomy*

The specimen is preserved as medium brown mineralized bone, usually well preserved, and variably crushed by sediment compaction. Rapid burial, hostile benthic conditions or both are indicated by the almost complete lack of epifaunal growth on the bone, except for a few 'oysters' (*Exogyra* sp.) on the mandible. The incomplete taphonomic scatter map (figure 3; § 1) records only undisturbed elements, but shows several remarkable features.

The *in situ* assemblage was mainly cranial and cervical material but with several postcervical bones, including isolated phalanges and especially a group of associated dorsal vertebrae and a rib. The presence of postcranial material *in situ* suggests that the original corpse was substantially complete when it finally sank to the sea-floor; we are not dealing with an isolated head and anterior neck which fell off a drifting corpse, as Swansborough (1989, following M.A.T.) originally suggested. Plainly the skeleton was disarticulated and scattered before burial. The greater part was never recovered, and was perhaps destroyed by quarry machinery before discovery. We are not even certain of the animal's orientation, as it may have lain with its neck flexed (cf. Taylor 1992*a*). Disturbance may have been caused by gases of decomposition within the body cavity. Further evidence suggesting rupture of the abdominal cavity at the place of burial is the presence of three scutes directly associated with the pliosaur and possibly from its stomach contents.

Taylor *et al.* (1993) ascribed these scutes to an unidentified ornithischian dinosaur which the pliosaur had presumably scavenged.

Most teeth are present (§ 4*a*), but we are unable to account definitively for their arrangement. Many were found under, and to one side of, the inverted skull, with the mandible also lying upside down about 2 m away. This suggests that the pliosaur fell to the sea floor before the connective tissue holding the teeth rotted enough for the teeth to fall out of their sockets. The teeth may have been held in strips by remnants of gum tissue (cf. cetaceans figured by Schäfer (1962)). At a later stage, when the teeth were completely freed, some agent or agents moved the mandible to one side and then displaced the skull enough to move it over the teeth then lying in the mud. One possibility is attack by a large scavenger, but there is no evidence of toothmarks or of scavenging other than two teeth of rather small sharks which may be there fortuitously. Alternatively, the skull and mandible may have been dragged around by the body inflated with gases of decomposition. It does however seem unlikely that the connective tissue around the teeth roots loosened enough for the teeth to fall out, before gases of decomposition were able to escape from the body cavity.

Perhaps the skull itself became buoyant. Bones of turkeys (*Meleagris gallopavo*) decaying in sea water accumulate gas within pores and cavities, sometimes becoming positively buoyant (Dr D. M. Martill, personal communication 1990). The numerous cavities in the head of *Pliosaurus* would have acted as gas traps. The carcass of a large marine vertebrate may sink to the sea floor on death but eventually rises when the gases of decomposition make it buoyant, unless the water depth, and therefore pressure, sufficiently reduce the gas volume and buoyancy (Allison *et al.* 1991). We speculate that the water was just deep enough for the pliosaur's skull to rise until the disarticulation of the skull, teeth and mandible caused contained gases to escape. The various parts of the head then sank, shedding the teeth.

The collection contains other pliosaur material in the form of a limb girdle fragment and also pieces of the jaw ramus of a smaller individual, but these were found loose on the quarry slope below the site, and were not certainly associated.

3. CRANIAL OSTEOLOGY

(*a*) *Skull*

Our reconstruction of the skull (figures 4–7) largely conforms to the usual pliosauroid form. Our description therefore concentrates on areas of uncertainty or particular interest. The skull of BRSMG Cc332 is badly crushed dorsoventrally and somewhat obliquely. Corrections have involved estimation of the original vertical dimensions, affecting especially the lateral and posterior views.

As is usual in pliosauroids, the dorsal part of the snout is largely made up of the premaxillae (pmx) and maxillae (mx), with the external nares (en) at the junction between the premaxillae, maxillae and frontals (f). As usual in plesiosaurs, there are no nasals. The specimen is important in showing clearly the jugals (j), lacrimals (l), prefrontals (prf), postfrontals (pof), and postorbitals (po). The frontals are scarcely exposed dorsally, being almost completely covered by posterior extensions of the premaxillae which interdigitate with the parietals (p). However, on the ventral face of the skull roof, the frontals are more completely exposed. They meet in the midline between the nares and parietals. Ventrally each bears a sharp longitudinal crest above the orbit (orb), inclined inwards towards the opposite crest to form a median tunnel, presumably for the olfactory lobes, and similar to that figured in the Callovian pliosauroid *Peloneustes* by Andrews (1896). The anterior end of each crest ends at the median end of a low rounded ridge running outwards on the ventral side of the frontal anterior to the orbit, and presumably homologous to the much deeper antorbital flange of other pliosauroids such as *Rhomaleosaurus* (Taylor 1992*b*). Laterally and externally the lacrimal, forming part of the anterior border and interior wall of the orbit, appears to overlap the frontal mesially and to form part of the antorbital thickening. The postfrontal is dorsoventrally compressed and wide from front to back, bearing a low crest running posterolaterally. The postorbital tapers to an interdigitating suture with the mesial prong of the postorbital. As a whole, the median portion of the interorbital bar, roughly corresponding to the premaxillae, frontals and parietals, is relatively deep dorsoventrally, but the lateral portions, corresponding to the prefrontals, postfrontals, and other bones, are flatter.

The jugal is a large bone forming the lateral rim and apparently the posterolateral corner of the floor of the orbit. It contacts the lacrimal anteriorly, postorbital dorsally and squamosal posteriorly. The postorbital and squamosal contact briefly to exclude the jugal from the dorsal edge of the temporal fenestra. The ventral side of the jugal bears a long, shallow trough holding the tapering posterior extremity of the maxilla. Crushing obscures the exact relationships of the jugal, maxilla, ectopterygoid (ec) and suborbital fenestra (sof). The maxilla is here reconstructed as tapering without a posterior expansion, and the jugal as forming the mechanical junction between the maxilla, postorbital, squamosal and ectopterygoid. It is unclear whether the jugal excludes the maxilla and the ectopterygoid from contact with each other.

The fused parietals (p) form a massive median dorsal bar with a high sagittal crest bifurcated anteriorly to house the parietal fossa (pfo). They bear ventrolateral crests which meet the epipterygoids (ep). Each epipterygoid is a robust, laterally compressed pillar closely united to the pterygoid (pt) ventrally and bracing the parietals against it.

The braincase is greatly distorted by crushing, plastic deformation and fracturing. As far as can be seen, it is of the usual pliosauroid form as described by Andrews (1913), and little further can be said. The parasphenoid (ps) is roughly triangular in section, with a rounded ventral crest and flattened top. It

