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Functional Anatomy of the Head of the Large Aquatic Predator Rhomaleosaurus zetlandicus (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England

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Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England

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CONTENTS

SUMMARY

The skull and mandible of the type specimen of the large pliosauroid plesiosaur *Rhomaleosaurus zetlandicus* from the Toarcian of England are elongate, and adapted for powerful predatory activity in water. The mandible contains all elements found in primitive reptilian mandibles. The broadly caniniform dentition suggests that *Rhomaleosaurus* fed on a wide range of active prey, and forcibly dismembered larger prey by shaking and twisting them.

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The cranial musculature is reconstructed for the first time in plesiosaurs. It was adapted for feeding in water. The adductor musculature included a large anterior pterygoideus attached to the suborbital fenestra, a large posterior pterygoideus, and a group of large dorsal muscles including the adductor mandibulae externus. The anterior pterygoideus exerted maximum torque when the jaws were wide open, snapping them shut quickly, and the dorsal muscle mass exerted maximum torque when the jaws were closed on prey to subdue and dismember it. The role of the posterior pterygoideus is uncertain or intermediate. The musculature combines elements of the 'kinetic inertial' system ascribed to aquatic tetrapods by Olson (1961), with his 'static pressure' system ascribed to terrestrial tetrapods. Olson suggested that the large pterygoideus musculature typical of the 'kinetic inertial' system functioned to confer kinetic energy on the mandible. However, its function may instead have been to compensate for the inertia and drag of the mandible. The depressor musculature comprised the depressor mandibulae and the longitudinal pharyngeal muscles, and opened the jaw quickly against drag. The cervical musculature cannot be reconstructed in detail. There was a strong nuchal ligament.

The forces within the head are analysed by using box and girder beams as analogues. Gross form, shape of constituent bones, and sutural morphology confirm adaptations to resist great bending moments arising from the action of the muscles when biting on prey. When the jaws were closed, the pterygoid flange supported the mandible against the inward component of the adductor muscle force.

Rhomaleosaurus was a visual predator. The eyes were large. The stapes is present. Underwater olfaction was likely. There is no evidence for an eardrum, but it is not known whether this is the plesiomorphic reptilian state or secondarily derived from a tympanate ancestor. The ears were not acoustically isolated from the braincase, so underwater directional hearing was poor, and sonar was not possible.

The structure of the head of *Rhomaleosaurus* is a functional compromise between the needs to maximize structural strength and to maximize swimming and feeding efficiency. Especially important were the ability to sustain large muscle and reaction forces to provide an adequate bite force at the end of a long snout, and the wide gape allowing the swallowing of large pieces of prey. Even larger items were dismembered into smaller pieces by shake and twist feeding. The major unresolved problems are the effects of scaling factors, and the torsional loadings induced when biting asymmetrically, or twisting large prey to pieces.

1. INTRODUCTION

The plesiosaurs were a widespread order of predatory aquatic reptiles with a fossil record from the Rhaetian (uppermost Triassic) to late Cretaceous (Brown 1981*a*). They were mostly marine and swam with four limbs in a form of underwater flight (Robinson 1975; Godfrey 1984; Alexander 1989; Halstead 1989). Plesiosaurs are conventionally regarded as a monophyletic group of modified diapsids classed within the Sauropterygia with 'nothosaurs', the plesiosaur-like *Pistosaurus*, and perhaps placodonts (Brown 1981*a*; Carroll 1981; Kemp 1985; Sues 1987*a*, *b*; Rieppel 1989; Taylor 1989). Plesiosaurs varied mainly in the proportion and shape of the head and neck. The order Plesiosauria (vernacular name 'plesiosaurs') comprises two superfamilies, the Plesiosauroidea ('plesiosauroids') with small heads, and the Pliosauroidea ('pliosauroids' or 'pliosaurs') with larger heads. This reflects ecological differences (Massare 1987, 1988). Plesiosauroids included long-necked feeders on relatively small fish and cephalopods, as well as filter or straining feeders on smaller fish and crustaceans (Brown 1981*b*; Chatterjee & Small 1989). Pliosauroids had robust skulls and teeth with wider gapes, so could feed on a wider range of prey sizes. However, little work has been done on feeding in any plesiosaurs, except surveys by Massare (1987, 1988).

There are many good specimens of Rhaetian and Lower Jurassic plesiosaurs, mainly from Britain and Germany (Urlichs *et al.* 1979; Brown 1981*a*; Benton & Taylor 1984). However, they are poorly known although critical for our understanding of the origin, early radiation and palaeobiology of plesiosaurs. Moreover, old specimens benefit from modern preparatory techniques (Rixon 1976; Crowther & Collins 1987) and non-destructive examination by computed tomography (McGowan 1989; Cruickshank *et al.* 1991).

This paper therefore re-examines the holotype of the robust-snouted pliosauroid *Rhomaleosaurus zetlandicus*. The genus *Rhomaleosaurus* comprises several species of moderately sized Lower Jurassic pliosauroids (up to 6 m long), with a range of jaw shapes (White 1940; Benton & Taylor 1984). Some had robust snouts with stout teeth, like the Nile crocodile (*Crocodylus niloticus*), and by analogy probably fed on a wide range of prey, dismembering large prey in water by shaking or twisting (Taylor 1987).

The aims of this paper are: (i) a description of the cranial osteology of *R. zetlandicus*, as a contribution to knowledge of Lower Jurassic forms; (ii) the first reconstruction of the cranial musculature of a plesiosaur; (iii) the first functional analysis of a plesiosaur head, with special reference to the problems facing an aquatic predator feeding on large prey.

2. MATERIAL

(*a*) *Specimens and repositories*

This study is based on the holotype of *Rhomaleosaurus zetlandicus* (YORYM G503; repository abbreviation given below). Its provenance, taxonomy, preparation and taphonomy are only briefly summarized here (see Taylor (1992) for full discussion). Other genera used for comparison are here listed with relevant references. Closely similar Lower Jurassic forms are *R. cramptoni* (Carte & Baily 1863*a*, *b*), and *R. thorntoni* (Andrews 1922), both Toarcian; and *R. megacephalus*, Hettangian (Stutchbury 1846). Two smaller, less robust Toarcian species are *R. propinquus* (Watson 1910), and *R. victor* (Fraas 1910). Also used for comparison are the Callovian (Middle Jurassic) plesiosauroid *Cryptoclidus* (Brown 1981*a*), and the Callovian (Jurassic) pliosauroids *Liopleurodon*, *Peloneustes*, *Pliosaurus* and *Simolestes* (Andrews 1913; Linder 1913; Tarlo 1960). Repository abbreviation: YORYM, Yorkshire Museum, Museum Gardens, York YO1 2DR, UK.

(*b*) *Taxonomy and provenance*

Class: Reptilia
Subclass: Sauropterygia Owen, 1860
Order: Plesiosauria de Blainville, 1835
Superfamily: Pliosauroidea (Seeley, 1874), Welles, 1943
Family: Pliosauridae Seeley, 1874
Rhomaleosaurus zetlandicus (Phillips, in Anon., 1854)

Holotype: YORYM G503, an incomplete skeleton about 5.3 m long, comprising head (0.74 m long), neck (1.3 m long), vertebral column, portions of the ribs, limb girdles and limbs, and a gastrolith; undescribed except for brief discussions by Carte & Baily (1863*a*, *b*) and Tate & Blake (1876, pp. 249–250, plate 1, figure 5). The skull and mandible have been largely exposed by mechanical preparation, some done during the 19th century and some done during this study. The matrix in the interior of the skull is a hard, tenacious pyritous concretion which could not be wholly removed.

Referred material: none at present.

Locality and horizon: collected in or before 1852 from the Loftus (also Lofthouse) Alum Mine, a large coastal quarry about 2 km northeast of Loftus, and about 18 km northwest of Whitby, Yorkshire, England (U.K. National Grid Reference NZ 7420; Anon. 1853; Phillips 1854; Benton & Taylor 1984). Assuming that the specimen came from the strata mined for alum, then its source horizon fell within the upper or middle portion of the Alum Shale Member (formerly termed the 'Cement Shales' and 'Main Alum Shales'), Whitby Mudstone Formation, Lias Group, Lower Jurassic, and within the *Hildoceras bifrons* Biozone of the Lower Toarcian (Cope *et al.* 1980; Benton & Taylor 1984; Powell 1984).

3. SKULL

(*a*) *General*

The head (figures 1–4) is large, robust, broad and triangular, with a bluntly rounded snout and huge temporal fenestrae (tf). It is dorsoventrally rather flattened and is highest at the occiput. The reconstruction presented here is corrected for crushing. The main errors, if any, will probably lie in the vertical plane and the relative locations of the quadrates.

(*b*) *Dorsal elements*

The premaxillae (pmx) are massive bones with anterior toothbearing portions. The sockets for the large premaxillary caniniform teeth run backwards, inwards and upwards deep into the bone, towards the midline, as shown by crushing of the dorsal surface into empty sockets. The long, tapering facial processes (fac) run back along the midline between the nares to an apparently overlapping suture with the parietals (p). The facial processes form a low, obtuse dorsomedian crest (dmc) and separate to surround the dorsomedian foramen (dmfo). From in front of the foramen backwards, each premaxilla forms a low, rounded parasagittal crest (psc) which merges into the lateral wall of the foramen. The foramen occurs also in *R. cramptoni*, *R. megacephalus*, *R. propinquus*, and *R. victor*. Its function is unclear.

The marked marginal notch (no) between each premaxilla and maxilla (mx) is partly formed by the outward swelling around the sockets of large teeth. The skull is here dorsally convex from side to side. More posteriorly, it is slightly flatter in the middle but curves downwards on either side above the thick toothbearing margin. The maxillae bear gentle bumps and hollows apparently following the underlying sockets of the large maxillary teeth, which seem to extend backwards, inwards and upwards to near the midline. Each orbit (orb) is anteriorly closed by a curtain-like antorbital flange (aof) descending downwards and slightly backwards into matrix filling the ventral and medial portions of the orbits. A low antorbital crest appears to demarcate the anterior rim of each orbit from the facial surface. However, it may be an artefact caused by crushing of the facial surface downwards against the palate, with shearing at the top of the antorbital flange. An overhanging dorsomedial shelf (dms) forms the medial rim of the orbit. The lateral marginal bones of the orbit are not preserved.

The facial processes of the premaxillae appear to be hollow prisms with central cavities (pmc) meeting each other in deep interdigitating sutures, and the maxillae in deep butt joints (section 1, figure 2). Each maxilla comprises a heavy lateral tooth-bearing section, and apparently a hollow thin-walled medial portion with a central cavity (mxc). It butts against the vomer (v) ventrally. There is a central cavity (cc) between the premaxillae, maxillae and vomers. The paired vomers seem to comprise dorsal and ventral portions, but this may be an illusion caused by the section passing through a transverse foramen. In any case, the section is located in an area where the tooth roots are relatively short and so may not be typical of other parts of the premaxillae and maxillae.

Each external naris (en, figure 1) lies just in front of the orbit (orb). It is an anteroposteriorly elongate oval opening dorsally. Inside the anterior end is a shelf sloping posteroventrally into the matrix filling. The lateral and medial rims appear to be rounded edges. The posterior end is walled off internally by a vertical curtain of bone descending into the matrix. Sculpturing on the lateral rim, and a sculptured spiral (ssc) on the anterior internal shelf, may have been origins for muscles or ligaments controlling a narial flap or plug.

