

Cranial anatomy of the Lower Jurassic pliosaur *Rhomaleosaurus megacephalus* (Stutchbury) (Reptilia: Plesiosauria)

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SUMMARY

An account is given of the skull of a large pliosauroid plesiosaur from the lowermost Hettangian (Lower Lias; Lower Jurassic) of Barrow upon Soar, Leicestershire, identified as *Rhomaleosaurus megacephalus* (Stutchbury, 1846). It is proposed as the neotype of the species, as the holotype was destroyed in an air-raid on Bristol in November 1940. Details of the skull allow emendation of the diagnosis of the genus *Rhomaleosaurus*. Comparison of *R. megacephalus* with the Upper Liassic species, *Rhomaleosaurus zetlandicus*, shows that the former has a more gracile snout and a shallower lower jaw symphysis, and lacks squamosal–quadrate foramina. There may also be differences in the number and nature of the palatal grooves associated with presumed underwater olfaction. Lack of iron pyrites in the matrix surrounding the specimen allowed computed axial tomography (CAT)-scan sections to be obtained, which in association with the little-distorted nature of the skull, permitted a confident reconstruction of the skull. It shows a complete ring of circumorbital bones, and a suborbital fenestra. The braincase can be reconstructed from sagittal break-sections allied with CAT-scan sections. A stapes is identified. A poorly preserved dentition comprises conical, striated, teeth with caniniforms on each premaxilla and at the front of each maxilla. Although very similar to the later species, this skull is not so well adapted for apprehending and dismembering large prey, as is *R. zetlandicus*.

1. INTRODUCTION

Plesiosaurs are large, extinct, aquatic predatory reptiles, of diapsid descent. By the lowermost Jurassic they appear to have been fully adapted to an open-water habitat, ultimately evolving a mode of under water ‘flying’ (Taylor 1981; Riess & Frey 1991; Storrs 1993). Underwater flight (and loss of nasal bones) seems to be the unifying feature of the Plesiosauria.

Currently the Order Plesiosauria de Blainville, 1835

is classified into two superfamilies: the Pliosauroidae (Seeley, 1874) Welles, 1943, and Plesiosauroidae (Gray, 1825) Welles, 1943, characterized by contrasting sets of characters of the skull, neck and skeleton (Brown 1981, pp. 339–341). Within the former, two families are known, the Pliosauridae and Polycotyliidae, and within the latter, there are several: Plesiosauridae Gray, 1825, Cryptoclididae Williston, 1925, and Elasmosauridae Cope, 1869 (Brown 1981).

The pliosauroids are plesiomorphic with regard to

the plesiosauroids in a number of features of their heads and lower jaws. The lower jaw contains the same number and distribution of bones as do more primitive reptiles, such as the captorhinomorphs, and they retain suborbital fenestrae in the palate (Taylor 1992*b*). The symphysis of the lower jaw has a variable number of tooth positions, usually five or more pairs, and the snout is elongated. In early forms the teeth are substantial, conical, striated and typically those of generalized predators which subject their skulls to extremes of stress while dismembering prey (Massare 1987; Taylor 1992*b*).

In the plesiosauroids the lower jaw loses the coronoid bones in all except the very early elasmosaurs, and the prearticulars are very much reduced or lost. This results in the lower jaw of plesiosauroids often being found with the dentaries and postdentary bones separated. Functionally it means that the lower jaw of plesiosauroids is adapted to resisting only dorso-ventral stresses (Cruickshank 1994*b*), as opposed to the situation in the pliosauroids discussed by Taylor (1992*b*). The palate of plesiosauroids is closed (Brown 1981; Storrs 1991), and they do not have downturned pterygoid flanges, such as are found in the species of *Rhomaleosaurus* at least (Taylor 1992*b*; figure 2 below). Also in contrast to the pliosauroids, the teeth of plesiosauroids are much more lightly built, being very sharp, slim and recurved. Massare (1987) has suggested that this derived type of dentition is adapted to apprehending soft-bodied prey, or was used as a filter for feeding on small aquatic invertebrates. These characters can be regarded as being 'derived' as far as the Plesiosauria are concerned.

Therefore among the Plesiosauria, the pliosauroids are the more generalized predators, and this is confirmed by the functional analyses that are available (Taylor 1992*b*; Taylor & Cruickshank 1993*b*; Brown & Cruickshank 1994). There are no up-to-date synoptic reviews of the Order Plesiosauria. Tarlo (1960) reviewed the Upper Jurassic pliosauroids, and Brown (1981) redescribed the English Middle and Upper Jurassic plesiosauroids, concluding his review with a classification of the Plesiosauria. Little attention has been paid to Lower Jurassic plesiosaurs until recently (Taylor & Cruickshank 1989, 1993*a*; Taylor 1992*a,b*; Cruickshank *et al.* 1991). This paper is a contribution to the revision of the Lower Jurassic Pliosauroidae, and fills some gaps in the information available for a period very early in their history, adding details to those recorded for *Rhomaleosaurus zelandicus* (Taylor 1992*a,b*). It also provides a basis for a reconsideration of some aspects of plesiosaurian palaeontology.

Abbreviations of repositories referred to in this paper are as follows: BMNH, Palaeontology Department, Natural History Museum, Cromwell Road, London SW7 5BD; BRSMG, Bristol City Museum and Art Gallery, Queens Road, Bristol BS8 1RL; LEICS, Leicestershire Museums, Arts and Records Service, 96 New Walk, Leicester LE1 6TD; NMING, National Museum of Ireland, Geology Department, Kildare Street, Dublin 2, Ireland; PETMG, Peterborough City Museum & Art Gallery, Priestgate,

Peterborough, PE1 1LF; WARMS, Warwickshire Museums Service, Market Place, Warwick, CV34 3SA; YORYM, Yorkshire Museum, Museum Gardens, York, YO1 2DR.

2. MATERIAL AND METHODS

(a) *The specimen*

As part of a programme to define the nature of Liassic plesiosaurs more closely (Taylor 1992*a,b*; Taylor & Cruickshank 1993*a*; Cruickshank 1994*b*), the large, almost complete and little distorted skull of a mounted skeleton (LEICS G221.1851) was dismantled and prepared for description (Cruickshank 1994*a*).

Preparation followed conventional mechanical techniques. The matrix was removed with the use of compressed air driven Airpens and Burgess Professional Vibrotools and the exposed bone surface was protected with a 5% solution of Paraloid B72 in acetone. Repairs were effected with HMG commercially available adhesive (Paraloid B72 in acetone).

Additional information (particularly on distorted and damaged areas) was obtained from a series of computed axial tomography (CAT)-scans done on the Queen's Medical Centre, Nottingham University, 'Picker' Synerview 1200SX machine (Cruickshank *et al.* 1991).

The block containing the skull and lower jaw came away from the mount in five major pieces: the anterior snout, the mid-portion of the skull, a block containing most of the braincase from the pineal foramen back to the occipital condyle, and the left and right quadrate regions, which split away from the braincase through the bones of the braincase side-walls. One further line of natural weakness failed during preparation, causing the left orbital region to come away from the rest.