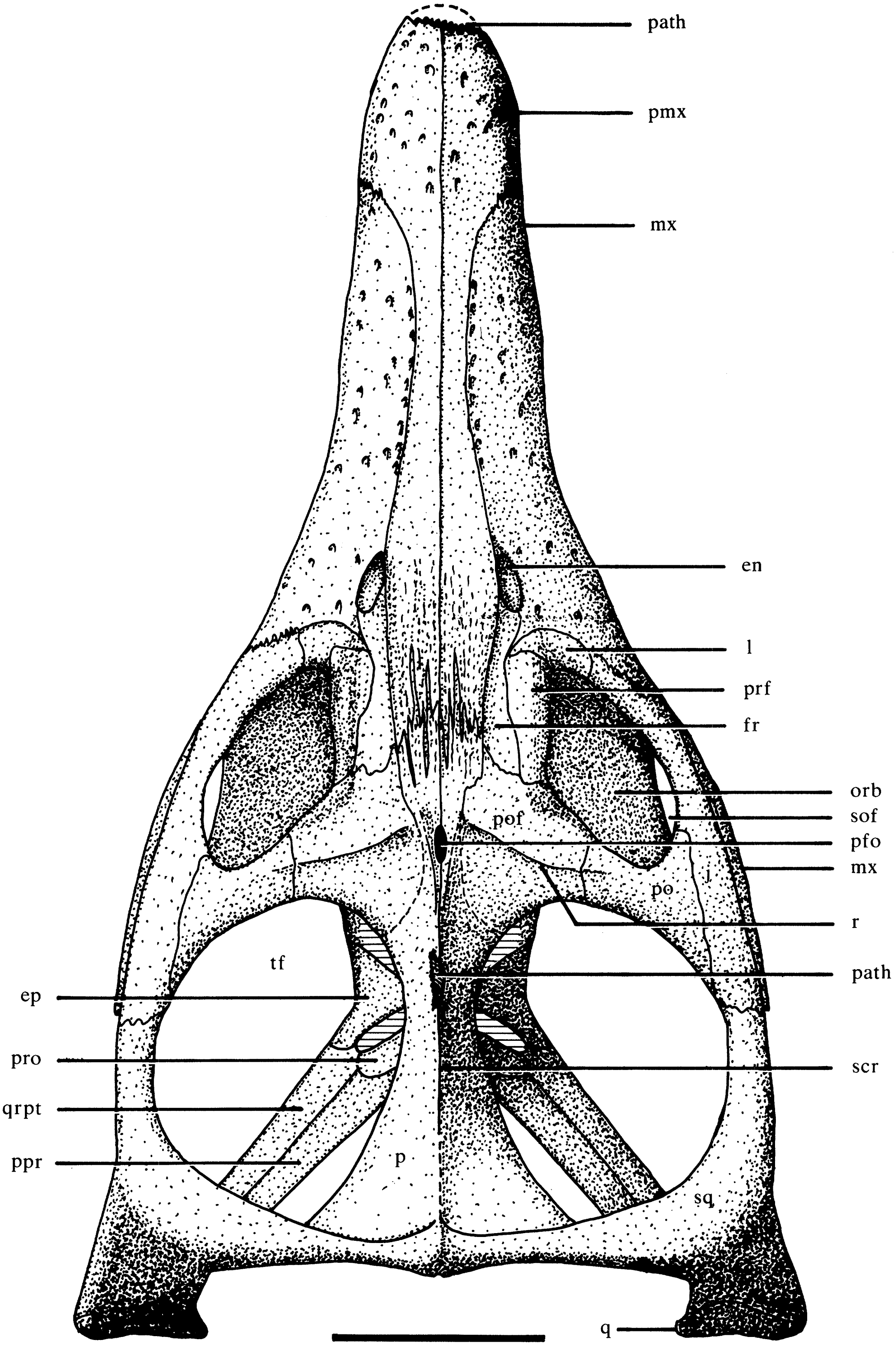

Figure 4. *Pliosaurus brachyspondylus*. Reconstruction of skull in dorsal view. Scale bar, 25 cm.

divides the two posterior interpterygoid vacuities (piv). The parasphenoid has a strong interdigitating suture with the pterygoids anteriorly. Posteriorly, the braincase is ventrally overlapped by the pterygoids. The massive basioccipital (bo) bears the rounded occipital condyle (oc), which is wider than it is deep, and carries several irregular pits and a central notochordal pit. It is not possible to reconstruct satisfactorily the pillar-like portions of the exoccipital-opisthotics on either side of the foramen magnum (fm), or the supraoccipital. The paroccipital processes (ppr) of the exoccipital-opisthotics are long and laterally compressed, running posterolaterally to the quadrates and leaving elongated posttemporal fenestrae (pfe) above

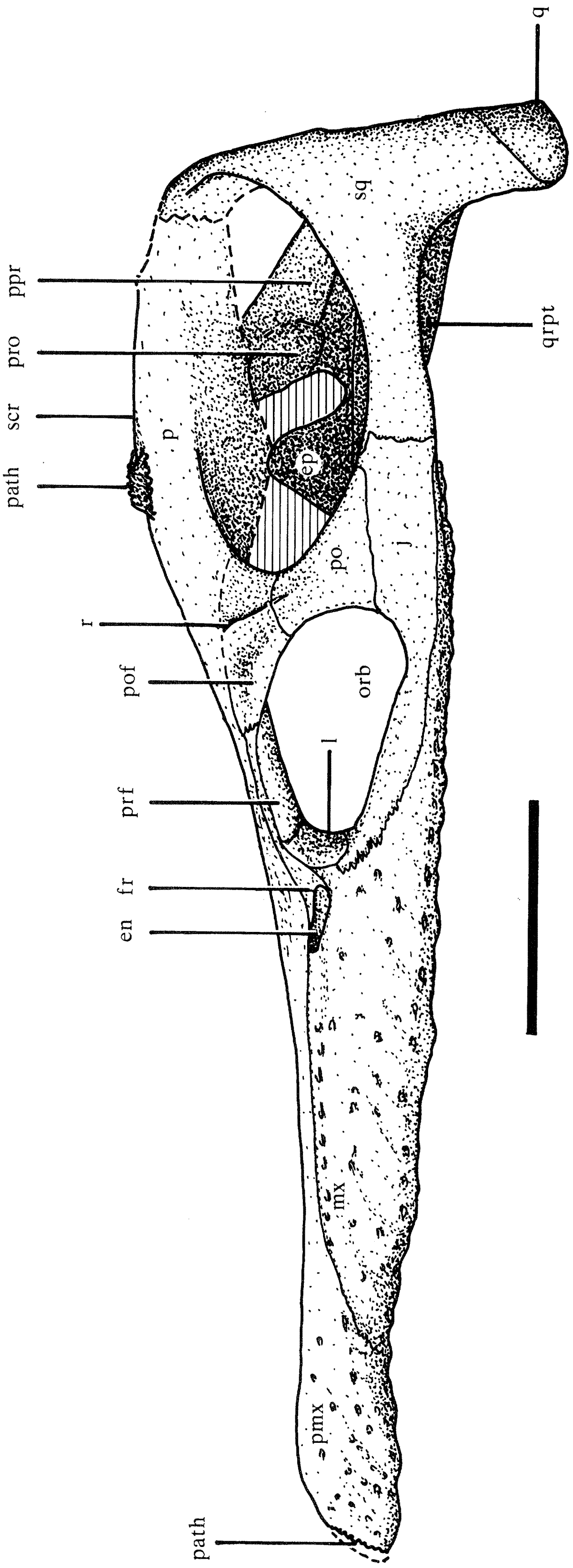

Figure 5. *Pliosaurus brachyspondylus*. Reconstruction of skull in lateral view. Scale bar, 25 cm.

them. Only the left prootic is visible, an irregularly polygonal bone severely crushed onto the pterygoid.

The palate is almost intact but has suffered localized damage and distortion, which obscures the precise locations of many sutures. It is more or less flat. The dental alveoli are carried within the margins of the premaxillae and maxillae, within a strip of variably textured bone demarcated from the remainder of the palate. The paired vomers (v) are partly fused with obliteration of the anterior half of the median suture. They are greatly elongated, running forward between the premaxillae to end at the posterior end of a median ventral boss (vb) formed by the premaxillae. The vomers appear to extend posteriorly to extraordinarily small paired internal nares (in) which are bounded by the vomers and laterally by the maxillae. Each internal naris opens anteroventrally and merges smoothly into the posterior end of a shallow inverted trough running forwards along the palate. Each palatine (pal) is a long strip running from the vomer to the ectopterygoid. Anteriorly, it is stiffened by a low ridge on its dorsal surface. It appears to meet the maxilla in a butt joint. Posteriorly the medial edge is punctuated by a large foramen (palf) where it meets the pterygoid.

Both ectopterygoids (ec) are damaged. Each seems to be a roughly triangular bone overlapping the pterygoid ventrally, meeting the palatine anteriorly, and forming part of the medial edge of the suborbital foramen (sof), much as in the Callovian pliosauroids figured by Andrews (1913).