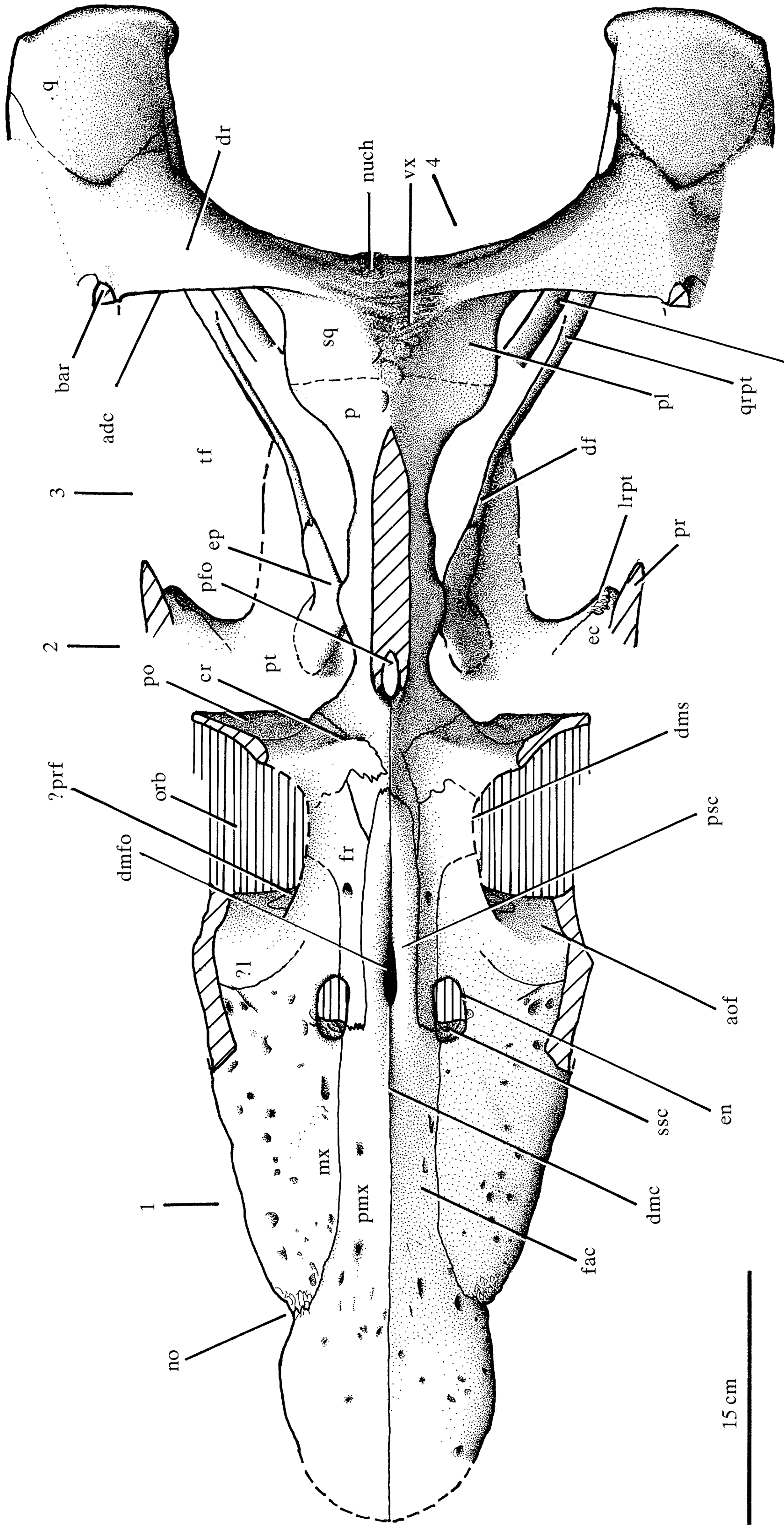

Figure 1. *Rhomaleosaurus zetlandicus*. Reconstruction of skull in dorsal view, including locations of planes of sections 1–4 (see figure 2). Figures 1–8 show damaged or sectioned bone as diagonal hatching, and matrix obscuring any deeper structures as transverse hatching and toning.

The presence of nasal elements in plesiosaurs is uncertain (Brown 1981*a*). They cannot be confirmed or refuted in YORYM G503 because of crushing between the nares and orbits. The nasals are here presumed absent; if so, the maxillae meet the frontals (fr). The posterior terminations of both frontal-maxillary sutures are lost because of damage.

A bone here interpreted as the lacrimal (?l, figures 1 and 2) overlaps the maxilla slightly in a curved suture running in front of, and parallel to, the antorbital crest. The lateral and medial ends of both sutures are lost because of damage. No lacrimal foramen is visible. This bone may, alternatively, be the anteromedial termination of a large jugal but this cannot be resolved as the lateral portion of the orbit is missing.

An element interpreted as the prefrontal (?prf) forms the medial antorbital flange, overlapping the presumed lacrimal. Crushing makes it impossible to determine whether it extended onto the dorsal surface of the skull. (If the 'lacrimal' is in fact the jugal, then the 'prefrontal' would be the true lacrimal.)

In external view, each frontal (fr) meets the premaxilla, maxilla, parietal and postfrontal (pof), in overlapping sutures which may conceal its actual size. The frontal forms a shallow longitudinal trough between the rounded median crest and the edge of the orbit. It appears to overlap the premaxilla anteriorly, but more posteriorly it is overlapped by the posterior end of the premaxilla and the postfrontal. It forms an interdigitating suture with the postfrontal. The deep structure of the frontals cannot be resolved in this specimen; they are reinforced by ventral flanges in *Cryptoclidus* and *Peloneustes*.

Supraorbitals, palpebrals and sclerotic plates are absent, although sclerotic plates are known from other plesiosaurs.

The postorbital bars (figure 1; section 2, figure 2) comprise postfrontals (pof) and postorbitals (po). Their distal portions and dorsal edges are missing, and their anterior and ventral sides are buried in matrix. The bars are strongly jointed to the median bones. Each has a deep vertical flange. It probably extended outwards and slightly downwards and backwards to meet the lateral bars of the orbits, with a small triangular fillet of bone in the dorsal posterolateral corner of the orbit, as in *R. cramptoni* and *R. propinquus*. The postfrontals form the dorsal portions of the bars. Medially each merges smoothly with the frontal and parietal in an interdigitating suture, sending a thin anteromedial lamina to overlap the parietal. There is a transverse crest (cr) on the posterodorsal edge of the postfrontal. Anteriorly, the postfrontal is concave and forms the posterior portion of the overhanging dorsomedial edge of the orbit. The postorbitals meet the postfrontals in a complex suture. They deepen suddenly lateral to their brief sutures with the parietals, forming large rounded bosses.

The paired parietals (p) join in an interdigitating median suture, and bear a long median crest. In YORYM G503 the dorsal portion of this crest is missing between the parietal foramen (pfo) and the squamosals (sq). Behind the foramen, the parietals form a pitched roof above the braincase (section 2, figure 2). The parietals expand slightly ventrolaterally, and their ventrolateral edges thicken to form the sockets for the epipterygoids (ep). More posteriorly, the parietals become shallower (section 3, figure 2), and then expand into two plates (pl, figure 1) set at a more obtuse angle over the posterior braincase.

The fused parietal–squamosal suture forms a band of roughened bone running ventrolaterally from the anterior apex of the flattened, triangular occipital vertex (vx), and marking a change in orientation of surface texture. A break in the left squamosal, under the median end of the anterodorsal crest (adc), shows an interdigitating suture, suggesting that the parietals extend posteriorly under the squamosals to at least this point. The bone texture also suggests a possible fused parietal–squamosal suture along the posteroventral edge of the dorsal skull bones below the vertex and along each post-temporal bar. Fusion of this suture has been reported in other plesiosaurs, which vary, however, in the extent to which the squamosals overlap the parietals dorsally (Fraas 1910; Andrews 1913; Brown 1981*a*).

The squamosals (sq) and quadrates (q) are damaged and partly obscured by matrix. Each squamosal and quadrate together have the characteristic triradiate structure of plesiosaurs (cf. *R. victor*, figure 5*b*). The dorsal rami (dr, figure 1) of the squamosals meet in the dorsal midline in an interdigitating suture, and widen anteriorly to form part of the plates (pl) overhanging the braincase roof. Each ramus is inflected to give an anterodorsal crest (adc) forming the posterior rim of the temporal fenestra and overhanging the plates, and it also has a rounded ventral crest (vc, section 4, figure 2).

The anterior ramus of each squamosal (ars, figure 5*b*) is missing except for its base on the left squamosal (bar, figure 1). It would have projected forward to form the posterior portion of the lateral temporal bar, probably forming an interdigitating suture with the bones of the anterior portion (as in *R. victor*, figure 5*b*).

The ventral ramus of the squamosal sends ventromedial and ventrolateral flanges (vmf, vlf) either side of the quadrate (figures 1, 3, 5*b*). The ventral crest of the dorsal ramus continues posterodistally into the ventromedial edge of the ventromedial flange.

The ventral ramus of the squamosal and the quadrate together form a broad bone which is convex dorsally and concave ventrally, thus an inverted 'U' in section, sloping steeply posteroventrally (sections 5 and 6, figure 2). The squamosal–quadrate suture is an inverted 'V' with the apex at the squamosal–quadrate foramen (sqf, figure 3). Each paroccipital process (ppr, figure 1) is now displaced but fitted into a shallow recess in the medial face of the squamosal just above the squamosal–quadrate suture, as in some plesiosauroids (Brown 1981*a*). The quadrate ramus of the pterygoid (qrpt, figures 2*a* and 3) articulates with a socket at the anteromedial corner of the quadrate, and sends a lamina posteriorly to overlap the flattened medial face of the quadrate almost as far back as the condyles.

The quadrate has thickened lateral and medial edges and swollen articular condyles merging into the