The mandible has been very firmly pushed up against the inside of the upper jaw, so that the coronoid eminences and crowns of the mandibular teeth are hardly visible; many teeth are seen in section where the specimen has been damaged, but only one or two are preserved well enough for illustration. The midline of the snout has been slightly depressed, and the braincase region has been disrupted so that the vertex is bent down compared to the line of the rest of the sagittal crest. At the same time the heads of the quadrates have been pushed forward and downward. This is most clearly seen on the left side where the quadrate is positioned more horizontally than it was in life, with the head overlapping the broken posterior end of the anterior ramus of the squamosal by about 35 mm. The anterior ramus of the right squamosal has broken away from the jugal arch, and is lying, bent in two, in the matrix infilling the supratemporal fenestra. All this disruption has caused the mandible to be drawn back, relative to the cranium, by about 30–40 mm. The anterior cervical vertebrae turn and run behind the right quadrate, which obscures detail in that region. However, it has been possible to clean much of the matrix from the posttemporal fenestra on that side.

The snout has been cleaned only on its outer

surface; the teeth are in a very poor state and about 30 mm of bone has been eroded away from the tip of the premaxillae since 1851, exposing the roots of the anteriormost teeth in section. Matrix was not cleaned from between the anterior jaw rami. The mid-region of the skull, back to level with the postorbital bars, has been cleaned on its outer surface, but once again the teeth are poorly preserved. The left orbit and palatal surface have been freed of matrix, as has the dorsal surface of the lateral rami of both pterygoids.

The bone is well preserved, but very brittle. Surprisingly little damage had been done to the bone surface by the Victorian preparators, apart from the undersurface, where the block had been planed, so as to make it lie flat on the mount (Cruickshank 1994a). The brittle nature of the bone, and the need to retain the integrity of the skull for display, led to a decision not to clear the entire specimen from its containing matrix.

The skull and lower jaw are reconstructed in figures 1–10, taking into account all the information listed above. Bone from the retroarticular processes was removed by the original preparators. No hyoids or sclerotic bones are preserved.

(b) *Locality and horizon*

This specimen was collected by William Lee, ‘Farmer and Limeburner’, of Barrow upon Soar (NGR SK 57 17), in the County of Leicestershire, sometime prior to 1851, and sold to the Leicester Literary and Philosophical Society by that date (Anon, 1851, 1852; Taylor & Cruickshank 1989). The actual pits or quarries from which Lee obtained his material for sale have not been identified in general, in spite of much effort (Martin *et al.* 1986; LEICS archives), but it is believed LEICS G221.1851 came from the Village Delft, in the village centre, now backfilled and built over.

The horizon is the Bottom Floor Limestone (Harrison 1877), of the *planorbis* sub-zone of the *Psiloceras planorbis* zone of the Hettangian (Lowermost Jurassic). The sub-zone is the lowest in the Lias, and the limestone horizon one of the lowest within that, being barely 2 m above the local Rhaetian (Martin *et al.* 1986). Many small ammonites can be seen in the matrix surrounding the skeleton, but their preservation is not good enough for formal identification. The description of a well-preserved pliosauroid from such a low horizon in the Jurassic is of importance and adds considerably to the understanding of the group as a whole.

3. LIST OF ABBREVIATIONS USED IN TEXT AND FIGURES

a	angular
aiv	anterior ininterpterygoid vacuity
ar	articular
ars	anterior ramus of squamosal
artc	anterior transverse crest of glenoid fossa
base	base of tooth
bo	basioccipital

bs	basisphenoid
ce	coronoid eminence
cr	crest
crown	crown of tooth
d	dentary
damage	damage on crown of tooth
dep	depression
df	descending flange of epipterygoid
dfl	dorsal flange of pterygoid
dia	diastema
dmfo	dorso-median foramen
drs	dorsal ramus of squamosal
ec	ectopterygoid
en	external naris
eo	exoccipital–opisthotic
ep	epipterygoid
fac	facial process of the premaxilla
fmag	foramen magnum
fo	foramen
fr	frontal
gl	glenoid fossa
in	internal naris
j	jugal
l	lacrimal
lc	lateral condyle
lg	lateral groove
mc	medial condyle
mg	median groove
mto	mature tooth
mx	maxilla
no	notch
oc	occipital condyle
orb	orbit
p	parietal
pa	prearticular
pal	palatine
palv	primary alveolus
pfo	parietal foramen
pitfoss	pituitary fossa
piv	posterior interpterygoid vacuity
pmx	premaxilla
po	postorbital
pof	postfrontal
ppr	paroccipital process
prf	prefrontal
pro	prootic
ps	parasphenoid
psc	parasagittal crest
pt	pterygoid
ptb	pterygoid boss
ptf	pterygoid flange
q	quadrate
qrpt	quadrate ramus of the pterygoid
r	ridge
rap	retroarticular process
sa	surangular
salv	secondary alveolus
scc	semicircular canal(s)
sh	shelf
so	supraoccipital
sof	suborbital fenestra
sp	splenial
sq	squamosal

sta	stapes
sym	symphysis
tf	supratemporal fenestra
tr	trough
ut	utricle
v	vomer
vlfs	ventrolateral flange of squamosal
vmfs	ventromedian flange of squamosal
V,X	cranial nerves
1-4	sections through skull

Diagonal ruling=broken bone, or bone in section (except for figure 5).
Horizontal ruling=apertures in skull.
Machine stipple=matrix.
Solid line=confident reconstruction.
Broken line=restored reconstruction.

4. SYSTEMATIC PALAEONTOLOGY

Class: Reptilia
Subclass: Sauropterygia Owen, 1860
Order: Plesiosauria de Blainville, 1835
Superfamily: Plesiosauroidea (Gray, 1825) Welles, 1943
Family: Pliosauridae Seeley, 1874
Genus: *Rhomaleosaurus* Seeley, 1874
Type species: *Plesiosaurus cramptoni* Carte and Bailly, 1863
Plesiosaurus megacephalus Stutchbury, 1846
Selected synonymy:
1846 *Plesiosaurus megacephalus* Stutchbury, 1846.
1851 *Plesiosaurus macrocephalus* (sic) recte *megacephalus* Stutchbury, 1846. Anon, 1851.
1852 *Plesiosaurus megacephalus* Stutchbury, 1846. Ansted, pp. 14-15 in Anon, 1852.
1889 *Thaumatosauros megacephalus* (Stutchbury, 1846). Lydekker, 1889, p. 166.

1989 '*Plesiosaurus*' *megacephalus* Stutchbury, 1846. Taylor & Cruickshank, 1989, pp. 20-24.
Type specimen: *Plesiosaurus megacephalus* Stutchbury. BRSMG Cb2335.
Referred material: LEICS G221.1851. Here designated the neotype. Skeleton displayed from the dorsal surface. WARMS G10875. Skeleton displayed from the ventral surface. NMING F10194. Skull and partial skeleton.

The need arises to designate a neotype for *Plesiosaurus megacephalus* Stutchbury, 1846, because of the loss of the type in an air-raid on Bristol in November 1940.

The holotype of *P. megacephalus* was a complete skeleton and skull, displayed latterly from the ventral surface (Swinton 1948; Taylor & Cruickshank 1989; Taylor 1994). Descriptions, illustrations and measurements of the species, based on the holotype (Stutchbury 1846; Sollas 1881; Swinton 1931, 1948) are inadequate for modern purposes, although they are sufficient to show that the breadth and length of the skull, among other characters, are indistinguishable from the specimen described here. The specimens are almost exactly the same length, to within 2%. All other measurements, including relative skull length and width, and relative neck length are also of this order of similarity (table 1). This similarity extends to Stutchbury's (1846) qualitative descriptions of the type, before it was embedded in plaster of Paris for display.