The pterygoids (pt) are complex bones, as in other pliosauroids, with anterior, lateral, posterior and quadrate rami. The anterior ramus is large and flat and meets the vomers anteriorly. Medially the anterior rami part to form the anterior interpterygoid vacuity (aiv). The lateral rami of the pterygoids are wide and flat bones. There is no development of a significant pterygoid flange, other than a low, rugose elevation (ro) on the ventral face of the lateral ramus. The posterior rami of the pterygoids meet in the midline posterior to the posterior interpterygoid vacuities (piv) to cover the ventral basicranium. The ventrolateral flange (vlf) of the posterior ramus runs from the rear edge of the lateral ramus of the pterygoid and meets its opposite in the midline. The transverse shelf (sh) is formed by the posterior rami under the occipital condyle, and merges laterally into the ventromedial edges of the massive quadrate rami of the pterygoids. These quadrate rami are crushed, but their distal portions were rounded in cross-section, deeper than they were wide, and thicker ventrally than dorsally.

The crushed and sheared squamosals (sq) and quadrates (q) together form a massive arch. The reconstruction presented here as a best estimate shows the jaw articulations projecting laterally somewhat beyond the sides of the skull, but it should be noted that this overhang does not seem to be present in the Callovian material figured by Andrews (1913). The squamosals and quadrates have the characteristic plesiosaurian triradiate structure. The anterior ramus of the squamosal is compressed from side to side. It

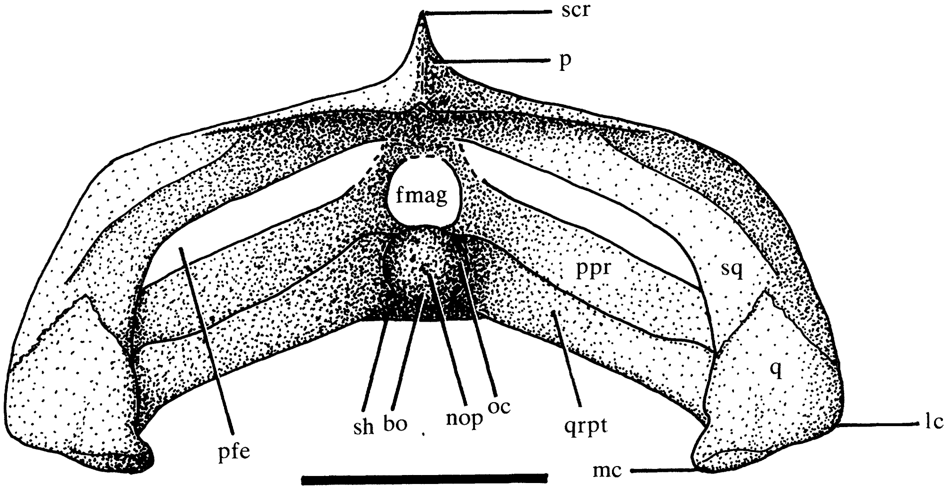

Figure 6. *Pliosaurus brachyspondylus*. Reconstruction of skull in occipital view. Scale bar, 25 cm.

tapers gradually and curves inwards anteriorly to meet the jugal and also, briefly, the postorbital on the dorsomedial edge of the bar. The dorsal ramus of the squamosal, extending medially to the parietals, is deep and complex. Dorsally it widens laterally and merges into the anterior ramus. The ventral portion of the ramus expands into the dorsal roofing plates of the braincase. The squamosal holds the quadrate wedged into itself. Ventrally the squamosal meets the paroccipital process. The posterior end of the quadrate ramus of the pterygoid is damaged on each side, but it is concave inside, and convex outwards, in cross-section. The external edge is covered by a lamina from the quadrate. The quadrate bears the usual plesiosaurian double condyle structure, with shallow lateral (lc) and deep medial (mc) condyles.

The remains of at least five sclerotic plates are present, most still in the floor of the left orbit. They are irregular, rather thick bones without any clear sclerotic sulcus.

The anterior extremity of the premaxillae shows damage (path) which combines a break or erosion with the development of a roughly textured irregular growth of bone. The parietal crest also bears an asymmetric, rugose growth (path). This proliferative, presumably pathological, growth may be a tumour or a reaction to some form of trauma, perhaps an infection or wound. Possibly the original loss of premaxillary bone happened when a tooth broke off when handling large prey. Wells (1964) reported bone damage of uncertain cause, combining erosion and proliferative growth, in the epipodials and tarsus of a specimen of the Kimmeridgian pliosauroid *Liopleurodon macromerus*.

(*b*) *Mandible*

The mandible is crushed dorsoventrally, leading to fracturing and lateral spreading, especially in the region of the posterior end of the dentary and the adductor fossa. The height and width are estimated in the reconstructions (figures 8 and 9). The symphysis is missing except for the posterior termination of the symphyseal facets on the coronoids, which allows an estimate of the total length of the postsymphyseal portion by comparison with the rostrum. The distance between the jaw rami is taken from the positions of the quadrates in the skull reconstruction. Comparison with the skull reconstruction indicates that the mandible had a relatively long, narrow rather than spatulate symphysis, bearing about 10 or 11 pairs of symphyseal teeth. The symphysis has been reconstructed in outline following data in Tarlo (1960).

As far as can be seen, the structure of the mandible is typical of pliosauroids as in, for example, *Rhomaleosaurus* (Taylor 1992*b*) and *Peloneustes* (Linder 1913). It is composed largely of the dentary (d) and coronoid (co) anteriorly, and surangular (sa) and angular (a) posteriorly, with the articular (ar) sheathed ventrally by the angular. Crushing and damage make it impossible to trace the full outlines of the elements, especially the coronoids, splenials and prearticulars, and the precise extent of the adductor fossa. The prearticular (pa) appears to be present as a narrow tongue forming the medial rim of the adductor fossa, with the pointed rear end lost in the articular-surangular suture below the glenoid, and the anterior end extending at least as far as the coronoid eminence. The splenial (sp) is a robust bone fitting into a groove in the angular. The glenoid fossa (gl) was borne on lateral and medial flares of the mandibular ramus (lflr, mflr). It had the usual kidney-shaped pliosauroid form in dorsal view, with shallow lateral and deeper medial cavities to match the quadrates, and demarcated anteriorly and posteriorly by transverse crests (atrc, ptrc).

4. DENTITION

(*a*) *Description*

Most of the teeth were found loose, many are broken and incomplete, and some are completely fragmented, making an accurate count impossible. Counting tooth