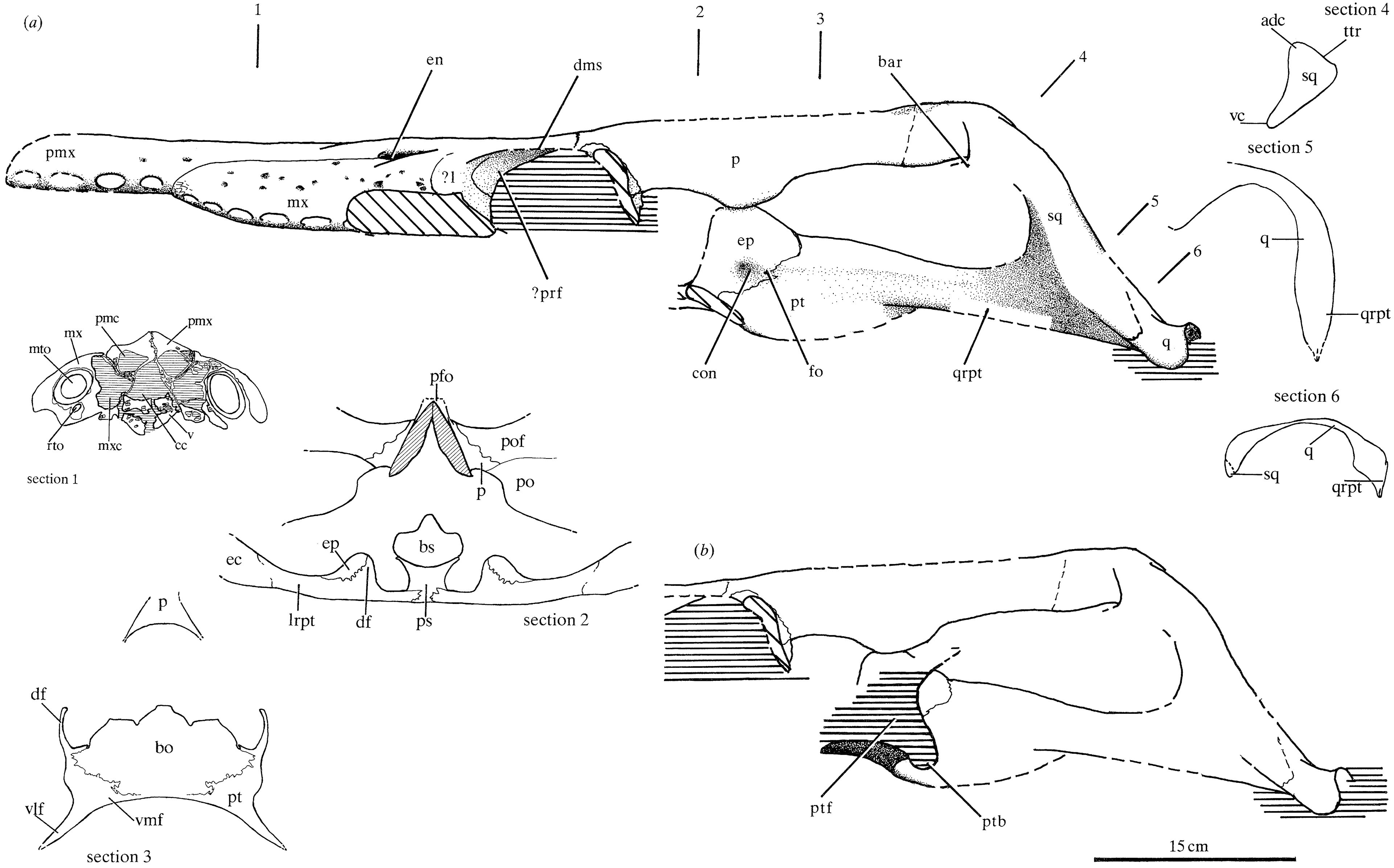

Figure 2. *Rhomaleosaurus zetlandicus*. Reconstruction of skull in lateral view, (*a*) including locations of planes of sections 1–6, and (*b*) posterior portion with pterygoid flange. Sections 1–6 to approximate scale. For shading, see figure 1.

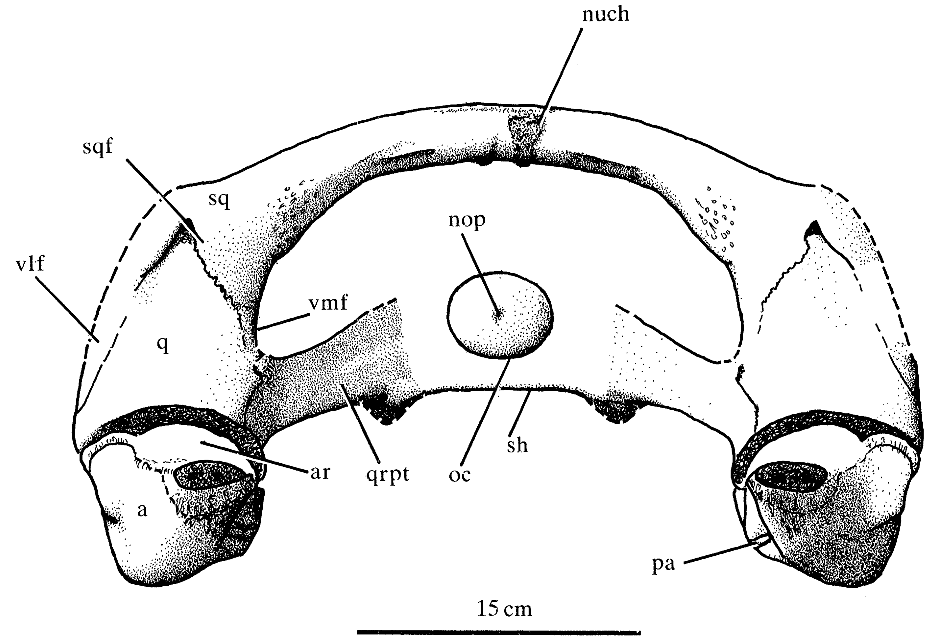

Figure 3. *Rhomaleosaurus zetlandicus.* Reconstruction of skull and mandible in occipital view.

low, rounded transverse ridge on the posterior edge. The articular condyles are obscured but are presumably the normal plesiosaurian type with a lateral and a rather larger medial condyle (lc, mc) separated by a parasagittal sulcus (pss), as in *R. victor* (figure 5*b*). There is a small foramen (fo) on the ventral side (figure 4).

Damage makes it impossible to confirm or refute the presence of quadratojugals, which probably do not occur in plesiosaurs (Brown 1981*a*, *contra* Andrews 1910).

(*c*) ***Braincase***

The disarticulated and largely obscured braincase of YORYM G503 can be interpreted by using reviews by Andrews (1910, 1913) and Brown (1981*a*). At the parietal foramen (pfo), at or close to the dorsum sellae (section 2, figure 2), the basisphenoid (bs) is closely applied to the dorsal surface of the parasphenoid (ps), which meets the pterygoids (pt) in interdigitating sutures at the immobile basipterygoid articulation. The parasphenoid is ventrally keeled between the two posterior interpterygoid vacuities (piv, figure 4), and disappears posteriorly under the pterygoids. Behind the posterior interpterygoid vacuities a section (3, figure 2) shows the basicranium to be deep, wide and probably composed solely of the basioccipital (bo), sheathed laterally and ventrally by the pterygoids.

The occipital condyle (oc, figures 3 and 4) is damaged. In shape it is between a hemisphere and a truncated cone, slightly wider than high or long. A groove runs round the base on the ventral and lateral sides; the dorsal side of the base is not visible. A small central pit may be a notochordal pit (nop). Both ventrolateral tubera are only partly visible. They are coarsely roughened and pitted.

The rest of the braincase is largely obscured. In lateral view the left pro-otic is an irregularly polygonal bone not markedly different from that of *Peloneustes*. The supraoccipital is displaced and hardly visible. Both fused exoccipital-opisthotics are largely obscured except for the paroccipital processes (figure 5*a*). Several breaks through the right process show that it tapers to its midpoint then expands once more into a laterally compressed and truncated distal end which fitted into a socket on the medial face of the squamosal above the quadrate.

(*d*) ***Palate***

Although the palate is damaged, it is here described in detail because of the many areas of uncertainty and because of its functional importance. The lateral margins are missing in the orbital region. The dorsal side of the palate is wholly unknown except from two breaks (sections 2 and 3; figure 2). The posterior portion of each pterygoid bears a dorsal flange (df) at the level of the basicranium, bearing the robust epipterygoid (ep). Each flange continues anteriorly for an unknown distance beneath the postorbital bars. A major area of uncertainty is how the palate connects to the dorsal skull elements, especially in the regions of the cheeks and antorbital flanges.

The anterior palate (figure 4) and internal nares are poorly exposed. The internal nares (in) are located anterior to the external nares. Each vomer and maxilla meet at the posterior end of the internal naris in a suture that appears to be a simple butt joint. The suture runs posteriorly and slightly laterally to contact the palatine (pal). The interdigitating vomer–palatine suture runs posteromedially to the midline, but is not clear because of damage or perhaps partial fusion. At the midline, the vomers appear to have been separa-

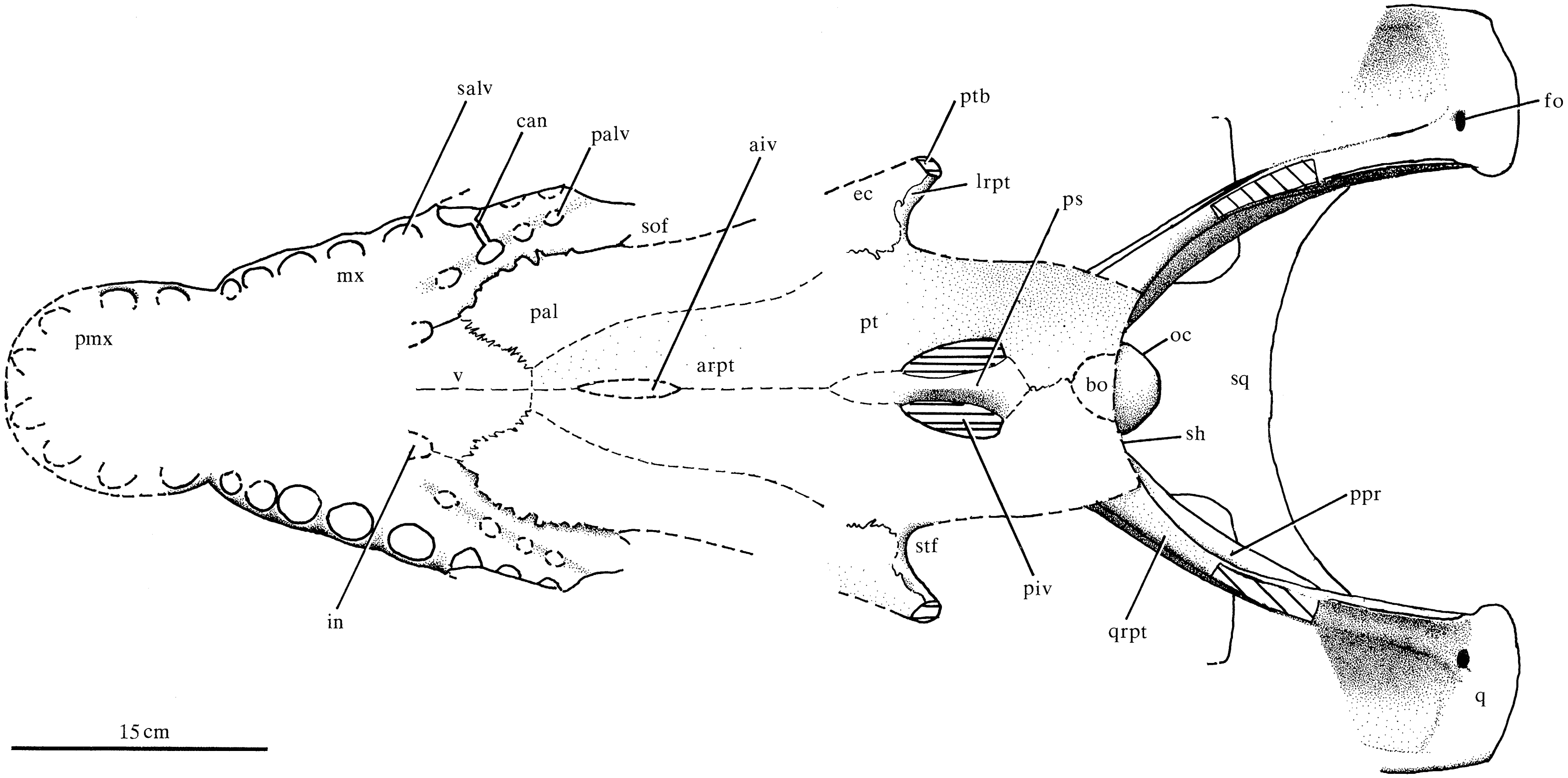

Figure 4. *Rhomaleosaurus zetlandicus*. Reconstruction of skull in ventral view. For shading, see figure 1.