The genus *Rhomaleosuarus* is currently unrevised, except for *R. zetlandicus* (Phillips, in Anon, 1854) (Taylor 1992a). However, some aspects of the genus are dealt with below (§ 5a).

As this is the only large (more than 3 m) species of Rhaeto-Hettangian (Lower Jurassic) pliosauroid known to me in Britain, I therefore refer the specimen described in this paper to the species *Rhomaleosaurus megacephalus* (Stutchbury, 1846). In the known loss of

Table 1. Measurements of *Rhomaleosaurus megacephalus* (Stutchbury, 1846)

Stutchbury characters	type (BRSMG Cb2335)	LEICS G221.1851
1 snout-l.jaw articulation	2'8''/813 mm	2'9''/838 mm
2 l.surface on mid-line	2'0½''/622 mm	2'0''/610 mm
3 l.surface snout-int.nares	1'6''/457 mm	—/—
4 l.jaw symphysis	0'5½''/140 mm	0'5''/127 mm
5 breadth muzzle	0'5½''/132 mm	0'5''/127 mm
6 widest across occiput	1'3½''/394 mm	1'3½''/394 mm
7 top head to front nares	0'9½''/241 mm	0'10½''/267 mm
8 length nasal opening	0'1 ⅓''/28 mm	0'1''/25 mm
9 width nasal opening	0'0½''/13 mm	0'0½''/13 mm
10 width between nasal op.	0'1 ⅓''/28 mm	0'1 ⅓''/32 mm
11 ant.muzzle-ant.orbits	0'11½''/292 mm	0'12½''/318 mm
12 columellar(=hyoid) length	0'5 ⅓''/145 mm	—/—
13 collumellar diameter	0'0 ⅓''/15 mm	—/—
additional characters		
overall length	16'8''/5080 mm	17'0''/5182 mm
length of neck	4'1''/1240 mm	4'4''/1321 mm
proportions (overall length=100)		
length of skull (%)	16	16.2
length of neck (%)	24.4	25.5
width skull posteriorly (%)	7.8	7.8

the holotype I also designate it the neotype of that species.

Discussions of the provenance of the holotype of *R. megacephalus* have led to mistaken references to its locality, and by inference, its horizon. Swinton (1948) refers it to 'Street', a well-known fossil vertebrate locality southwest of Glastonbury, yielding specimens from the 'pre-*planorbis* beds'. However Taylor (personal communication 1991) notes that the original catalogue (BRSMG Geol. MS. no. 23) records the locality for Cb2335 as being 'Street-on-the-Fosse', a small village about 4 km south of Shepton Mallet and 12 km east of Glastonbury. The MS. entry equates the horizon with that at Street, and is thus also of pre-*planorbis* age. Street-on-the-Fosse is known to lie on Lower Liassic rocks and the specimen may therefore be ascribed to the Lower Lias, and perhaps the Triassic–Jurassic boundary. Stutchbury (1846) merely ascribed the specimen to 'Somerset'. *Rhomaleosaurus megacephalus* is therefore a pliosauroid of the very earliest Hettangian (Lowermost Liassic).

Diagnosis of the genus *Rhomaleosaurus*: Based on Taylor (1992a) for the species *R. zettlandicus* (YORYM G503), but with additional information now available from *R. megacephalus* and other species, the generic diagnosis is:

Pliosauroid of moderate length (ca. 5 m). Head length about 15% of overall length. Head subtriangular with snout bearing rosette of intermeshing large teeth. Length: width ratio of skull about 2:1. Enlarged, spatulate, symphysis with five pairs of teeth. About 30 teeth in each mandibular ramus. Teeth circular in section. Dorso-median foramen between facial processes of premaxillae. Medially facing trough on the prearticular and anterior face of the articular. Well-developed pterygoid flange bearing ventrally projecting lateral boss. Neck with about 28, possibly more, vertebrae; about 25% of overall length. At least 58 presacral vertebrae. Hettangian–Toarcian (Lower Jurassic).

Tarlo (1960) pointed out that the Upper Jurassic Pliosauroidae could be divided into four groups, based on the genera *Simolestes*, *Liopleurodon*, *Pliosaurus* and *Peloneustes*. One of the principal distinguishing characters he used was the length of, and hence the number of teeth in, the lower jaw symphysis. *Liopleurodon* had a spatulate symphysis with five pairs of teeth, as opposed to *Simolestes* with a rounded symphysis bearing a similar number of teeth, and the other two genera with symphyses holding up to 14 pairs of teeth. *Rhomaleosaurus* is similar to *Liopleurodon* in this respect, and clearly different from the other three genera.

***R. megacephalus*: specific diagnosis:** Skull more gracile than *R. zettlandicus*. Snout width-to-length ratio 1:1.25. Palate with pair of channels on each side, the medial one of which runs to the internal nares and the lateral one to a large, more posteriorly placed foramen. Lower jaw symphysis more shallow than in *R. zettlandicus*. Tooth-crown ornament a more dense pattern of longitudinal ridges when compared with *R. zettlandicus*; striations all round crown. No quadrate-squamosal foramen.

See § 6a for further discussion on the species of *Rhomaleosaurus*.

5. DESCRIPTION

(a) *Skull* (figures 1–5)

This specimen provides information concerning areas missing in *R. zettlandicus* (Taylor 1992b), particularly the cheek region, postorbital bar, occipital arch and braincase.

In dorsal view (figure 1), the skull is triangular in shape with a narrow snout that is only slightly expanded over the tip of the premaxillae (pmx). It is typically pliosauroid in structure, with large, kidney-shaped, dorsally facing orbits (orb) at about the midpoint, followed by much larger temporal fenestrae (tf). The pineal foramen (pfo) lies behind the level of the orbits, and just behind the external nares (en), on the midline of the snout, is a small dorso-median foramen (dmfo). Narrow suborbital fenestrae (sof) are seen through the orbit. The quadrates (q) project behind what appear to be weak squamosal bars (drs). The small external nares (en) lie in troughs (tr) on the upper surface of the snout, very close to the orbits. The posterior ends of the maxillae (mx) protrude from the smooth line of the skull margins.

The premaxillae (which support five pairs of teeth) send back long facial processes (fac) between the external nares (figure 2, sections 1 and 2); the processes are flanked by the maxillae and the relatively small frontals (fr). A circumorbital series of bones includes jugals (j), lacrimals (l), prefrontals (prf), postfrontals (pof) and postorbitals (po). They are arranged in very much the same way as in *R. zettlandicus* (Taylor 1992b). Lacrimals are not normally reported in plesiosaurs, but in this specimen a change of texture of the bone surface in front of the orbit in the same place as the positive confirmation of a lacrimal in *Pliosaurus brachyspondylus* (Taylor & Cruickshank 1993b) is suggestive of the presence of a lacrimal here. On the midline of the skull, the frontals, meet in the midline between the parietals and premaxillae. The parietals (p) swell out towards the rear of the supratemporal fenestrae, are covered by the dorsal processes of the squamosals, and are underlain by the supraoccipital (so). Visible through the supratemporal fenestrae are the bones forming the sidewall of the braincase, whose structure is discussed below.

In side view (figure 2) the skull is shallow. Observations from natural breaks and CAT-scan sections (figure 2; sections 1–3), confirm this, indicating little distortion in the skull anterior to the braincase. What is noticeable is the manner in which the line of sockets for the anterior dentition (salv; section 1, figure 2) is turned outwards, so that the upper limits of the tooth sockets curve upwards onto the sidewall of the premaxillae. Projecting down below the line of the jugal bar is the pterygoid flange (ptf), with its attendant boss (ptb), followed by the quadrate ramus of the pterygoid (qrpt).