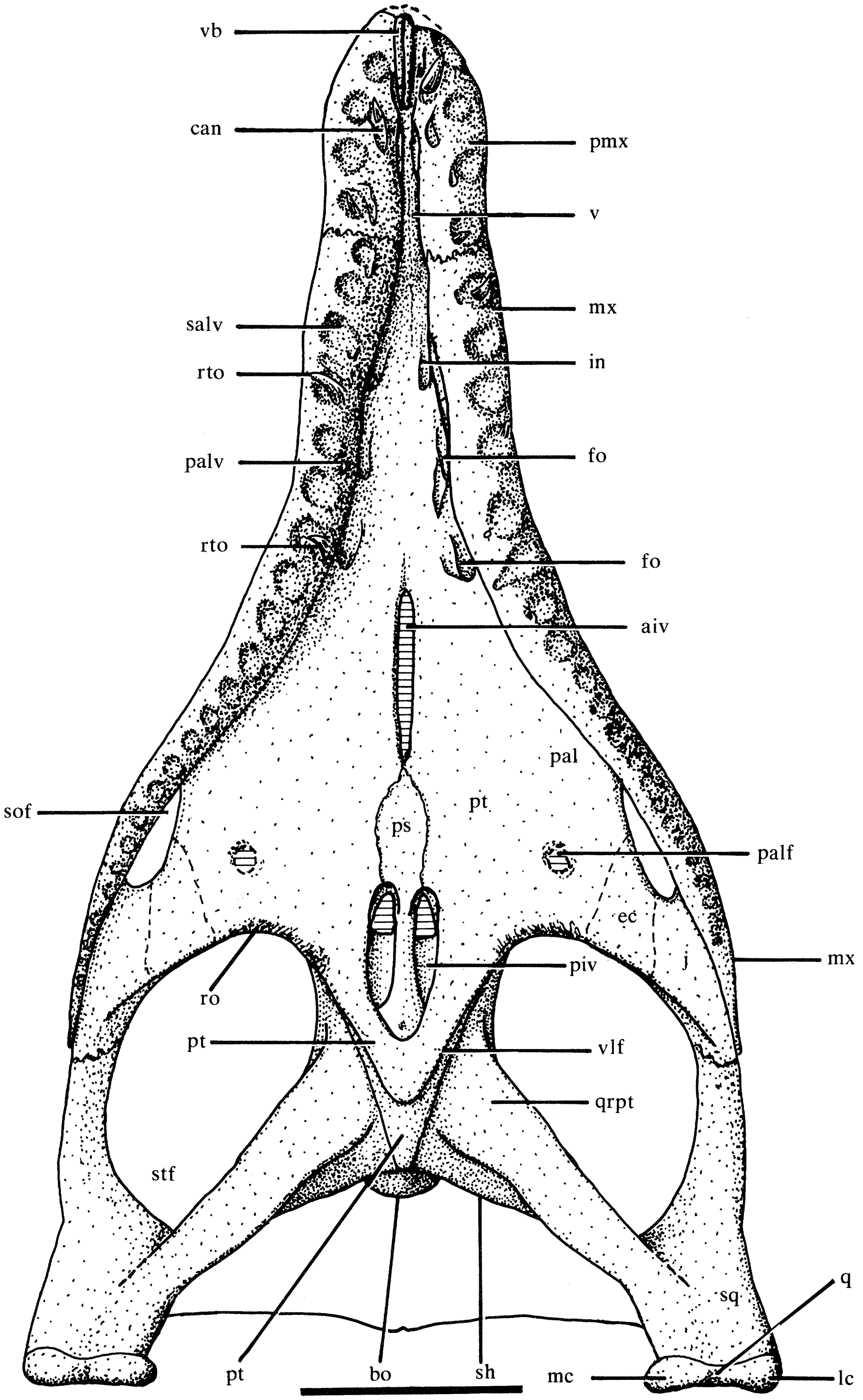

Figure 7. *Pliosaurus brachyspondylus*. Reconstruction of skull in ventral view. Scale bar, 25 cm.

crowns suggests that about 99 teeth are represented in BRSMG Cc332, including developing replacement teeth (but not counting a very few replacement teeth which were probably too small to displace the previous mature tooth). Each premaxilla carries five tooth sockets. We estimate that the right maxilla carries 24 sockets, and the left maxilla 25, giving a total of 59 functional sockets in the skull. The mandible as preserved bears 42 sockets and we estimate a further 20 or 21 on the missing portion, by comparison with the skull, giving a total of 62 or 63 sockets. The total of about 122 sockets compares well to the total of 99 teeth in the material available to us, allowing for a proportion of empty sockets before death, possibly some loss before burial, and some collection failure.

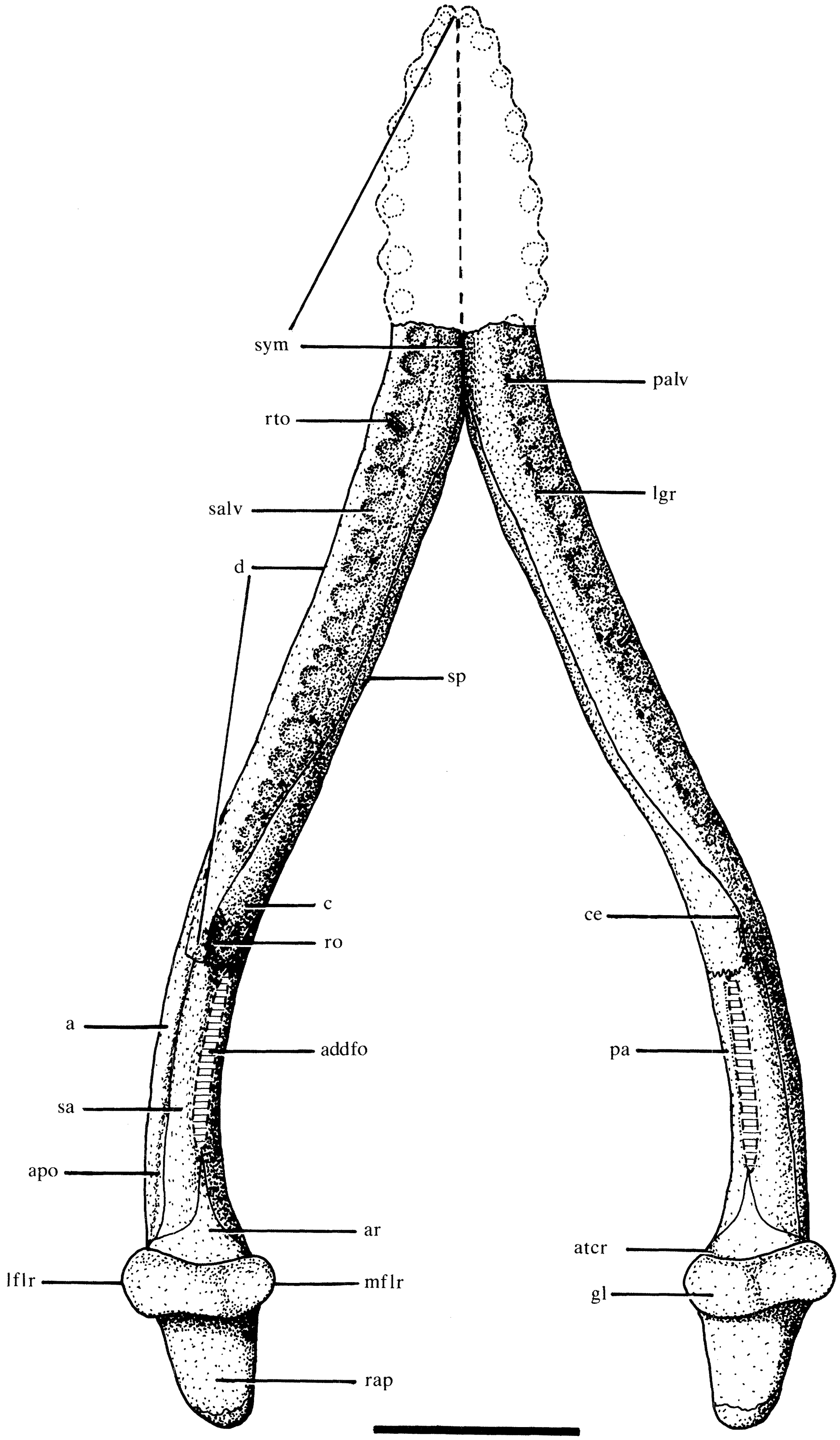

Figure 8. *Pliosaurus brachyspondylus*. Reconstruction of mandible in dorsal view. Scale bar, 25 cm.