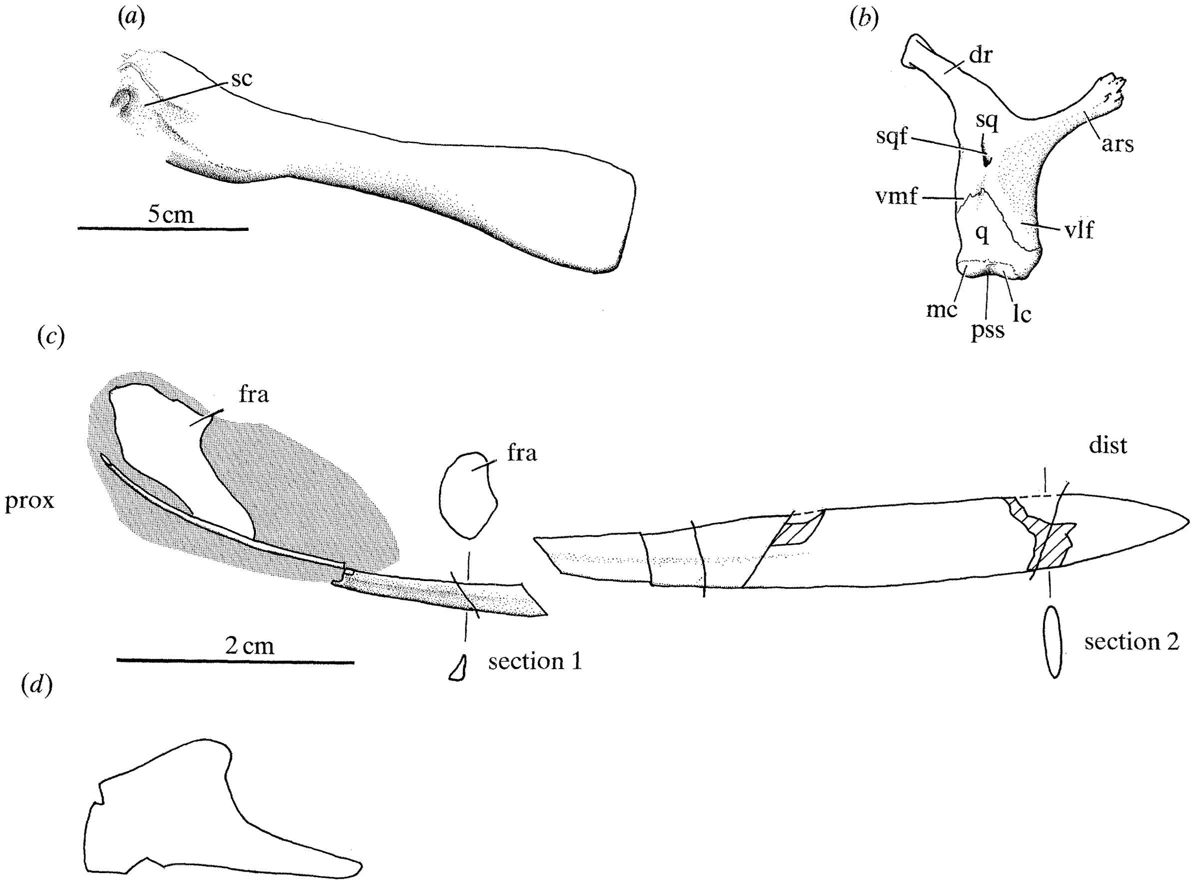

Figure 5. (*a*) *Rhomaleosaurus zetlandicus*. Lateral view of paroccipital process of left exoccipital-opisthotic. (*b*) Diagram of structure of right squamosal–quadrate of *Rhomaleosaurus* (after *R. victor*, Fraas 1910, plate 10, figure 2). (*c*) *Rhomaleosaurus zetlandicus*. Right stapes as preserved, from medial aspect, with two sections (1, 2). (*d*) *Rhomaleosaurus zetlandicus*. Unidentified bone, possibly part of hyoid apparatus. For shading, see figure 1.

ted by damage. The vomers seem to meet the pterygoids posteromedially between the palatines, but they are too damaged to confirm this.

The secondary dentary alveoli (salv) are set in the ventral side of the rounded margin of the maxilla, which is slightly flared around the lateral edges of each alveolus. The posterior portions of the maxillae are missing.

The left palatine (pal) is roughly flat ventrally. Laterally it meets the maxilla in an apparent scarf joint, overlapping the maxilla with a lip. More posteriorly the maxilla is missing ventrolateral to the orbit. The now mutilated but robust lateral edge of the palatine here formed the medial rim of the suborbital fenestra (sof), confirmed by the free lateral rim of the right palatine. This fenestra was almost certainly a long, narrow oval formed by the maxilla laterally and the palatine and ectopterygoid medially; it is partly preserved in *Rhomaleosaurus thorntoni* and wholly in *R. megacephalus*, and is known from other pliosauroids. The posterior terminations of the palatines are missing; they presumably contacted the ectopterygoids (ec).

Each pterygoid (pt) comprises anterior, lateral and posterior rami. The ventrally comparatively flat anterior ramus (arpt) forms much of the median palate below and anterior to the orbits. Damage makes it difficult to verify the nature of the midline suture between the pterygoids, which appears to be interdigitating, or the size of the anterior interpterygoid vacuity (aiv).

The ectopterygoid (ec) and the lateral ramus of the pterygoid (lrpt) together form the main lateral member of the palate, a robust dorsoventrally flattened bar linking the median palate with the marginal skull bones and forming the anterior rim of the subtemporal fenestra (stf). This area is missing on the left, but almost complete on the right. The pterygoid–ectopterygoid suture is extensively overlapped and ventrally interdigitated. From the midline laterad, the bones tilt increasingly posteroventrally to form the pterygoid flange with a marked pterygoid boss (ptb, figures 2*b* and 4). The middle portion of the palate, just behind the orbits, is thus slightly convex ventrally from side to side (section 2, figure 2). The junctions with both jugals are mostly missing except for a broken process (pr, figure 1) of the right ectopterygoid extending posterodorsally and laterally over the pterygoid flange and mandible. The link between the palate, postorbital bars, and lateral temporal bars is poorly known in plesiosaurs, and the literature is confusing. Pliosauroid specimens show variation in the extent of ventral emargination of the cheek and I leave the question open to avoid the risk of circular argument.

The complex posterior ramus of the pterygoid (prpt) overlaps the sides and floor of the braincase. It sends a quadrate ramus (qrpt) posterolaterally to the quadrate. Anterior to the quadrate ramus (section 3, figure 2) each pterygoid comprises: a dorsal flange (df) which posteriorly contacts and projects dorsal to the lateral side of the basicranium; a ventromedial flange (vmf) applied to the ventral side of the basicranium and anteriorly merging with the lateral ramus; and a projecting ventrolateral flange (vlf) the lateral edge of which forms the medial rim of the anterior portion of the suborbital fossa. The flanges blend into a thickened central union which forms the base for the long quadrate ramus which is set somewhat dorsal to the ventrolateral flange and is in side view a continuation of the dorsal flange.

The ventromedial flanges of the pterygoids open out to form the two oval posterior interpterygoid vacuities (piv) divided by the parasphenoid, with which they form an interdigitating suture. The palate is here ventrally concave from side to side. The pterygoids meet again at the posterior end of the vacuities, and then appear to part to expose the basioccipital. The pterygoids and basicranium thus form the transverse shelf (sh, figures 3 and 4) below the occipital condyle, merging into the proximal end of each quadrate ramus. The pterygoids ventrally overlap the posterior braincase to a variable degree in pliosauroids (see, for example, Andrews 1896, 1913; White 1940). They form a strong, interdigitating suture (section 3, figure 2) with the braincase to create a single mechanical unit.

The ventrolateral flange of each pterygoid (vlf, figures 2*a*, 3 and 4) slopes downwards and outwards. It is a thinner posterior continuation of the lateral ramus. The flange is damaged, but its edge appears to have been much sharper than the anterior rim of the subtemporal fossa and to have terminated on the ventral side of the posterior transverse crest just medial to the base of the quadrate ramus.

The dorsal flange of the pterygoid (df, figures 1 and 2*a*, section 3) is oriented approximately vertically and runs longitudinally and slightly anteromedially along, and then forwards from the sides of the basicranium, to which it is closely apposed. Anterior to the epipterygoid the flange is relatively shallow. Posterior to the epipterygoid the flange is much higher, concealing the basicranium and perhaps the lower portions of the exoccipital-opisthotics from lateral view. Posteriorly to the basicranium the dorsal flange merges into the dorsal portion of the quadrate ramus.

The epipterygoid (ep) is a laterally compressed, thick blade tapering dorsally to a truncated apex. It leans medially slightly, and rests in a wide, shallow socket (section 2, figure 2*a*) on the dorsal flange of the pterygoid, forming a heavily overlapped, interdigitating suture. Its anterior edge is thicker and rounded anteriorly. The free posterior edge is thinner and sharper, and runs posteroventrally to meet and overlap the dorsal flange. The dorsal and ventrolateral flanges of the pterygoid together form a dorsolaterally opening shallow concavity which is terminated anteriorly by the outward flare of the anterior portion of the base of the epipterygoid. Inside this is a more marked, smaller concavity (con). The pterygoid–epipterygoid suture here contains a small V-shaped crest delimiting a small foramen (fo). The medial sides of both epipterygoids and pterygoids are obscured.

The quadrate rami (qrpt) of both pterygoids are badly damaged. Each is a long, laterally compressed process running posterolaterally and slightly ventrally from beside the occipital condyle to the anteromedial corner of the quadrate below the squamosal-quadrate contact. Proximally the ramus is deep. Its ventral portion is continuous with the heavy central portion of the pterygoid between the three flanges, and has a thickened, rounded ventral edge. Its dorsal portion is thinner with a sharp dorsal edge continuous with the dorsal flange. More distally it becomes shallower in side view and the dorsal edge becomes thicker and more rounded. The ventral edge is still rounded until a point just over halfway along the ramus. Henceforth it is missing on both sides. A wide and very shallow flat-bottomed depression runs along the lateral face of the ramus for almost its whole length. Distally the ramus is laterally compressed and forms an interdigitating suture in a socket on the anteromedial corner of the quadrate, also sending a thinner lamina posteriorly to form an overlapping, interdigitating suture over the flat vertical medial face of the quadrate.

(*e*) *Stapes and hyoid elements (figure 5 c, d)*

Stapes are rarely found in plesiosaurs, perhaps because of collection failure. Stutchbury (1846; also Swinton 1948) reported a 'columellar bone', apparently a hyoid, in *R. megacephalus*. Williston (1907) described a short, stout stapes in the Cretaceous pliosauroid *Dolichorhynchops*, but this needs verification as the bone was not found *in situ*, differs from that described here, and may even have come from another animal. Therefore this description deals in detail with the two stapes of YORYM G503 as the first undoubted plesiosaurian stapes.

Each stapes is a long, thin, curved ribbon of bone lying very close to its life position. It runs from the vicinity of the fenestra ovalis, back between, and parallel with, the paroccipital process and the quadrate ramus of the pterygoid, towards the quadrate. The two stapes lie in different orientations and the life orientation is unknown.