The cheek bar is formed from the long jugal which curves round the lower orbital rim to contact the anterior ramus of the squamosal (ars) in an interdigitating suture. The postorbital contacts the jugal from above, with a squamous overlap on the inner surface of the cheek bar. The postorbital suture just fails to

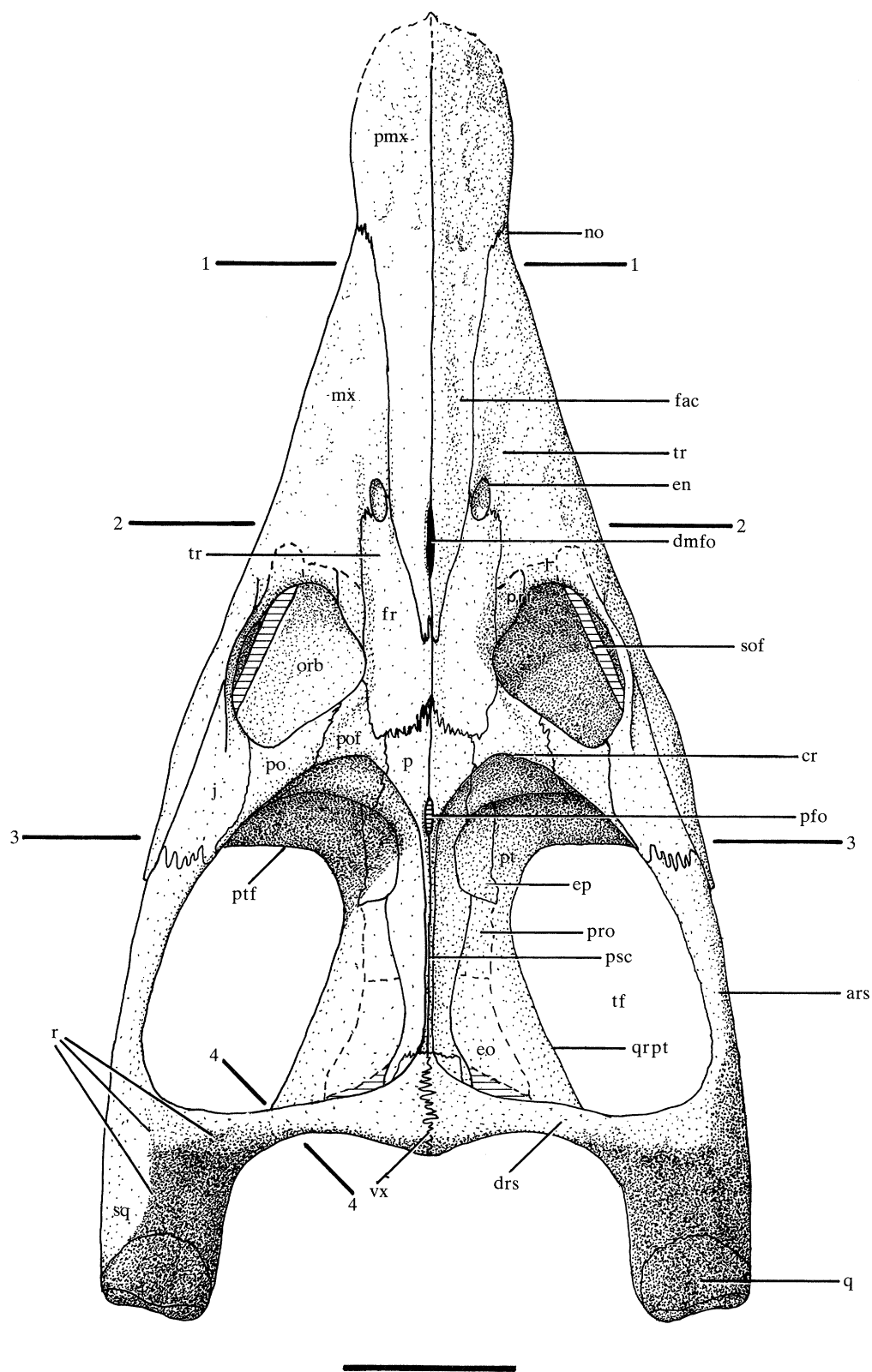


Figure 1. Dorsal view of *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). Scale bar = 50 mm. Sections 1–4 see figure 2. For abbreviations used in this and other figures see pp. 249–250.

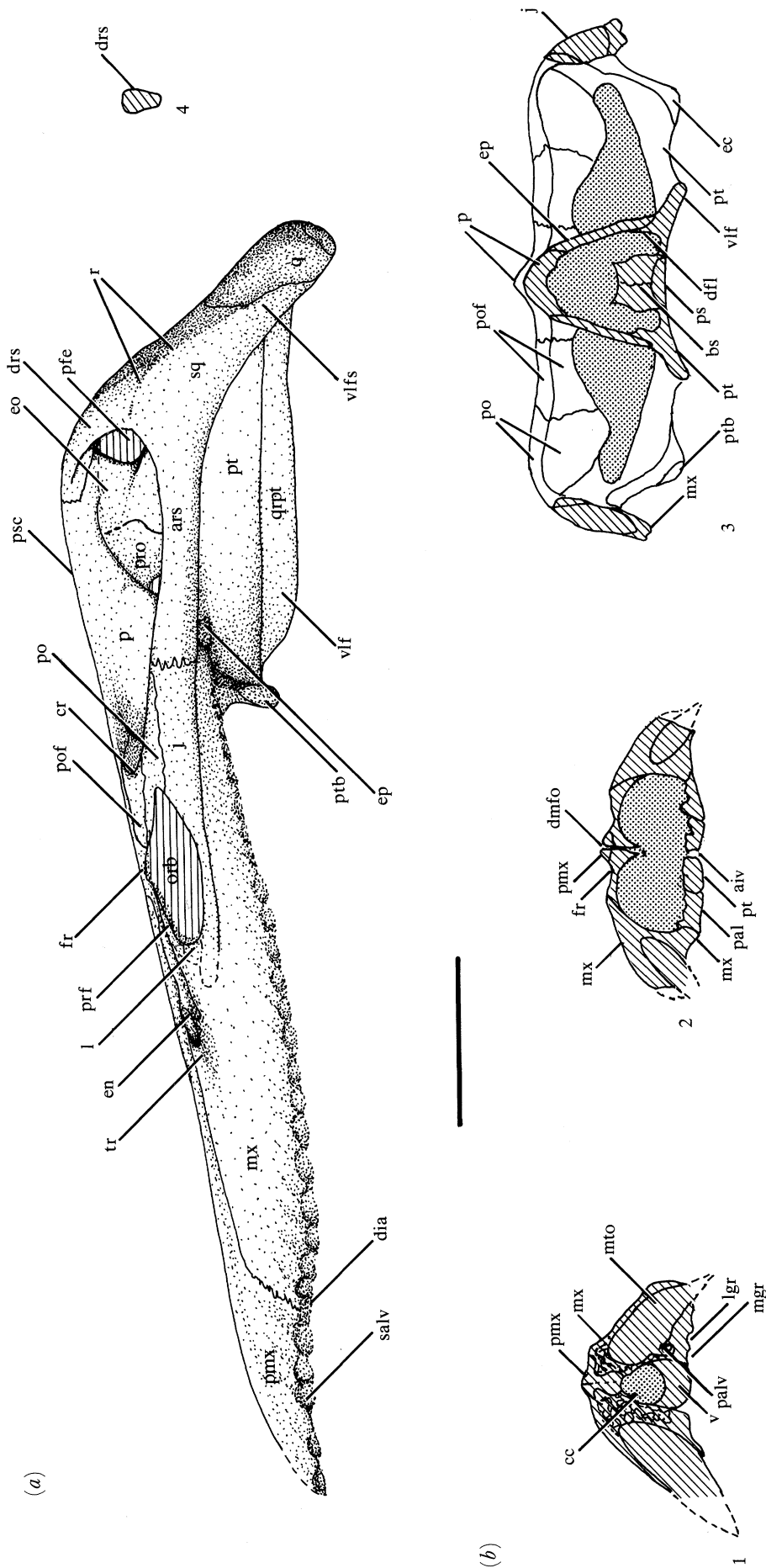


Figure 2. (a) Left lateral view of skull of *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). Scale bar = 50 mm. (b) Sections 1–4 where indicated on figure 1.