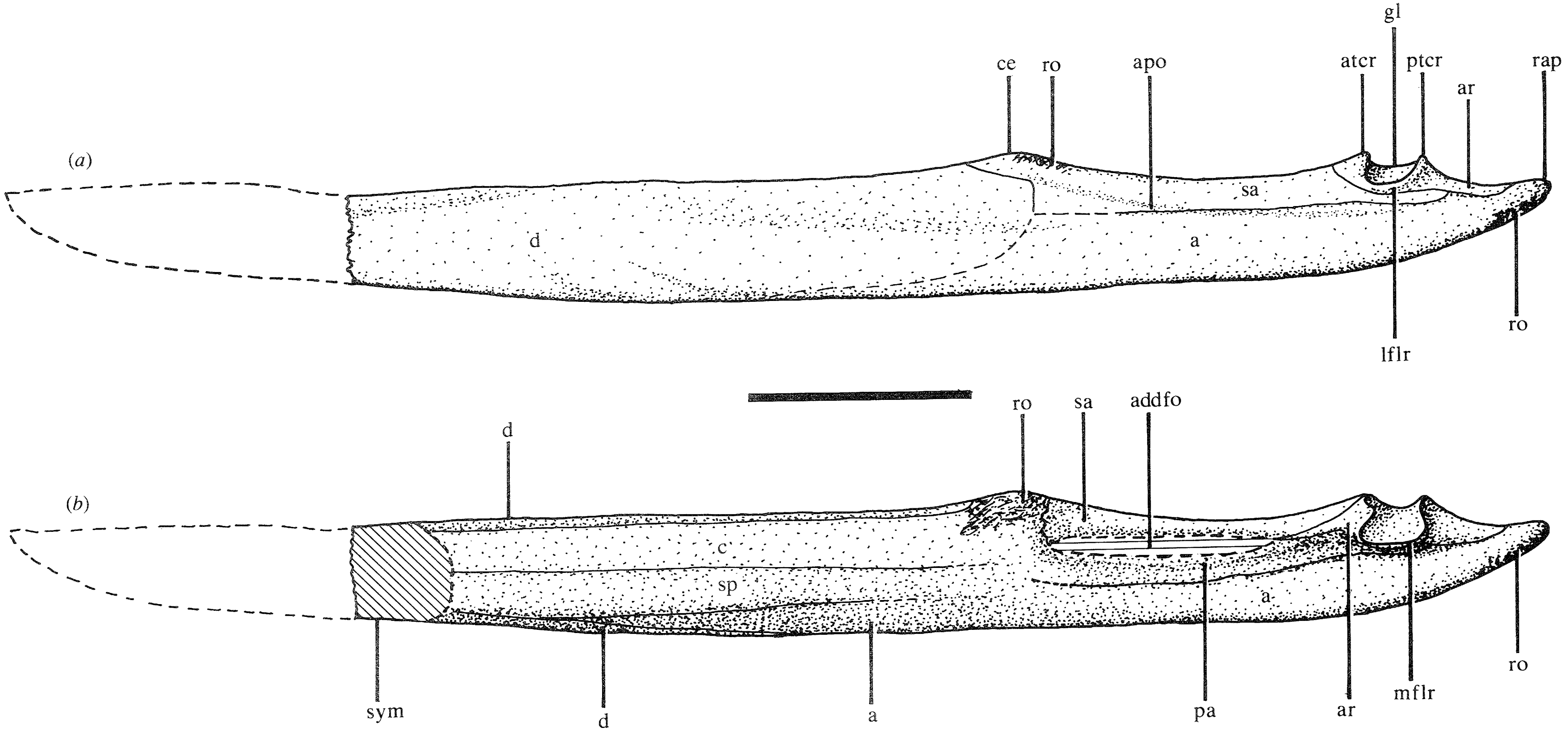

Figure 9. *Pliosaurus brachyspondylus*. Reconstruction of mandible, (*a*) in lateral view, and (*b*) in medial view. Scale bar, 25 cm.

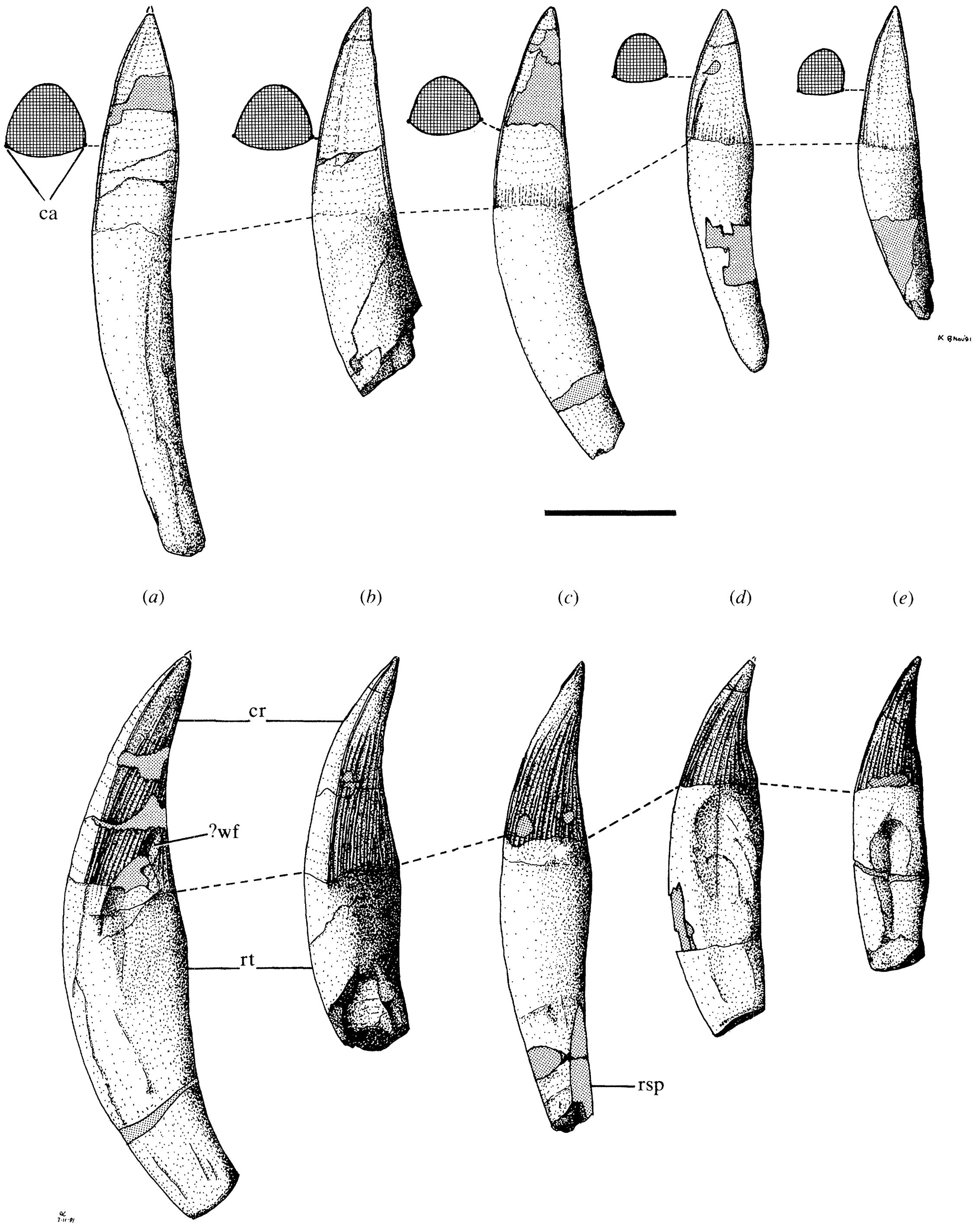

Figure 10. *Pliosaurus brachyspondylus*. Larger teeth. Rectangular crosshatching represents section of tooth at position indicated, showing paired carinae on larger teeth, and increasingly rounded cross-section of smaller teeth. Toning indicates damage or matrix. (*a*)–(*e*) Lingual and axial views. Scale bar, 5 cm. Dashed line indicates division between crown and root.

The teeth all consist of the typical plesiosaurian form of a curved conical crown and slightly bulbous root. However, they vary greatly in size and proportions from about 223 mm in length (crown 90 mm in length) to 25 mm (crown 15 mm), and appear to fall into two main types, with a few intermediates.