The left stapes has been mutilated. The distal end is missing, and the proximal end is buried within the matrix just above and lateral to the occipital condyle. It is slightly bowed laterally, as it lies now. The right stapes is exposed medially, as it lies now. It is broken and its pieces displaced. The proximal portion is not visible. The remaining distal portion is a long, slender leaf-shaped bone without a visible foramen. It is twisted along its length through about 90 degrees, and bowed convexly downwards within a plane sloping

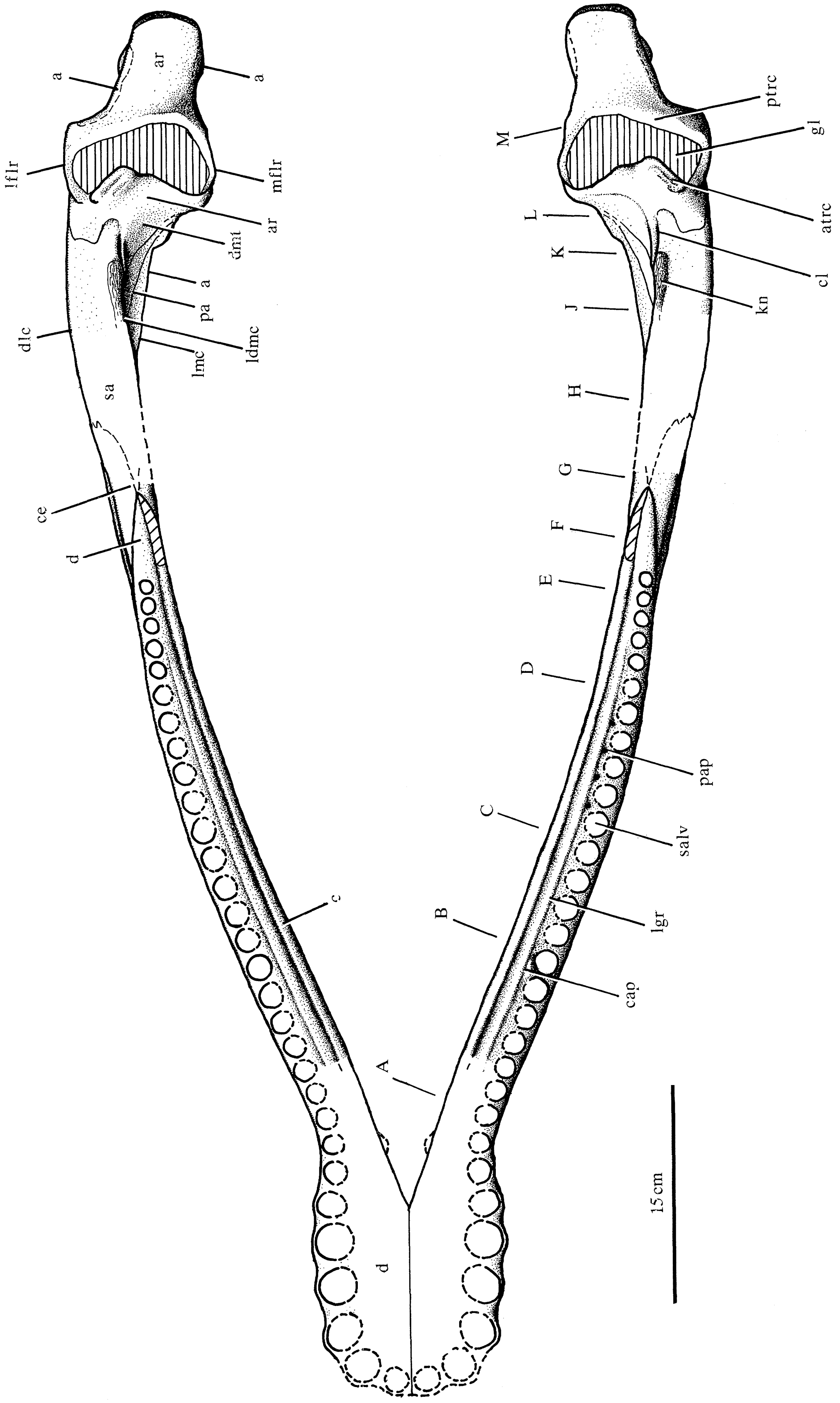

Figure 6. *Rhomaleosaurus zetlandicus*. Reconstruction of mandible in dorsal view, showing lines of section through mandible (figure 7). For shading, see figure 1.

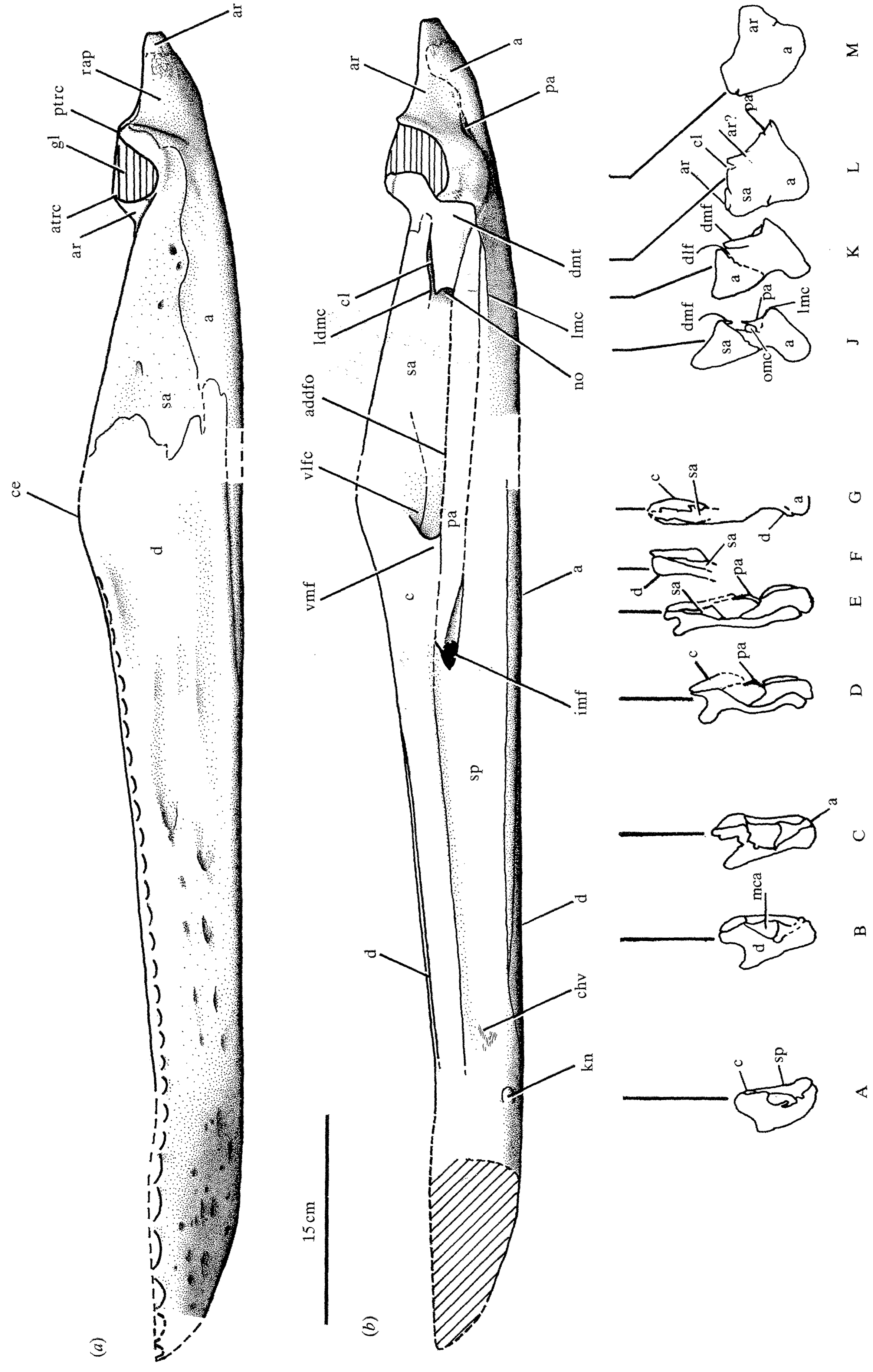

Figure 7. *Rhomaleosaurus zetlandicus*. Reconstruction of mandible, (*a*) in lateral view, and (*b*) in medial view. Positions of sections approximate (see figure 6 for actual lines of section); section H is not illustrated here but described in the text. For shading, see figure 1.

ventromedially. Along the 'medial' side runs an ill-defined longitudinal depression. The stapes is slightly triangular in section at the broken proximal end (prox, section 1, figure 5*c*). The flattened distal end (dist, section 2) ends in a leaf-like point which lies medial and rather anterior to the end of the right paroccipital process, so that it apparently did not extend to the quadrate. Presumably it ended in a cartilaginous extrastapes. There are two unidentifiable fragments of bone (fra).

The robust hyoid elements, known from other plesiosaurs (first ceratobranchials (Romer 1956)), are missing from YORYM G503. A thin, irregularly quadrilateral bone (figure 5*d*) lies near the distal portion of the left pterygoid's quadrate ramus. It may be another hyoid element, possibly an ossification within the second ceratobranchial (cf. crocodilians (Romer 1956)).

4. MANDIBLE (figures 3, 6, 7 and 8)

The mandible is damaged and incompletely exposed but can be reconstructed from both rami and from natural breaks (sections A–J, figures 6 and 7; section H is too incomplete to figure but is described in the text). The width between articulations is taken from the reconstructed distance between the quadrates. The literature on plesiosaur mandibles is confusing and has not been used to avoid circular argument. *Rhomaleosaurus* contains all elements, including splenial, single coronoid and pre-articular, seen in primitive reptiles such as *Eocaptorhinus* (Heaton 1979).

The mandibular rami meet in a deep akinetic symphysis, which is laterally expanded with a ventromedian crest where the two ventrolateral faces meet at about 90 degrees. The anterior edge is missing. The symphysis contains the deep secondary alveoli (salv) of the large anterior caniniform teeth, which extend ventromedially and posteriorly almost to the ventral midline, as shown in a break.

From the symphysis backwards each ramus is increasingly laterally compressed and becomes more vertical. The ramus is thus thinnest in section, and approximately vertically oriented, in the region of the coronoid eminence (ce). Posterior to the coronoid eminence the ramus broadens on both sides to form a heavy rounded ventrolateral flange (vlf), and a thickened dorsal portion with an acutely angled but terminally rounded dorsolateral crest (dlc). Only the anterior and posterior extremities of the adductor fossa (addfo) are visible in the specimen. It is here restored as a long, narrow opening with a straight medial rim, although the only positive evidence for this is the constant size of the pre-articular at the ends and in section H (see below). The fossa seems to have opened dorsomedially and is thus not visible from the dorsal aspect. The glenoid fossae (gl) lie in the top of the mandible, in expanded lateral and medial flares (lflr, mflr). There is a strong retroarticular process (rap).

The dentary (d) forms most of the ramus anterior to the coronoid eminence and almost all the symphyseal region. The coronoid (c) is long, transversely compressed, and slightly twisted. It extends anteriorly to near the symphysis although may not actually enter into the symphysis. The dentary is almost wholly hidden in medial aspect, perhaps explaining why Fraas (1910) apparently described the coronoid of *R. victor* as part of the dentary. Posteriorly the coronoid deepens over the Meckelian canal (mca) to form a ventromedial flange (vmf), whose posterior margin bears a concavity forming the anterior end of the adductor fossa. From just forward of this point a ventrolateral flange (vlf) runs posteriorly, covering and forming an interdigitating suture with the medial face of the surangular (sa), visible at section H.

The splenial (sp) is a long, transversely compressed bone forming the ventral portion of the median face of the ramus, and apparently taking part in the symphyseal suture, as in *R. thorntoni*. It forms the anterior and ventral rims of the elliptical intermandibular foramen (imf) which opens medially and slightly posteroventrally. The splenial sends a short prong backwards above the foramen to overlap the anterior pre-articular (pa). Posteriorly, the splenial is a thin bone closely applied to the medial face of the angular (a) at least as far back as the coronoid eminence and perhaps as far as the end of the dentary, as in *R. victor*, although its posterior termination is missing or obscured in YORYM G503.

The pre-articular (pa) is poorly known in plesiosaurs. In *R. zetlandicus*, it is long, narrow, compressed from side to side, and runs from the intermandibular foramen back to the glenoid, ending on the median side of the jaw posteroventral to the glenoid fossa. Anteriorly (sections D and E) it is thin, and kinked into dorsal and ventral laminae. The dorsal lamina forms a prong extending anterodorsally over the foramen to contact the splenial. Posteriorly the ventral lamina becomes shallower and forms the lateral wall of a trough running posteroventrally from the foramen into the Meckelian canal. The bone is displaced from its life position which is reconstructed as underlapping the coronoid dorsally and butting against the splenial and angular ventrally (sections D and E).