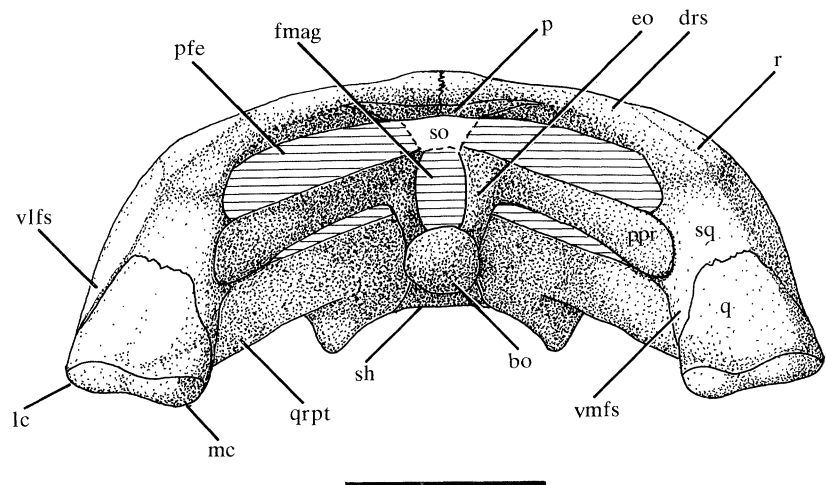


Figure 3. Occipital view of skull of *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). Scale bar = 50 mm.

meet the squamosal on the outer surface. Running below the jugal is the maxilla, which terminates in a shallow blunt point, behind the last tooth socket, and behind the jugal–squamosal suture.

Each postorbital bar (figures 1 and 2; section 3) is formed from the postorbital and postfrontal. A flange formed from both bones turns downward at a crest (cr) to define the anterior margin of the supratemporal fenestra; the junction between postorbital and postfrontal is an oblique suture which largely excludes the postfrontal from the orbital margin. The postfrontal and postorbital form about equal portions of the front wall of each supratemporal fenestra.

The descending rami of the squamosals (vlfs, vmfs) and the quadrates in combination form strongly built, sloping pillars (figure 3). A very marked Y-shaped ridge (r) on the outer surface of each squamosal, running onto the outer edge of each quadrate, outlines the probable attachment of the skin (and muscles?) of the neck. There is no squamosal–quadrate foramen in this specimen; the possibility exists that it might have been closed by dorso-ventral compression during fossilization, but this seems unlikely considering the overall lack of distortion of the skull. A similar lack of the foramen is apparent in colour slides of NMING F10194.

Much of the anterior of the palate and the mandibles (figures 2 and 4) is obscured by matrix, so that the inner limits of the tooth rows are only seen in CAT-scan section. However, some of the detail that was obscured in the palate of *R. zetlandicus* is visible.

The vomers (v) are long, paired, bones forming a rounded swelling on the midline of the palate (figure 2, section 1; figure 4), terminating almost one third of the way back along the skull, level with the internal nares (in). Flanking the vomers, on the inner portions of the palatal shelves of the maxillae, are paired grooves; the inner of which (mgr) terminates in the internal nares, and the outer (lgr), in a large foramen (fo) some distance behind the nares. Running out anteriorly, both grooves curve towards the premaxillary–maxillary junction on the palatal rim, where there is a gap in the tooth row (dia). This point marks the greatest embayment (no) of the profile of the snout

region. The outline of this notch is variable in *Rhomaleosaurus*, being most marked in the broad-snouted species such as *R. zetlandicus*.

In all plesiosaurs which have been examined during the course of this research, the internal nares are positioned some distance in front of the external nares. It has been proposed that the narial system formed a hydrodynamically driven olfactory system (Cruickshank *et al.* 1991). This system sampled water currents driven along the palatal grooves and past sensory epithelium contained within the snout, and out via the dorsally placed external nares. Negative pressures generated in the troughs (figure 1, tr) on the roof of the skull by motion through the water would assist this action (Cruickshank *et al.* 1991).

Suborbital fenestrae (sof) are present, bounded on their inner surfaces by depressions (dep) and ridges (r) on the palatal surfaces of the palatines (pal). Behind the suborbital fenestrae, the palatines and ectopterygoids (ec) butt against the inner surface of the jugals and maxillae. The ectopterygoids are laterally expanded bones ventral to the pterygoids (pt), forming a downturned flange (ptf) which ends laterally in a strong boss (ptb) to bear against the coronoid bone on the inner surface of the mandible (figure 2, section 3). Anterior (aiv) and posterior (piv) interpterygoid vacuities are present.

The structure of the pterygoid follows that of *R. zetlandicus* closely (Taylor 1992b), with strong ventro-lateral flanges (vlf) and quadrate rami (qrpt). The basioccipital (bo) is seen principally as the occipital condyle (oc) (figure 5a,b), with only a very small exposure on the midline of the palatal surface (figure 4).

The apparently weak dorsal rami of the squamosals (drs) are buttressed by ventral flanges (figure 2, section 4), which markedly increase their resistance to bending and shear moments. Large paroccipital processes (ppr) and quadrate rami of the pterygoids (qrpt) reinforce the rear of the skull. A small, but poorly preserved, supraoccipital (so) underlies the occipital arch, being separated from the fused squamosals by a narrow exposure of the parietals.