The larger teeth (figure 10*a–e*) are roughly caniniform, massive, trenchant, and deeply rooted for more than half their length. They vary in size. They are triangular in transverse section, bearing the characteristic two finely crenulated carinae (ca) of Kimmeridgian pliosauroids, dividing the crown surface into a relatively flat outer portion and a rounded inner portion. The teeth are asymmetric, and apparently arranged so that the carinae were placed on the outside of the tooth row, demarcating the labial and lingual surfaces of the crowns. The asymmetric curvature would match the anterolabial inclination of the larger tooth sockets. All teeth, as in some other pliosauroids, bear ornament in the form of sharply demarcated prismatic ridges, usually confined to the axial and lingual sides. These teeth are the classic

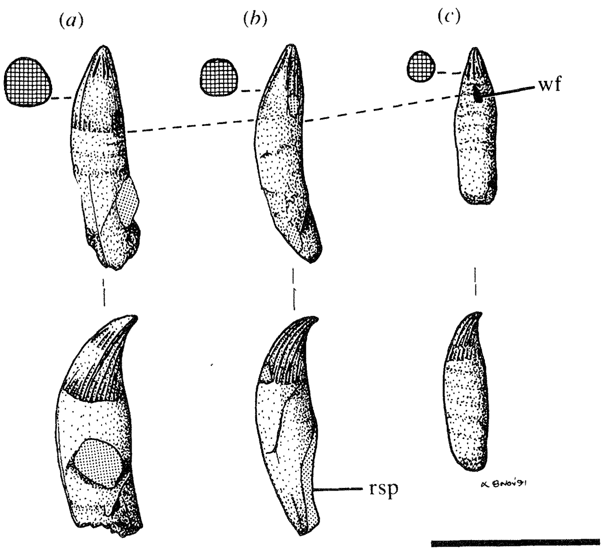

Figure 11. *Pliosaurus brachyspondylus*, smaller teeth. (*a*)–(*c*) Lingual and axial views of three small 'ratchet' teeth. Scale bar, 5 cm. Legend as in figure 10.

'pliosaur' type as figured by, e.g. Tarlo (1960). Several bear wear facets (e.g. figures 10*a* and 11*c*, ?wf) apparently fortuitously caused by opposing teeth rubbing against each other. Some teeth bear resorption pits (e.g. figures 10*c* and 11*b*, rsp).

The smaller teeth (figure 11*a*–*c*) are much less asymmetrical and were presumably oriented more vertically in their sockets, consistent with the much reduced inclination of the posterior sockets. These teeth have much less distinct carinae but bear sharply recurved, sometimes actually hooked, crowns. In transverse section they are subcircular, with the presumably labial surface almost free of ornament.

It is not possible to estimate the exact relative numbers of the two types of teeth or whether there is a sharp demarcation between them. However, there is a noticeable diminution in the diameter of the tooth sockets just in front of the last ten sockets on each maxilla, and the last eight on each dentary. Perhaps these small rear sockets held the small hooked teeth. This is consistent with a total of about 38 sockets for small hooked teeth, comparing with at least 29 markedly hooked crowns estimated as represented in the collection. However, the most posterior few sockets are very shallow. This is not apparently due to crushing, raising the possibility that these sockets may not have been functional, as might be expected from their location apparently alongside the adductor musculature. Damage to the smaller teeth makes it impossible to assess the length of their roots but one tooth, preserved in matrix, appears to show an exceptionally short root and may have come from one of the shallow sockets.

(*b*) *Functional analysis*

Massare (1987) and Taylor (1992*b*) discussed the structure and function of pliosauroid teeth. The large anterior caniniform teeth of *P. brachyspondylus* are robust penetrating teeth to hold, kill and cut up prey, with skin penetration helped by the serrated carinae and the sharp ornament. The relatively robust crown, lack of a narrow or sharply pointed tip, moderate curvature, and deep root indicate that these teeth were adapted to withstand great loadings, much as mammalian carnivores' canines do. The carinae would have had some cutting action, especially when penetrating prey. They would probably also have helped to extend and unite the holes made by the teeth when the pliosaur was trying to shake or twist a piece off its prey. Massare (1987) assigned pliosauroids with such teeth to her 'Cut Guild', probably the highest order predators in a given fauna. These animals could apparently subdue and dismember large fish and reptiles, although they could opportunistically attack smaller prey.

The posterior teeth are small and have recurved crowns directed backwards towards the gullet, suggesting that they were used not to penetrate prey but to prevent it from slipping out of the mouth or even escaping while it was being swallowed, as in *Rhomaleosaurus zetlandicus* (Taylor 1992*b*). The recurved crowns would act as ratchets, providing little resistance to rearwards movement, but immediately digging into and stopping any forwards motion. This would help the pliosaur swallow large prey items using its strong tongue and hyoid musculature (judging from the robust bars found in other *Pliosaurus* species, (Andrews 1913)) or when using inertial feeding (Taylor 1987) to jerk the food back into its gullet.

5. MUSCULATURE

Taylor (1992*b*) carried out the only prior reconstruction of the cranial musculature of a plesiosaur, the Toarcian *Rhomaleosaurus*. Our reconstruction of *Pliosaurus* (figure 12) is essentially similar in gross morphology and function, and we do not attempt to reconstruct small differences as we consider this unjustified within the limits of accuracy of the methods involved (see Taylor 1992*b*). *Pliosaurus* is here reconstructed as having two main functional muscle masses.

The first muscle mass (figure 12*a*) is the M. adductor mandibulae externus (mame) and other muscles (mpst, mamp) originating in and around the upper temporal fenestra. They insert into a bodenaponeurosis (boden) attached to the coronoid eminence, and presumably also to the dorsal and medial portions of the mandibular ramus between the coronoid eminence and articulation, and also the adductor fossa, either directly or via tendinous sheets. The coronoid eminence bears an area of heavily roughened bone (ro, figure 12*b*) on both lateral and medial faces, the medial side being more extensive than the lateral; this is excellent evidence for the insertion of a strong bodenaponeurosis. The muscles' line of action was oriented dorsally and somewhat posteriorly, in such a way that the lever arm of most of the muscles was least when the mouth was as widely open as possible, and increased progressively as the jaw shut. This muscle group was presumably most efficient, and had the