The pre-articular forms the ventromedial rim of the adductor fossa. Here it is largely obscured or missing but probably was a roughly straight, laterally compressed, vertically oriented bone, running back to the articular region. In section, at section H, it is rather thicker than it is at the front end of the adductor fossa, slightly convex medially and slightly concave laterally. At the posterior end of the adductor fossa (section J), the pre-articular, in section, tapers to a dorsal crest, and has a thickened ventral edge lying in a trough in the angular. More posteriorly, it is flattened, running within a trough to where the medial longitudinal crest ends posteriorly against the medial flare. It is very narrow where it runs over the crest onto the ventromedial surface where it is visible externally as a thin tongue curving down and backwards below the medial flare of the articular (ar) and above the angular. Posteriorly the pre-articular appears to be fused with these bones, and demarcated only by ridges and folds.

The surangular (sa) forms the bulk of the dorsal

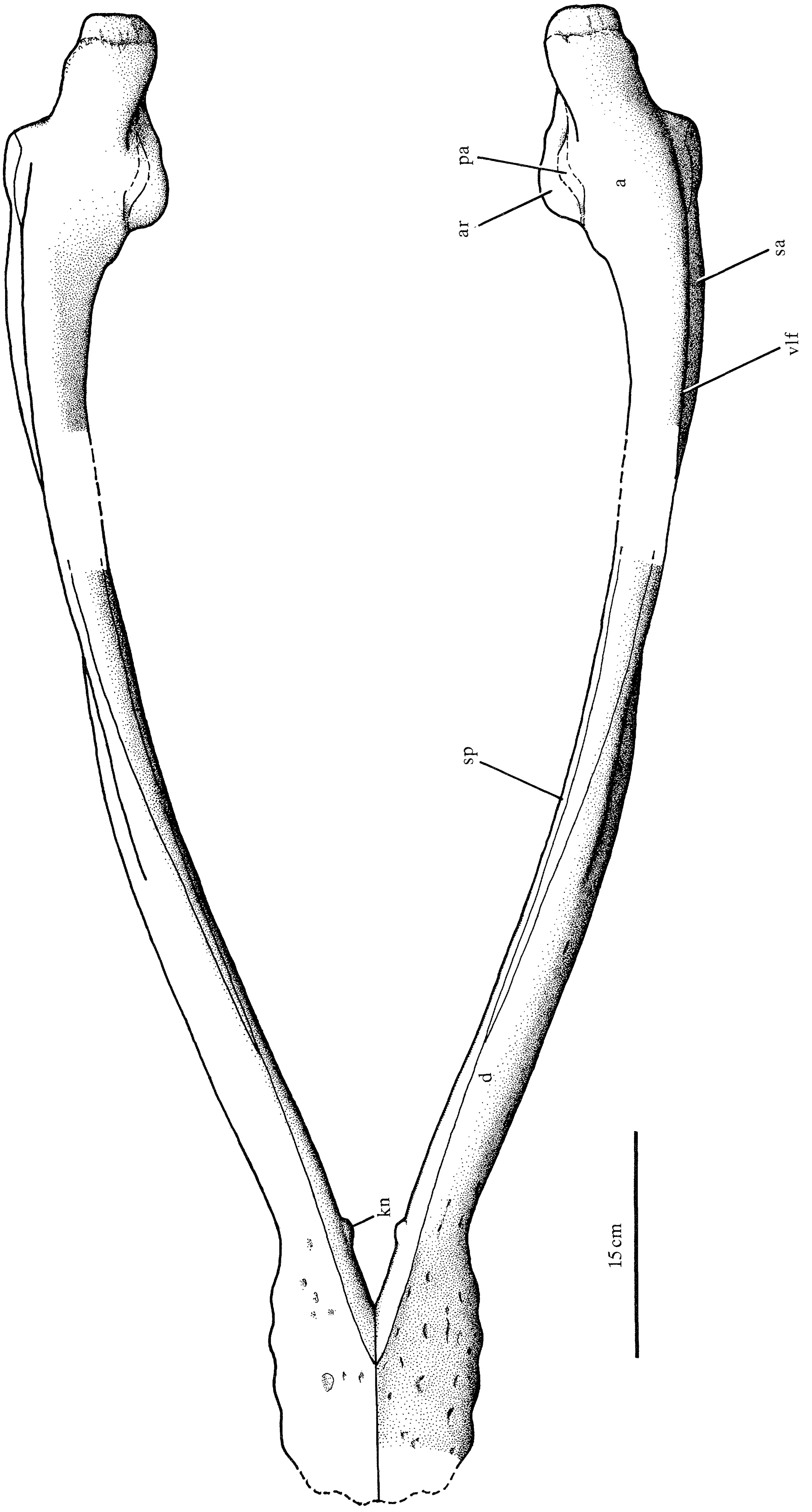

Figure 8. *Rhomaleosaurus zetlandicus*. Reconstruction of mandible in ventral view.

ramus between the coronoid eminence and glenoid fossa. It is missing or obscured in the region of the adductor fossa. At section H it is roughly laterally compressed, and is dorsomedially diagonally truncated by an interdigitating suture with the coronoid. The ventral portion is not clearly visible but appears to show an excavation on its medial side, thus enlarging the adductor fossa. At the posterior end of the adductor fossa (section J) the surangular is rather thicker and subtriangular in section. Its ventromedial face forms an interdigitating suture with the angular. Its dorsolateral crest underlaps the anterodorsal tip of the articular. In external view the surangular-articular suture runs anteriorly from a point beneath the lateral rim of the glenoid, crosses dorsally and then medially across the dorsal surface of the surangular, and runs back posteriorly for a short distance. It then appears to curve back anteromedially to the posterior end of a deep cleft (cl), but this junction is obscured for a few millimetres by damage to the bone. The cleft bounds the surangular medially and runs anteriorly to the posterior end of the adductor fossa with which it is apparently confluent. It may be a posterior vestige of the Meckelian canal.

The angular (a) runs almost the whole length of the ramus posterior to the symphysis. Its tapered anterior portion is wedged between the dentary and the splenial, and hardly visible externally. The angular is damaged or missing underneath the adductor fossa. Hereabouts is the anterior end of the heavy rounded ventrolateral flange (vlf) extending backwards under the glenoid fossa. At the posterior end of the adductor fossa (section J) the angular dorsally forms a broad interdigitating suture with the surangular. This suture may be fused internally as it is not visible in sections K and M anterior and posterior to the glenoid fossa (section L is obscured by mineral deposits). Posterior to the glenoid, the suture is externally partly obliterated by fusion. The angular thus seems to form a trough around the ventral and lateral surfaces of the articular, as in plesiosauroids (Brown 1981*a*).

Immediately behind the posterior end of the adductor fossa, section K shows a complex structure of two dorsal flanges continuous with the main body of the angular. The dorsomedial flange (dmf) forms the dorsal portion of the medial face of the ramus behind the adductor fossa, above the pre-articular and within the dorsomedial trough (dmt) of the jaw ramus. It is anteriorly compressed from side to side, with a notch (no) in its anterior end forming the posterior end of the adductor fossa. Dorsolaterally it comes close to the surangular, but is divided from it by the cleft (cl). Posteriorly it appears to be continuous with the anterior transverse crest (atrc) of the glenoid fossa. It is interpreted as part of the articular.

The dorsolateral flange (dlf) lies at the bottom of the cleft (cl), sutures laterally with the surangular and is medially covered by the dorsomedial flange (dmf). The dorsolateral flange could be part of the angular, or part of the articular–Meckel's cartilage complex. An element which seems to be part of an ossified Meckel's cartilage (omc) is present more anteriorly at the posterior end of the adductor fossa (section J), underlying the dorsomedial flange of the articular, and lying medial to a flange of the articular which may be continuous with that described above at section K. I tentatively interpret the dorsolateral flange as part of the angular.

The *articular* (ar) is a robust bone exposed mainly dorsally and forming the dorsomedial flange of the jaw ramus between surangular and pre-articular, the glenoid fossa and most of the retroarticular process. The anterior transverse crest of the fossa (atrc) is divided into a higher, dorsally flatter and thicker lateral portion and a lower, sharply crested medial portion. The lateral and medial rims are low. The posterior rim (ptrc) is a low rounded transverse crest.

5. DENTITION

(*a*) *General*

The dentition is severely damaged and there has been some loss of teeth from the sockets before burial. Only a few teeth, and none of the mature teeth, have intact crowns. The anteriormost few dentary and premaxillary teeth are lost. The posterior maxillary teeth are also missing. However, the dentition appears to be similar to that of *R. cramptoni*, *R. thorntoni*, and pliosauroids in general, especially *Simolestes*.

(*b*) *Tooth structure*

See figure 9. The teeth vary in size and shape according to position in the jaws, and ontogenetic age. Each tooth has a large, slightly bulbous and hollow base (base) opening at the end, and a tapering conical crown (crown). The tooth is recurved, the crown more than the base. The bases of the anterior teeth were somewhat recumbent because the deep roots were housed in a shallow skull or anterior mandible and were oriented somewhat dorsomedially and somewhat posteriorly. This was compensated by the curvature of the teeth, which protruded outwards slightly before turning towards the other jaw. This outwards projection was, however, relatively minor, presumably because it tended to weaken the teeth by causing bending rather than compressive loads during feeding. It is not apparently as marked as in feeders on small prey, such as *Cryptoclidus* and the Gharial *Gavialis*, which do not require such robust teeth.

Each tooth is circular in cross-section without carinae, except perhaps a faint broadening of the distal crown into an incipient carina on each axial face. The apex is not needle-pointed, but is still sharp enough to pierce flesh. Longitudinal ridges run from the foot of the crown towards the apex for varying distances. Each is a sharply crested triangular prism clearly demarcated from the otherwise smooth surface of the crown. There are more ridges on the inner, lingual side than on the buccal side. Only a few ridges run right to the apex. The smaller teeth seem to have a semicircular area free of ridges on the buccal side immediately adjacent to the base, and in larger teeth this area expands to cover the entire buccal side, similar to *Simolestes*. The smallest teeth, in the rear of

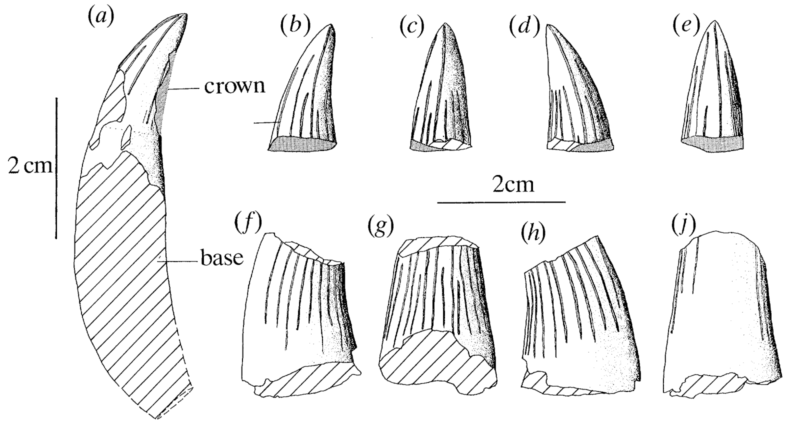

Figure 9. *Rhomaleosaurus zetlandicus*. Dentition. Diagonal hatching indicates damage and tone indicates areas covered by matrix. (*a*) immature tooth; (*b*)–(*e*) axial, lingual, axial and buccal views, respectively, of the apical portion of the crown of the immature second right maxillary tooth. (*f*)-(*j*) axial, lingual, axial and buccal views, respectively, of the broken crown of the mature fifth left dentary tooth, one of the large symphyseal tusks.

the jaws, appear to have had sharply recurved tips pointing posteriorly.