The sidewall of the braincase is exposed on both sides of the rear-central block of the skull, as sections through

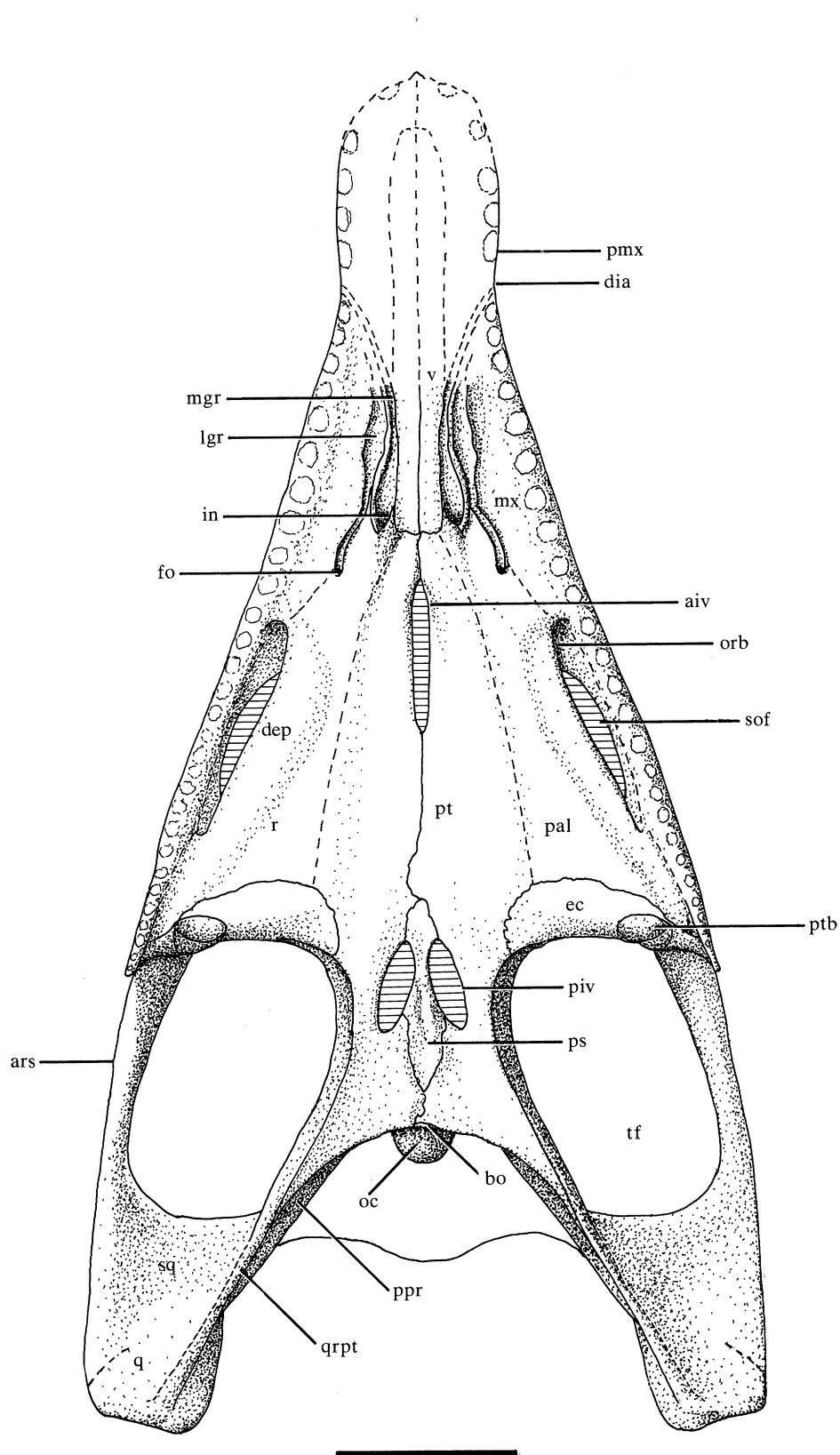


Figure 4. Ventral view of skull of *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). Scale bar = 50 mm.

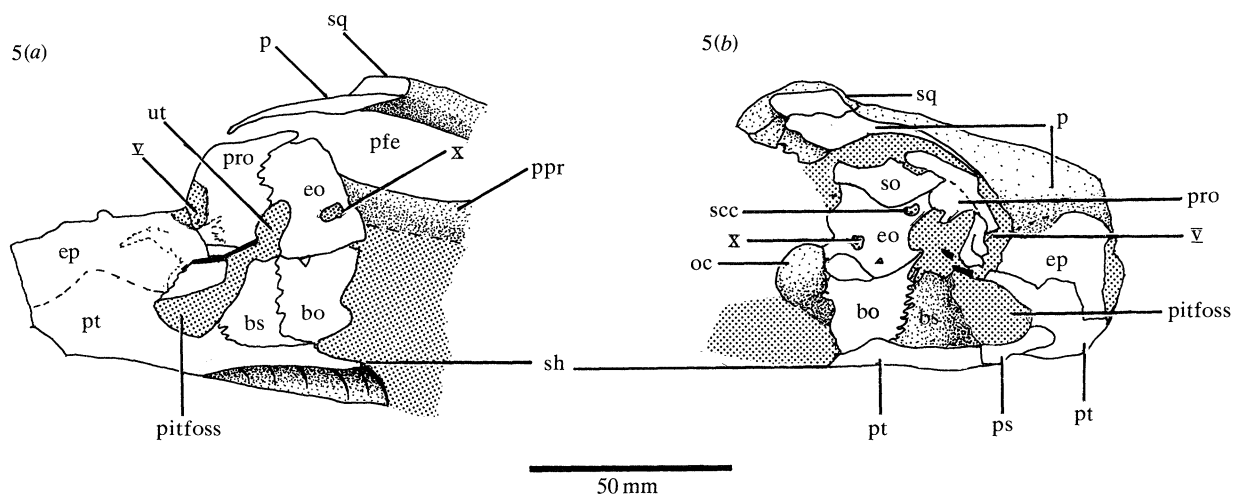


Figure 5. (a) Break section through right wall of braincase, looking outward. *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). (b) Break section through right wall of braincase, looking inward. *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). Scale bar = 50 mm. In this figure only, bone in section is unornamented.

the bones (figure 5a,b) of the right side, and slightly offset laterally on the left (figure 6). The reconstruction of the braincase depends on interpretation of the detail (figures 1, 2 and 6), but without more information from other sources, e.g. three-dimensional reconstructions based on CAT-scanning, the detailed relationship of the parasphenoid (ps) remains unclear (figure 2, section 3; Cruickshank 1994b).

The floor of the braincase is formed from the conjoined basioccipital and basisphenoid (bs). No sign of the 'basipterygoid' processes can be seen in section (Cruickshank 1994b), but a large pituitary fossa (pitfoss) runs across the body of the basisphenoid. The exoccipital-opisthotics (eo) are the main components of the side of the braincase behind the prootics (pro), and lie with a broad contact on the basioccipital. The supraoccipital bridges the dorsal gap between the exoccipital-opisthotics and contacts the thin lamina of the parietals dorsally. It appears that the prootic does not contact the basioccipital at all, but joins the front of the exoccipital-opisthotics and basisphenoid. The epipterygoids (ep) form a substantial part of the sidewalls of the braincase, overlapping the descending flanges of the parietals on their outer surface, and resting on

the dorsal flanges (dff) of the pterygoids (figure 2, section 3).

On the left side of the braincase (figure 6, sta) a short section of what may be the left stapes is exposed between the quadrate ramus of the pterygoid and the paroccipital process (ppr). It seems to be robust, and cannot be traced further using mechanical preparation techniques, but it has been detected running forward in the CAT-scan sections.

(b) Mandible (figures 7–9)

Only the outer surfaces of the lower jaws are well exposed (figure 7), and the CAT-scan sections contribute little that has not been described already (Taylor 1992b). The general shape is the same as in *R. zelandicus*, except that both articular regions are very badly damaged so that the true profile of the retroarticular processes (rap) cannot be determined. The depth of the symphyseal region (sym) is much less than that in *R. zelandicus*. On the inner surface of the left ramus, the trough (figure 8, dmt) formed from the anterior face of the articular (ar) and the prearticular (pa) for muscle insertions has been exposed. The rear of the splenial (sp) is squeezed between the prearticular and angular, which confirms their provisional identification by Taylor (1992b) in *R. zelandicus*. The coronoid is obscured here by matrix. Further forward, opposite the pterygoid flange, the coronoid forms a curved bar to bear against the pterygoid boss (ptb).