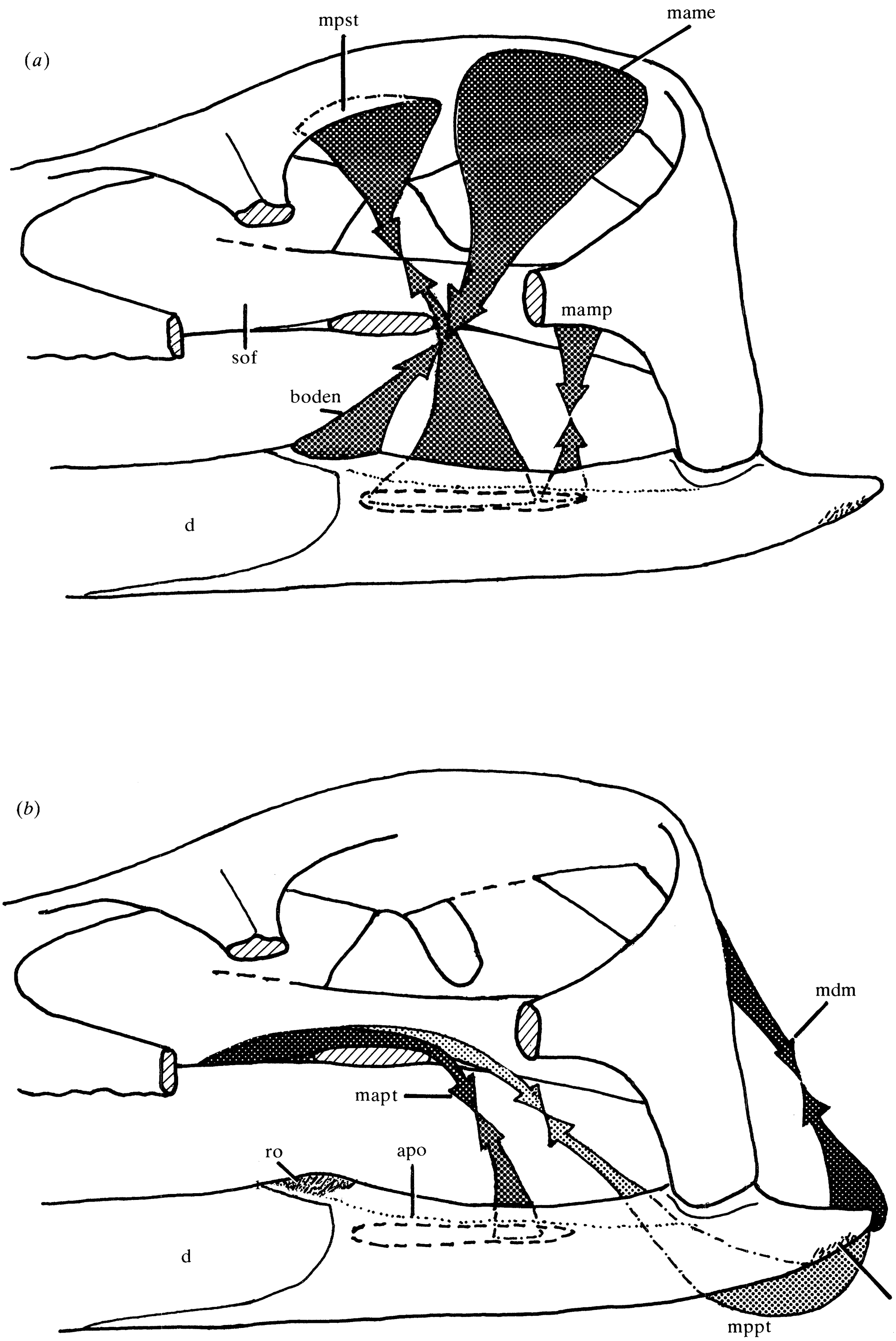

Figure 12. Diagrammatic reconstruction of mandibular adductor musculature. (*a*) Dorsal musculature; (*b*) ventral musculature.

primary function of exerting force, when the jaw was clamped shut onto prey.

The second muscle mass is the pterygoideus musculature (figure 12*b*). The M. anterior pterygoideus (mapt) is reconstructed as originating from the dorsal surface of the palate, including the tendinous fascia over the suborbital fenestra, and inserting onto the medial side of the mandibular ramus below the adductor fossa. The M. posterior pterygoideus (mppt) originated from the anterior and medial rims of the subtemporal fossa, which are locally roughened presumably for tendinous aponeuroses. It inserted as a strong tendinous sheet into a heavily roughened area (ro, figure 12*b*) on the ventral side of the mandibular ramus below and posterior to the articulation. The muscle would have curved backwards, downwards and outwards under the jaw ramus. Its true line of action thus sloped much more ventrally, and it had a much longer lever arm around the articulation, than one would expect from drawing a straight line from origin to insertion (see Taylor (1992*b*) for full discussion). Both pterygoideus muscles had lines of action sloping posteroventrally such that their moment arms were greatest when the jaws were widest open and decreased as the jaws closed. Taylor (1992*b*) argued that these muscles in *Rhomaleosaurus* served to produce strong closing torques against the inertia and drag of the mandible, and we infer a similar function in *Pliosaurus*.

Like *Rhomaleosaurus*, *Pliosaurus* is thus reconstructed as having a dual-function muscle mass combining the 'Static Pressure' and 'Kinetic Inertial' systems of Olson (1961). The pterygoideus musculature closed the jaw shut onto mobile prey, and the dorsal adductor musculature clamped the jaws tightly onto the prey to hold and kill it with the long anterior caniniform teeth. However, the two muscle groups were not mutually exclusive: the pterygoideus group would have made a useful contribution to holding the jaws shut, and the dorsal group would have helped accelerate the closing of the jaws. A similar dual-purpose system appears to occur in the 'nothosaur' *Pachypleurosaurus* (Rieppel 1989) and may well be primitive for plesiosaurs and at least some other sauropterygians.

Little can be said about the mandibular abductor and pharyngeal floor musculature except that the retroarticular process provided a long lever arm for the insertion of the M. depressor mandibulae (mdm, figure 12*b*), which presumably originated on the posterior face of the squamosal and quadrate. The M. depressor mandibulae would have been important in opening the jaw when pursuing prey in water, whose density reduces the opening effect of gravity and whose drag slows opening. The M. depressor mandibulae was presumably assisted by the longitudinal musculature of the floor of the mouth, as in *Rhomaleosaurus* (Taylor 1992*b*). Robust hyoid bars have been reported from Callovian species of *Pliosaurus* (Andrews 1913) but have not been recovered from BRSMG Cc332.

6. FUNCTIONAL ANATOMY OF HEAD SKELETON AND CONCLUSIONS

The present study is only the second functional analysis of the head of a pliosauroid. The other study, of the Toarcian *Rhomaleosaurus zetlandicus*, contains a full functional analysis and discussion of methodology (Taylor 1992*b*), while Taylor (1987) discusses the problems of tetrapods feeding in water. We present a brief complementary analysis here.

The skull and mandible of *Pliosaurus* were most heavily loaded when it bit into prey. The skull and mandible were then loaded primarily in dorsoventral bending and shear, with a muscle force loading the temporal region of the skull and coronoid region of the mandible; a reaction force at the articulation directed dorsally and somewhat anteriorly; and a much smaller reaction at the bite point.

Pliosaurus has much the same adaptations to resist dorsoventral bending as *Rhomaleosaurus*. The skull is relatively long and low, to reduce drag in water as the jaws were snapped onto prey, at the cost of dorsoventral strength (Taylor 1987). Bending moments rather than shear forces become the main determinant of structure in such long, thin beam-like structures, and the skull shows adaptations to resist bending moments. It is highest posteriorly, with the sagittal crest summit at about the position of highest bending moment. This is also near the neck joint where added height confers the least added inertia and drag to a head being swung laterally underwater. The median dorsal elements would tend to buckle under the compressive loadings induced by bending, but they are supported by ventral flanges between the orbits and along the median parietal bar. The ventral elements of the skull appear to be well arranged to resist the complementary tensile loadings. The pterygoids are apparently strongly sutured to the quadrates and basicranium posteriorly and anterior palate and maxillae anteriorly. Furthermore, the basicranium, pterygoids, epipterygoids, and occipital arch together form a strong box beam supporting the parietal bar. The coronoid eminence does give the mandibular ramus maximum depth at roughly the point of maximum bending moment, although little more can be said about the design of the mandible.

The rather flat skull of *Pliosaurus* seems poorly adapted to resist torsional loadings involved in twisting pieces off prey too large to swallow whole as crocodilians do today (Pooley & Gans 1976). Indeed, an interesting difference between *Rhomaleosaurus* and *Pliosaurus* is in the design of the ectopterygoid area. In *Rhomaleosaurus* the ectopterygoid and pterygoid form a strong boss – essentially a pterygoid flange – buttressing the flattened medial face of the mandibular ramus against inward loadings, as would have occurred when the animal was holding struggling prey and twisting it to pieces. In contrast, *Pliosaurus* lacks any sort of pterygoid flange. Its ectopterygoid is a flattened bone almost flush with the rest of the palate, and the inner face of the mandibular ramus is rounded. The double-condyle quadrates fitting into the deep glenoid fossae give the jaw joint considerable strength, but provide least support when the symphysis is loaded transversely. Yet the teeth are suited to tackling large prey. Maybe *Pliosaurus* was simply big enough to swallow prey whole, or maybe its head was so massive that it did not need the special adaptations to resist transverse loadings, thus keeping the palate clear of potential obstructions to swallowing large prey. This problem can only be resolved by an analysis of the scaling factors involved.

Further evidence that *Pliosaurus* was less specialized to eat relatively large prey than *Rhomaleosaurus* lies in palatal structure. The origins of the pterygoideus musculature, along the ventrolateral flanges of the pterygoids, extend to the midline in *Pliosaurus* although they would have tended to encroach upon the buccal cavity, unlike *Rhomaleosaurus* where the midline of the palate was apparently kept clear.

Another striking difference is that *Pliosaurus* has a relatively long, thin snout and posteriorly placed temporal fenestrae compared to *Rhomaleosaurus*. The massively built posterior skull, including the squamosal-quadrate complex and the posterior pterygoid-braincase unit, may simply be a response to the more posterior concentration of muscle forces, with relatively weak forces at the bite point but relatively great reactions at the jaw joints.