(*c*) *Arrangement*

It is here assumed that larger sockets held teeth with longer and larger crowns. The dentition is fully thecodont with early replacement teeth in primary alveoli (palv) lingual to deep secondary alveoli (salv) housing mature teeth (Edmund 1960). Each premaxilla (figure 4) contains a small first socket (not shown in the figure), and four large sockets running posterodorsally and medially deep into the bone, although the anteriormost sockets are severely damaged. The first few maxillary teeth are small but increase in size backwards to give a second group of teeth of about the same size as the large premaxillary teeth, and also deeply rooted (figure 2). Section 1 (figure 2) shows a mature tooth (mto) in a secondary alveolus and a developing replacement tooth (rto) in a primary alveolus which connects to the secondary alveolus. The left maxilla carries a shallow, indistinct longitudinal depression (dep, figure 4) parallel to the jaw margin and containing the primary alveoli. Four primary alveoli are visible on the left and two on the right. One shows the temporary canal (can) for the replacement tooth to migrate to the secondary alveolus. The remaining alveoli are missing, but in *R. cramptoni* and *R. thorntoni*, the teeth then decrease in size backwards, with a marked reduction in size beneath the anterolateral corner of the orbit.

Each dentary bears about 30 secondary alveoli (figure 6). The primary alveoli lie between and medial to the secondary alveoli in a rough longitudinal groove (lgr) lateral to and parallel to the dentary-coronoid suture. They vary according to developmental stage. Some are open pits (pap) and others are capped with bone (cap). The lateral wall of the groove is formed by the confluent rims of the secondary alveoli. The primary and secondary alveoli lie in coarsely textured bone between the lateral rim of the dentary and the groove, presumably reflecting the constant remodelling of the bone during eruption and laterad migration of replacement teeth.

The anterior rim of the symphysis is missing but the deeper portions of the bases and roots of the small first teeth are preserved. Next there are four large teeth in deep sockets, then a sixth slightly smaller but still large tooth. The seventh and more posterior teeth of *R. zetlandicus* are smaller, and about equal in size, except for the most posterior whose sockets decrease in size posteriorly.

Proceeding from back to front, the sockets are first almost vertical but tilt increasingly laterally and then increasingly anteriorly. The large teeth of the premaxillae and symphyseal region of the dentary thus form a radiating pattern with their crowns bending to intermesh with each other around the rather rounded snout. This ‘rosette’ of tusks strongly resembles a pair of human hands with the fingers half-bent inwards and brought together so that the fingers interlock. A similar pattern is found in *R. cramptoni* and *Simolestes*. Just behind this rosette the mandibular teeth projected upwards into the premaxillary–maxillary notch. More posteriorly the maxillae flare laterally over the dentaries so that the upper teeth seem to have overlapped the lower teeth, as in crocodiles. The situation in the most posterior tooth row remains unclear.

The teeth probably intermeshed without touching. They are too damaged to assess the presence of tooth wear caused by hard prey, known from other pliosauroids (Massare 1987).

(*d*) *Functional analysis*

The larger teeth strongly suggest a generalized carnivorous diet, with a proportion of large prey that had to be subdued and then dismembered, either by shaking from side to side, or by twisting to pieces, as in the modern Nile crocodile *Crocodylus niloticus* (Taylor 1987). The sharp but not needle-pointed crowns pierced flesh and smashed cephalopod shells. The recurved tips of the smaller posterior teeth acted as catches to secure large items of food moving backwards through the mouth to the gullet.

Each of the larger anterior teeth resembles a mammalian carnivore's canine (Van Valkenburgh & Ruff 1987), adapted to pierce and hold prey which is struggling forcibly. The deep root anchors it against longitudinal and transverse stresses. The crown is a slightly recurved and robust cone, adapted to resist the vertical stresses of penetration and the longitudinal and transverse stresses of prey manipulation and dismemberment. Its moderate recurvature ensures that the crown is aligned normal to the prey surface and loaded mainly under compression when the jaws are opened during attack (Frazzetta 1966). Any greater curvature, whether anteriorly (spearing prey as in some rhizodont fish (Andrews 1985), carcharhinid sharks (Frazzetta & Prange 1987), pythons (Frazzetta 1966), or pterosaurs (Wellnhofer 1980)) or posteriorly (to trap prey as in the angler-fish *Lophius* (Alexander 1974)), would subject the tooth to a higher risk of failure from the tensile component of bending loads (cf. Rieppel 1979). This suggests that the teeth were heavily loaded during life. As the crown is not blunt enough for a durophagous diet, the teeth must have been used to subdue and presumably dismember large, powerful animals. The ridges may have helped the tooth to penetrate and withdraw from prey by breaking the suction, like the groove or 'blood gutter' on a military bayonet. The absence of ridges on the lingual, convexly curved side, and nearer the crown, may be explained by the need to avoid concentrations of stress at the sharp junction between ridge and crown in areas that are highly stressed or under tensile loadings.

The teeth vary in height so that larger teeth on one jaw sometimes oppose smaller teeth on the other jaw, behind the anterior 'rosette'. This is reinforced by the changes in angle of the jaw margins, particularly at the posterior end of the mandibular symphysis. These features would help to capture large prey by driving some teeth particularly deep into the prey, thus holding it and delivering disabling wounds in vital parts, and by trapping part of the prey behind longer teeth. They occur in crocodilians feeding on larger prey, but not in piscivorous crocodilians such as the Gharial *Gavialis gangeticus* (Iordansky 1973).

The function of the anterior rosette, seen also in *Simolestes* and some other forms, may simply be to get a good grip on part of the prey before twisting off a piece. Crocodilians do not have such a rosette, perhaps because the anterior position of the nares preempts the space required for the roots of large anterior premaxillary teeth.

6. MUSCULATURE

(*a*) *Introduction and methods*

This is the first reconstruction of the cranial musculature of a plesiosaur. Plesiosaurs have no close living relatives as potential models, unlike varanid lizards and mosasaurs (Russell 1967), and reconstruction of their musculature is particularly dependent on the procedure used. The types of evidence used here are now discussed.

Gross morphology of the bone: tendons or tendinous sheets (bodenaponeuroses) commonly attach to a flat surface at an angle, or to a crest or other convexity, or to the connective tissue inside a suture, to avoid tearing the muscle–bone attachment by pulling away the periosteal membrane (Frazzetta 1968). In particular, the aponeuroses of pinnate jaw adductor muscles tend to attach to the edges of the temporal fenestrae. These rules do not apply to fleshy insertions.

Fine surface detail is well preserved in many, but not all, areas of YORYM G503. Most bone bears faint striae, presumably corresponding to the superficial layer of osteons. However, some areas are covered in variably developed ridging and furrowing, often with foramina countersunk within depressions or at one end of a short trough. This rougher texture is most strongly developed on the lateral sides of the mandible anterior to the coronoid eminence, and less strongly on the ventral aspect of the symphysis, extending upwards to the margins of the tooth sockets. The margins of the premaxillae and maxillae are less grossly roughened but also bear many countersunk foramina. All these regions are interpreted as bearing dermis and associated connective tissues which were so closely applied to the bone that nerves or blood vessels debouching from each foramen had to ramify within the depression around the foramen before serving the surrounding tissues.

The roughened anterolateral corner of the orbit anchored the dermis against the bulge of the eyeball. The roughened lateral face of the squamosal, anterior to the presumed insertion of the superficial cervical musculature (cr, figure 11, §6 *g*), presumably anchored the dermis of the neck. The coarsest texture, on the lateral mandible, gave the dermis firm anchorage against tensions caused by the stretching of the floor of the mouth when the animal was snapping its jaws shut or eating large pieces of food. The texture around the tooth sockets suggests that, like modern crocodilians, *Rhomaleosaurus* lacked fleshy lips. This probably helps the animals to open the mouth quickly underwater by allowing the rapid initial entry of water (Chernin 1974).

Bone surface detail alone is, however, an unreliable guide to the presence and relative size of muscles. McGowan (1979) could only identify a quarter of the actual muscle insertions and origins when working on cleaned bone specimens of the hindlimb of the Kiwi *Apteryx*, with little information on the relative sizes of the muscles, and Brown (1981*a*) argued that it was not possible to reconstruct the detailed musculature of the plesiosaurian humerus, as attempted by Watson (1924) and Robinson (1975). However, Nicholls & Russell (1985, p. 668) said in a study of the forelimb musculature of a theropod dinosaur that 'reconstruction of minutiae . . . seems beyond the scope of muscle scar evidence, but in strongly sculptured areas . . . bone architecture is probably a reasonable indicator of at least the major muscles'. I agree and, like them, confine myself to 'the attempted reconstruction of major muscles, for which good evidence, in the form of scars or major topographic features, seems to exist'.

The cranial musculature of living reptiles shows a common pattern presumably derived from their common ancestor and used as a basis for this reconstruction. Living reptiles, however, vary in the detailed subdivision of their musculature (itself somewhat arbitrary (Rieppel 1987)). Furthermore, no one living form is a suitable model for plesiosaurs as none is closely related or gives a sufficiently close functional analogy. *Rhomaleosaurus* has an apparently simple akinetic skull and orthally hinging mandible. Modern reptiles are all more or less specialized. Lizards have mobile quadrates with concurrent adaptations of the pterygoideus musculature (Smith 1980), whereas snakes and amphisbaenians are even more modified. Chelonians pack their musculature into a low skull and sometimes also have propalinal movement of the mandible (Schumacher 1973, Rieppel 1990). Crocodilians have a short adductor fossa, a jaw locking mechanism jamming a cartilage within the adductor tendon against the pterygoid flange (Drongelen & Dullemeijer 1982), and a vertically oriented basicranium in adults (Tarsitano 1985). *Sphenodon* chews food with propalinal movements of the mandible (Gorniak *et al.* 1982).

This reconstruction of *Rhomaleosaurus* is therefore done to the comparatively coarse level of subdivision which seems justified by comparison of various modern forms (Barghusen (1973) in general; Schumacher (1973) and Drongelen & Dullemeijer (1982) on crocodilians; Haas (1973) and Gorniak *et al.* (1982) on *Sphenodon*; and Haas (1973) on lizards).

Considerations of muscle structure and action are of relatively little use in reconstructing, rather than interpreting, musculature, partly because of the danger of circular argument from function to structure and back again. Also, each hypothetically reconstructed muscle should, of course, be capable of working reasonably efficiently throughout the presumed range of its action, and conversely, the best operation of each muscle has been used to suggest its function (see, for example, Kemp 1969; Bramble 1978). However, to be practicable, such work necessarily assumes constraints on the action of the muscle, commonly that it operates as a simple parallel-fibred muscle with the tension–length relation similar to a single fibre (see, for example, Gans & Bock 1965), so that its torque is predictably dependent on the angle to which the joint is opened. In fact, the jaw musculature of tetrapods is commonly pinnate, or mixed pinnate and parallel fibred, with a complex and strongly species-specific internal architecture. Such muscles are functionally flexible with varied angles of fibres within the same muscle, and complex activation patterns and length–tension relations (Alexander 1983; Bramble 1978; Gans 1982; Gans & Bock 1965; Gans *et al.* 1985; Gans & De Vree 1987; Herring 1975; Herring *et al.* 1979; Muhl 1982; Woittiez *et al.* 1984). In particular, the line of force is not necessarily along the direct line between the insertion of the muscle to the centroid of its fleshy origin, and there is no simple relation between the muscle's length and the torque exerted around the joint in question. Given the number of possible structures, it seems impossible to reconstruct the structure and operation of a muscle, especially in an animal like a plesiosaur which has no close living relatives. There are then no reliable data on which one can argue from operation to function.

I therefore do not attempt a quantitative analysis, but I do make qualitative remarks about the operation of individual muscles. I follow the muscle classification of Schumacher (1973) and Haas (1973), assuming for simplicity that each ontogenetic muscle mass has a single function (not always wholly valid (Gans 1982; Gorniak *et al.* 1982)).