The symphysis (figures 7 and 9) is broadly spatulate, and reinforced in the midline by diverging bars of bone on the undersurface of each ramus, formed from the dentaries (d). At least five tooth positions can be reconstructed on each side, over the limits of the broadened region of the symphysis. The surface is covered with a distinctive pocked ornament.

(c) Dentition (figure 10)

It is difficult to count the total number of teeth in each row, but there seem to be about 27 in each upper jaw ramus and over 30 in each lower jaw ramus. This

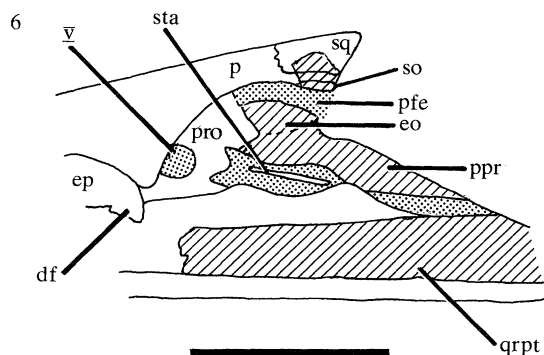


Figure 6. Left wall of braincase. *Rhomaleosaurus megacephalus* (Stutch), partly restored from figure 5a,b, showing portion of stapes (sta) exposed. (LEICS G221.1851). Scale bar = 50 mm.

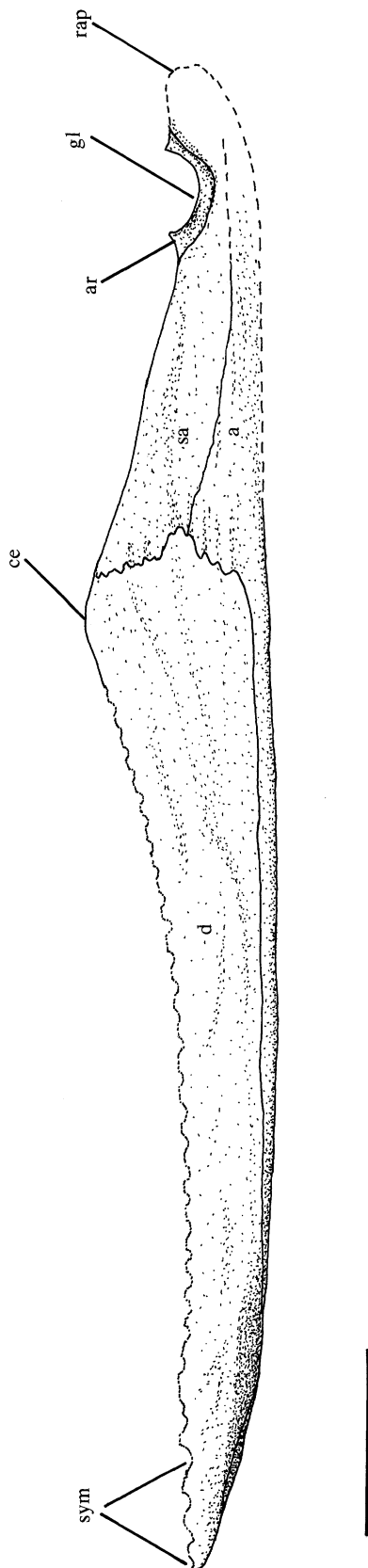


Figure 7. Outer view of left jaw ramus of *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). Scale bar = 50 mm.

count is within the known range for pliosauroids. The form of the teeth appears to be the same throughout, only the diameter varies with the tooth position. Extensive damage to virtually every tooth makes it difficult to be confident about their general morphology, but the most complete of those preserved on the surface of the snout (fifth tooth on the left premaxilla; figure 10) is a recurved, striated cone, with a blunt tip. There is a marked change in number of striae towards the tooth-tip; the number halving at about two-thirds of the distance. It is more heavily striated than those of *R. zelandicus* (Taylor 1992b).

The intermeshing anterior teeth projected outwards and forwards (figure 2, sections 1 and 2). On both the symphysis and the premaxillae there is a very small tooth flanking the midline. Examination of the snout shows the succeeding teeth to form a sequence which enlarges rapidly to a level with the maxillary suture, where there is a diastema (dia). Immediately behind the diastema the teeth become more upright and the tooth diameter diminishes slightly, but then increases over two or three positions. Thereafter there is a general diminution of tooth size. This dentition was one for grasping and piercing prey as described by Taylor (1992b) and Massare (1987).

Sections through the snout region (figure 2, section 1) show that the roots of the teeth deeply penetrate their supporting bones. In some of the anteriormost teeth, the roots almost touch on the midline of the skull. With closely arranged teeth, as in plesiosaurs, this composite 'material' of teeth reinforcing the dermal bones, must have made for a very strong, rigid structure.

6. DISCUSSION

(a) Comparison with other species

A number of species of English pliosauroids have been assigned to the genus *Rhomaleosaurus* Seeley, 1874. These are *Plesiosaurus cramptoni* Carte and Baily, 1863, the type species of the genus, *P. zelandicus*, Phillips, in Anon, 1854, *P. propinquus* Tate and Blake, 1876, *R. thorntoni* Andrews 1922, and *P. megacephalus* Stutchbury, 1846. Specimens assigned to the species *P. longirostris* Tate and Blake, 1876 have also been thought referable to *Rhomaleosaurus* (see Broadhurst & Duffy 1970), but this species has a jaw symphysis approximately 13 tooth positions long and therefore lies well outside the limit for *Rhomaleosaurus*. Swinton (1930) placed it in a separate genus, *Macroplata*, on the basis of its pectoral girdle characters, but the distinction holds good on skull anatomy as well.

The lower jaw of *Plesiosaurus propinquus* differs from that of *Rhomaleosaurus zelandicus* and *Rhomaleosaurus megacephalus* (Taylor 1992a,b; figures 7 and 8 herein) in that it has a prominent knob in the same position as the dorso-median trough described for *R. zelandicus* and *R. megacephalus*. It may therefore be a distinct species within the genus *Rhomaleosaurus*, but its full affinities must await complete description and analysis.

The other named species of *Rhomaleosaurus* can be provisionally divided into two groups for convenience:

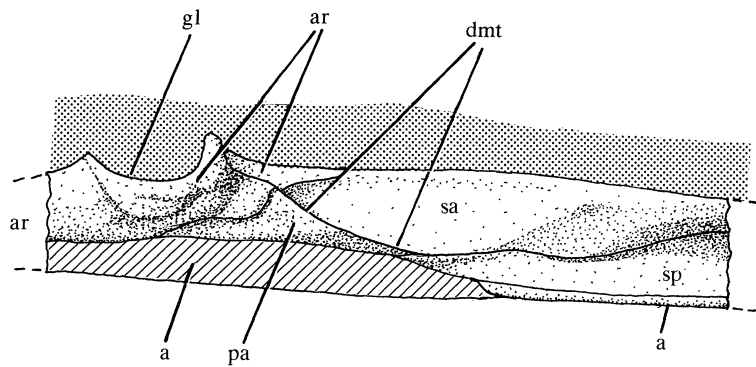


Figure 8. Ventral oblique view of inner articular region of left lower jaw. *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). Scale bar = 50 mm.