Pliosaurus, like *Rhomaleosaurus*, was a primarily visual hunter, possibly adapted to maximize visual acuity in the relatively dark waters in the lower part of the photic zone, or in the turbid, sediment-laden waters of coastal seas. The orbits are remarkably large, as usual in pliosauroids, and indicate large eyes, confirmed by the large size of complete rings of sclerotic plates in Callovian species of *Pliosaurus* (Andrews 1913; Linder 1913), while the lack of a sulcus on the sclerotic plates indicates underwater rather than subaerial vision (Taylor 1992*b*). Stapes have not been found in BRSMG Cc332, or at any rate recognized amongst the fragments. However, as in other plesiosaurs (Taylor 1992*b*), the otic capsules are not acoustically isolated, strong evidence that *Pliosaurus* was incapable of echolocation.

The internal nares are remarkably small and hard to locate (§ 3), seemingly far too small for the respiratory needs of such a large animal. However, modern marine mammals and crocodilians are misleading analogies. They breathe at the surface with dorsally located external nares, but they can do so only because they have secondary palates. *Pliosaurus* and other plesiosaurs did not have secondary palates, and could not have used their nares for respiration. The location of the nares may reflect the location of the long roots of the teeth within a dorsoventrally compressed skull, so that the nares were displaced posteriorly and dorsomedially to their present location. The nares could have been used for airborne olfaction. However, Cruickshank *et al.* (1991) suggest that *Rhomaleosaurus megacephalus* used its narial cavities for underwater olfaction rather than respiration. Perhaps *Pliosaurus* did the same; it also has inverted troughs on the palate, possibly conducting water to the internal nares. It is about twice as large as *Rhomaleosaurus*, yet its external nares are not much larger and the inner ones are about the same size. This is hard to explain if they were used for respiration. However, if they were used for olfaction, there is no functional reason why they should be considerably larger in the larger animal.

We thus reconstruct *Pliosaurus brachyspondylus* as a large visual predator, perhaps capable of underwater olfaction, and probably feeding opportunistically on a wide variety of food, including fishes, cephalopods, and other reptiles as available. It was apparently a dominant carnivore which despatched large prey such as fishes and reptiles with deep bites with its strong caniniform anterior dentition, and then used its broad, unobstructed palate, widened posterior gape and hooked posterior dentition to help move the prey down the gullet. BRSMG Cc332 is an individual with a gape of almost 0.75 m, capable of swallowing, say, ichthyosaurs several metres long whole, while there is evidence that it scavenged a dinosaur carcass (§ 2*d*; Taylor *et al.* 1993). Clarke & Etches (1992) report plesiosaurian propodials from the Kimmeridgian of Dorset and Wiltshire, two from the same *eudoxus* Zone as BRSMG Cc332, which show damage ascribed to the robust teeth of similar pliosauroids. Isolated portions of reptilian skeletons are relatively common in the Lower Oxford Clay (Callovian) of central England, and D. M. Martill (personal communication 1993) considers that they probably fell from carcasses being dismembered.

However, *Pliosaurus* probably also fed on smaller and so more abundant prey as opportunity offered (Massare 1987). Its relatively narrow anterior snout helped catch fish and cephalopods, though it would not have been so efficient on such prey as a reptile with a truly gracile snout (Taylor 1987). Cephalopod hooklets, presumably from prey remains, have been reported in another specimen of *P. brachyspondylus* (Massare 1987; Tarlo 1959*a*), and from a Callovian pliosauroid (Martill 1992). The main uncertainty is to what extent *Pliosaurus* dismembered its prey. It was not obviously specialized for twist-feeding. Perhaps it was simply big enough to eat most available prey whole. Furthermore, the relative abundance of potential prey decreases as prey becomes larger, so that it may have been worthwhile for the smaller *Rhomaleosaurus* to be specialized to attack and dismember prey its own size, whereas prey the size of *Pliosaurus* were so much scarcer as not to be worth specializing in.

The similarity in cranial anatomy between the Lower Jurassic *Rhomaleosaurus* and the Upper Jurassic *Pliosaurus* suggests that pliosauroids evolved a highly specific complex of adaptations that remained relatively unchanged since their initial evolution. Furthermore, a comparison with plesiosauroids (at least those described by Brown (1981)) suggests that pliosauroids are markedly more plesiomorphic than plesiosauroids, for example in retaining lacrimals, prefrontals, prearticulars, and coronoids, all presumably present in the common ancestor of plesiosaurs and lost in plesiosauroids. Furthermore, the presence of suborbital fenestrae in pliosauroids but not plesiosauroids or other sauropterygians conflicts with current phylogenies, although it may be a character reversal or autapomorphy. Recent work on plesiosaur and sauropterygian inter-relationships (e.g. Rieppel 1989; Sues 1989; Storrs 1991, 1993) thus needs to be refined, and significant progress depends on study of more of the Jurassic plesiosaurs.

This paper and the specimen's display are the culmination of many people's work. The Westbury Pliosaur was discovered by Professor T. Birkelund, Dr B. Buchart, Mr C. K. Clausen, Mr H. Nøhr-Hansen, and Miss I. Salinas (Institut for historisk geologi og palaeontologi, Copenhagen, Denmark), and Dr F. T. Fürsich (Institut für Paläontologie und historische Geologie, University of Munich, Germany). It was excavated by Bristol City Museums and Art Gallery staff (Dr M. L. K. Curtis, Dr M. D. Crane, Mr A. Mathieson, Ms S. A. Swansborough, and Ms J. L. Ratcliffe) assisted by Bristol University staff (Professor R. J. G. Savage, Dr D. Robinson, Mr M. E. White, Dr D. I. Whiteside, Mr J. D. Boyd, and Dr E. J. Loeffler), by the discoverers, and by Mrs R. H. B. Crane.

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KEY TO ABBREVIATIONS USED IN THE FIGURES

a	angular
addfo	adductor fossa
aiv	anterior interpterygoid vacuity
apo	aponeurotic sheet
ar	articular
atcr	anterior transverse crest
b	boss
bna	base of neural arch
bo	basioccipital
boden	bodenaponeurosis
bs	basisphenoid
c	coronoid
ca	carina
can	canal between alveoli
ce	coronoid eminence
cr	crown
cvc	centrum of cervical vertebra
d	dentary
dvc	centrum of dorsal vertebra
ec	ectopterygoid
en	external naris
ep	epipterygoid
fcr	facets for cervical rib
fm	foramen magnum
fo	foramen
fr	frontal
fs	subcentral foramina
gl	glenoid fossa
in	internal naris
j	jugal
l	lacrimal
lc	lateral condyle of articulation
lflr	lateral flare under glenoid fossa
lgr	lateral groove on dentary
mame	M. adductor mandibulae externus
mamp	M. adductor mandibulae posterior
mapt	M. anterior pterygoideus
mc	medial condyle of articulation
mdm	M. depressor mandibulae
mflr	medial flare under glenoid fossa
mppt	M. posterior pterygoideus
mpst	M. pseudotemporalis
mx	maxilla
nac	neural arch of cervical vertebra
nad	neural arch of dorsal vertebra
nop	notochordal pit
oc	occipital condyle
orb	orbit
p	parietal
pa	prearticular
pal	palatine
palf	palatine foramen
palv	primary alveolus
path	presumed pathological growth of bone
pfe	posttemporal fenestra
pfo	parietal foramen
ph	phalanx
piv	posterior interpterygoid vacuities
pmx	premaxilla
po	postorbital
pof	postfrontal
pro	prootic
ppr	paroccipital process
prf	prefrontal
ps	parasphenoid
pt	pterygoid
ptcr	posterior transverse crest
q	quadrate
qrpt	quadrate ramus of pterygoid
r	ridge
rap	retroarticular process
rb	rib
ro	roughened area

rsp	resorption pit
rt	root
rto	developing replacement tooth
sa	surangular
salv	secondary alveolus
scr	sagittal crest
sh	transverse shelf
sof	suborbital fenestra
sp	splenial
sq	squamosal
stf	subtemporal fenestra
sym	symphysis
t	tooth
tf	temporal fenestra
v	vomer
vb	ventral boss on premaxillae
vlf	ventrolateral flange
wf	wear facet

Tone: damaged bone or matrix
Horizontal hatching: openings in skull and mandible
Oblique ornament: bone in section