those from the Hettangian and those from the Toarcian. The former is restricted to *R. megacephalus*, but the latter comprises *R. cramptoni*, *R. zetlandicus* and *R. thorntoni*. The type of *thorntoni* (BMNH R4853) is a partial skull recently prepared, which shows several characters in common with *R. zetlandicus*. The most important of these are the anterior snout proportions, and the shape of the jaw symphysis in profile. The former is 1:1 in *R. zetlandicus* (Taylor 1992a) and *R. thorntoni*, whereas it is 1:1.25 in *R. megacephalus*. The symphysis in both Upper Liassic species is much deeper than in the Lower Lias species, *R. megacephalus*. Snout proportions similar to *R. zetlandicus* are found in *R. cramptoni*, although the symphyseal proportions cannot yet be determined for the latter species. Other differences between *R. zetlandicus* and *R. megacephalus* are the presence of a squamosal-quadrato foramen in *R. zetlandicus*, which is absent in *R. megacephalus*, and slightly differing overall skull proportions; that of *R. megacephalus* being more gracile than that of *R. zetlandicus*. The teeth of *R. megacephalus* are more finely striated than those of *R. zetlandicus* and *R. thorntoni*. The anterior of the palate is obscured in *R. zetlandicus*, so that the channels running forward from the internal narial region cannot be made out. However, in *R. thorntoni*, there is only one such channel,

with supplementary foramina lying within the walls of the internal nares. This condition differs from that in *R. megacephalus* where there are two grooves running forward, one from the internal nares and the other from a single prominent foramen, and no supplementary foramina are seen within the walls of the internal nares. In *Pliosaurus brachyspondylus* (Taylor & Cruickshank 1993b), apart from the internal narial opening, there are at least two other foramina almost as large. The condition of the palate in the region of the internal nares is therefore variable, and possibly significant for taxonomic purposes.

This brief comparison of the English Upper and Lower Liassic *Rhomaleosaurus* species implies that the large-headed Upper Liassic forms listed above may belong to the same species, with a corollary that there may well be only a single dominant predator species in each horizon; the more gracile *R. megacephalus* of the Hettangian being antecedent to the more robust *R. zetlandicus* of the Toarcian, but more research must be done to verify these views.

(b) Functional anatomy

The functional anatomy of the pliosauroid head has been discussed in depth by Taylor (1992b) and Taylor & Cruickshank (1993b). *Rhomaleosaurus megacephalus* differs from *R. zetlandicus* (Taylor 1992a,b) in relatively minor details, such as the relative proportions of the snout and lower jaw symphysis, the lack of a squamosal-quadrato foramen, and possibly the possession of paired palatal grooves. While these differences may be significant at a low taxonomic level, it is unlikely that they reflect major differences in function.

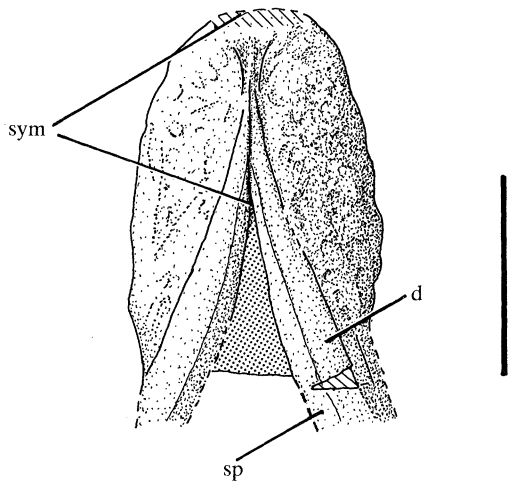


Figure 9. Ventral view of symphyseal region of lower jaw. *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). Scale bar = 50 mm.

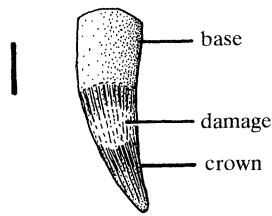


Figure 10. Fifth left premaxillary tooth in outer (buccal) view. *Rhomaleosaurus megacephalus* (Stutch). (LEICS G221.1851). Scale bar = 10 mm.

Two areas of the pliosauroid skull which can be further discussed are the braincase and the dorsal rami of the squamosals. In *R. megacephalus* the sidewall of the braincase is better exposed than in *R. zelandicus*, and the massive nature of the bones forming the braincase structure suggests that it must have absorbed considerable force during feeding. This confirms Taylor's (1992b, figure 18c) illustration which postulates forces acting on the rear of the skull. On the other hand, in contrast to the overall similarity of their braincases, the dorsal rami of the squamosals are significantly different; those of *R. zelandicus* being very much more stout than those of *R. megacephalus*. This seems correlated with the overall build of their respective skulls, where the very much more compact *R. zelandicus* was better able to resist bending moments in that part of the skull than was *R. megacephalus*. In both species however, the lower jaw is stabilized against lateral stresses, by the coronoids bearing on the large pterygoid flanges, and in the 'box-beam' like structure of the lower jaw. However, in some pliosauroids (e.g. *Pliosaurus brachyspondylus*) the pterygoid flange is lost through the development of an unrestricted gullet, presumably on becoming a 'bolt-feeder' (Taylor & Cruickshank 1993b). The lower jaw retains its 'box-beam' structure, but there is no longer any stabilization of the jaw against a pterygoid flange. In addition to the strengthening (lengthening) of the lower jaw symphysis, the function of the pterygoid flange was replaced in *P. brachyspondylus* by a strengthened occipital arch, with substantially widened and deepened dorsal rami of the squamosals allied to stronger paroccipital processes and much widened condyles on the very heavy quadrates (Taylor & Cruickshank 1993b). This may suggest that perhaps all pliosauroids were primarily 'twist feeders' (Taylor 1987), adapting their skull anatomy to the particular requirements of their specialist ecological niche. As far as *R. megacephalus* and *R. zelandicus* are concerned, the earlier form was less well adapted to coping with lateral and torsional stresses than the later.

7. SUMMARY AND CONCLUSIONS

1. The skull of a large, Lower Liassic, pliosauroid in Leicestershire Museum and Art Gallery (LEICS G221.1851), collected from a now inaccessible locality in Barrow upon Soar, Leicestershire, is described.
2. It is assigned to the genus *Rhomaleosaurus* Seeley, 1874, for which a revised diagnosis is given.
3. Comparison with other Lower Jurassic pliosauroids confirms that it is almost identical to the type of *Plesiosaurus megacephalus* Stutchbury, 1846, which was destroyed in an air-raid on Bristol in November 1940.
4. LEICS G221.1851 is declared the neotype of *Plesiosaurus megacephalus* Stutchbury.
5. Lack of iron pyrites in the matrix gave clear CAT-scan sections, which allied to the skull being very little distorted, provides a confident reconstruction of the skull.
6. The presence of a long jugal and suborbital fenestra is confirmed, along with a complete ring of circumorbital bones.

7. Details of the braincase are given. A stapes is identified.
8. The dentition comprises conical, striated teeth, with caniniforms on each premaxilla and anterior maxilla.
9. *Rhomaleosaurus megacephalus* was a powerful predator with a lifestyle similar to the Upper Liassic species, *R. zelandicus*.
10. Comparison of the Lower Liassic *R. megacephalus* with species from the English Upper Liassic emphasizes a number of differences. The Upper Liassic forms all share a broader, shorter, snout associated with a deeper symphysis of the lower jaw. Further study may show that *R. zelandicus*, *R. cramptoni* and *R. thornstoni* belong to the same species.

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