(*b*) *Mandibular adductor musculature*

See figure 10. The constrictor I dorsalis was presumably lost, as in crocodilians and chelonians (Schumacher 1973), as its primitive function was to move the palate upon the now-fused basipterygoid articulation. The levator bulbi cannot be verified as the orbital region is infilled with matrix.

The reptilian adductor mandibulae externus (mame, figure 10*a*) usually originates from the lateral portion of the posterior wall of the temporal fossa, including the post-temporal fossa and the underside of the temporal roof and upper cheek region, as well as aponeurotic membranes over the temporal fenestrae. It fills the posterior portion of the upper temporal fossa and inserts variously onto the dorsal, dorsomedial and dorsolateral portions of the lower jaw between the coronoid process and articulation, usually via the bodenaponeurosis attached to the coronoid process; sometimes some fibres insert directly onto the jaw (Barghusen 1973).

The adductor mandibulae externus of *Rhomaleosaurus* is reconstructed as originating around the post-temporal fossa, from a tendinous aponeurosis on the ventrolateral crest of the posterior portion of the median dorsal bar; on fleshy origins on the sides of this bar and the anterior face of the dorsal ramus of the squamosal, extending onto the anteroventral faces of the squamosal and quadrate; and another aponeurosis on the ventral crest of the dorsal ramus of the squamosal (not indicated in figure 10*a*) which continues to the posterior end of the ventrolateral crest of the median dorsal bar so that this aponeurosis may have been a continuation of the first. Further areas of tendinous origin may include the superficial fascia (supf, figure 10*a*) covering the temporal fenestra and attached to the posterodorsal crest of the postorbital bar (cr, figure 1), the lateral temporal bar, the dorsal extremity of the sagittal crest, the lateral edges of the vertex, and the anterodorsal crest of the dorsal ramus of the squamosal. Heavy sculpturing on the lateral face of the base of the paroccipital process and fainter sculpture on the lateral face of the pro-otic may indicate origins for minor aponeuroses, or the ventral edge of a membranous lateral wall of the braincase which could itself serve as an aponeurosis.

The insertion was presumably by a bodenaponeurosis (boden, figure 10*a*) attached to a coarsely pitted

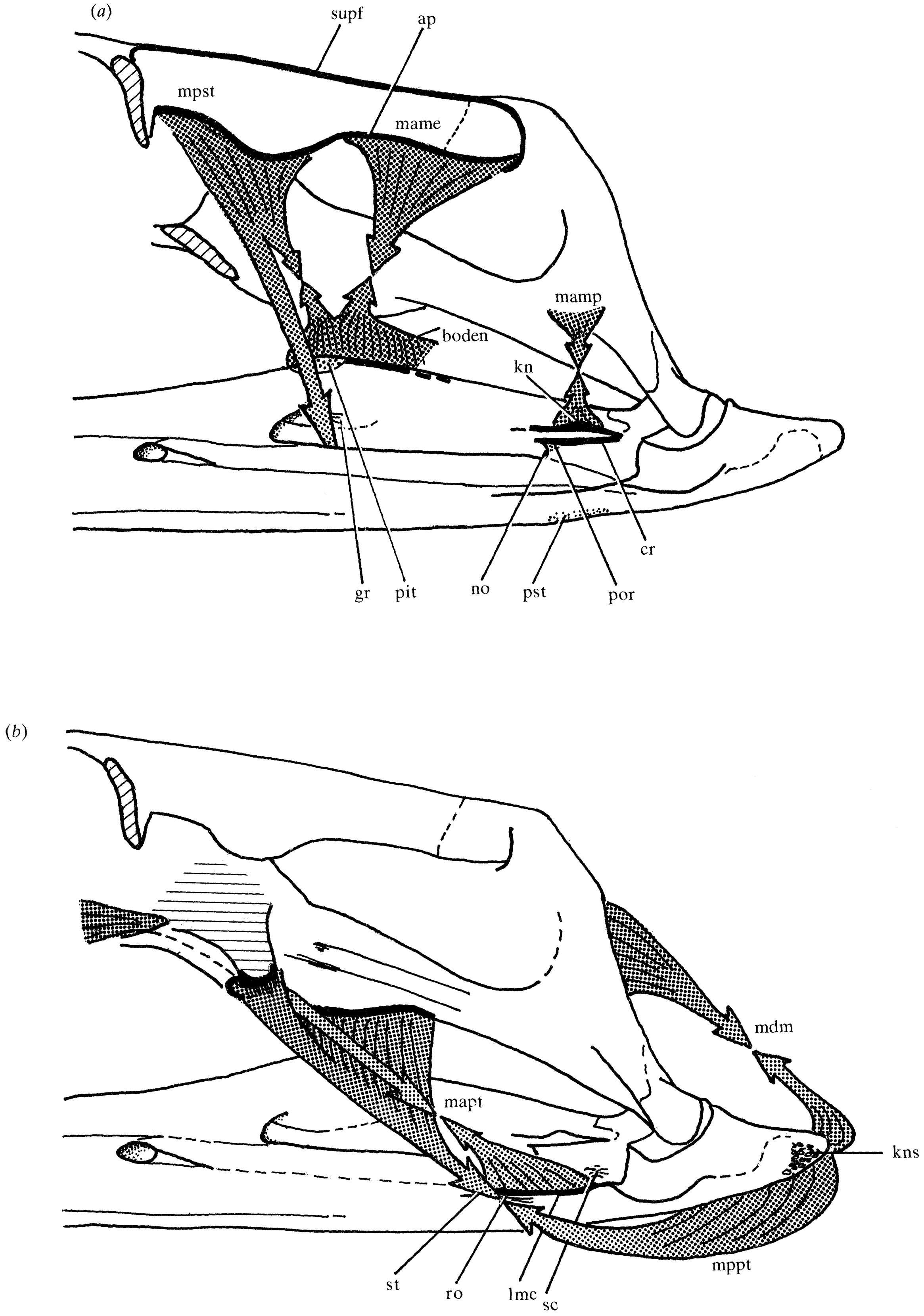

Figure 10. Reconstruction of mandibular adductor musculature showing the lateral aspect of the posterior skull (without lateral marginal bones) and the medial aspect of the mandible. Muscle reconstructions are diagrammatic, and show lines of action rather than actual bulk. Solid lining indicates the origins of major tendinous aponeuroses. (*a*) dorsal musculature, (*b*) ventral musculature.

area (pit) on the left coronoid eminence, and perhaps also to sutures between the dentary, surangular and coronoid. The bodenaponeurosis may have extended posteriorly along the sharp dorsolateral crest of the mandible. The muscle may also have sent a fleshy insertion onto the lateral face of the mandible as in *Sphenodon*, but there is no particular evidence for this.

The reptilian adductor mandibulae posterior (mamp, figure 10*a*), if present, usually lies within the posteromedial portion of the temporal fossa, originating from the medial portion of the anterior face of the quadrate and inserting into the adductor fossa or onto its edge (Barghusen 1973). This area is not well exposed in YORYM G503. The muscle is assumed present in *Rhomaleosaurus*, presumably originating on the thickened ventromedial edge of the quadrate and quadrate ramus of the pterygoid, and perhaps also tendinous aponeuroses on the ventromedial edge of the quadrate and less probably the weaker, more dorsolateral crest on the concave ventral surface of the quadrate. The origin may well have been primarily fleshy. The muscle apparently had a tendinous insertion onto the almond-shaped, sculptured knob (kn, figures 6 and 10*a*) on the dorsomedial edge of the surangular, and onto a narrower, less prominently roughened strip running posteriorly along the dorsomedial crest above the posterior end of the adductor fossa and onto the fossa's missing dorsal rim. Further insertions include the sharp dorsolateral crest (cr) of the articular and the deep cleft (cl, figure 6) and associated connective tissue between articular and angular, as well as a small region of porous bone (por, figure 10*a*) immediately posterior to the fossa. The smooth dorsomedial face of the articular between the crest and the porous bone may have borne a fleshy insertion. A further slip of muscle may have run over the notch (no) at the posterior end of the adductor fossa to insert into the fossa.

The pseudotemporalis (mpst, figure 10*a*) presumably originated in the anteromedial and dorsal portion of the temporal fossa, including the lateral face of the epipterygoid, the anterior portion of the parietal, and the posterior face and ventral boss of the medial portion of the postorbital bar. The sharp ventrolateral edge of the parietals anterior to the epipterygoid may have anchored a membranous lateral wall to the braincase or an anterodorsal aponeurosis, either of which provided origin for the pseudotemporalis. The thickened, sculptured ventrolateral crest immediately dorsal to the epipterygoid may have attached to a concentrated tendinous aponeurosis continuous with the anterodorsal aponeurosis anteriorly and the aponeurosis of the adductor mandibulae externus posteriorly.

There are several possible insertions, not necessarily mutually exclusive, in *Rhomaleosaurus*. The anterior and medial rims of the adductor fossa and the medial face of the splenial seem too weak. The pseudotemporalis probably inserted into the anterior portion of the adductor fossa and perhaps partly onto the bodenaponeurosis of the adductor mandibulae externus. The ventral portion of the medial face of the coronoid above the anterior portion of the fossa is imprinted by grooves (gr) which apparently bore blood vessels and nerves. As the oral mucosa probably did not extend here, this may indicate a tendon or tendinous sheet for the pseudotemporalis or the anterior pterygoideus, running over the bone here and inserting into the fossa.

The anterior pterygoideus (mapt, figure 10*b*) cannot be proved in the usual areas of origin, the dorsal surface of the palate and adjacent structures, as these are hidden. It probably originated in part on the membrane-covered suborbital fenestra, which can therefore be regarded as an adaptation for the attachment of this strong muscle, analogous to the temporal fenestra (Frazzetta 1968). However, the anterior rim of the subtemporal fenestra medial to the pterygoid boss is curved downwards, thickened and rounded as if to give free passage to the muscle, as in *Sphenodon* and crocodilians. The muscle may have inserted into the adductor fossa or on its rim, but this gives minimal torque about the articulation when the jaws are closed. It probably inserted, at least partly, onto an aponeurosis attached to the strong but fairly sharp longitudinal medial crest (lmc) which is directed dorsomedially and ends posteriorly by merging into the articular. A low step (st) continues its line and may represent a posterior continuation of the tendon. Slight roughening (ro) below the anterior portion of the crest, and sculpturing (sc) within the dorsomedial trough just lateral to the posterior end of the crest, may have borne subsidiary tendons. The muscle may also have had fleshy insertions.

The posterior pterygoideus (mppt, figure 10*b*) originated from the anterior and medial rims of the subtemporal fenestra, by means of a medial aponeurotic sheet on the sharp ventrolateral flange of the pterygoid, and a second aponeurosis concentrated on the pterygoid boss and perhaps extending dorsomedially onto the heavily sculptured dorsolateral corner of the pterygoid. The pterygoideus probably did not have any fleshy origin on the palate between the subtemporal fenestrae, as in crocodilians, thus easing the passage of prey into the gullet. The muscle may also have taken origin from more dorsal areas, including a subsidiary tendon from the textured anterodorsal rim of the concavity at the base of the epipterygoid (tend), and further minor tendinous sheets and aponeuroses on the dorsal edge of the trough running along the lateral face of the pterygoid and to striae (str) within the anterior end of the trough. The muscle may also have had a fleshy origin on the ventral and medial edges of the quadrate ramus.

The posterior pterygoideus had a strong tendinous insertion or insertions onto the ventromedial face of the retroarticular process, which is coarsely sculptured over much of its area into small knobs. This texture covers the hindmost portion of the ventral face of the articular and angular, and extends onto the lateral and medial faces of the jaw along the articular–angular suture. The angular is notably smooth beneath the glenoid flare, including the area ventral to the posterior portion of the medial crest where the mandible is slightly concave ventromedially. The

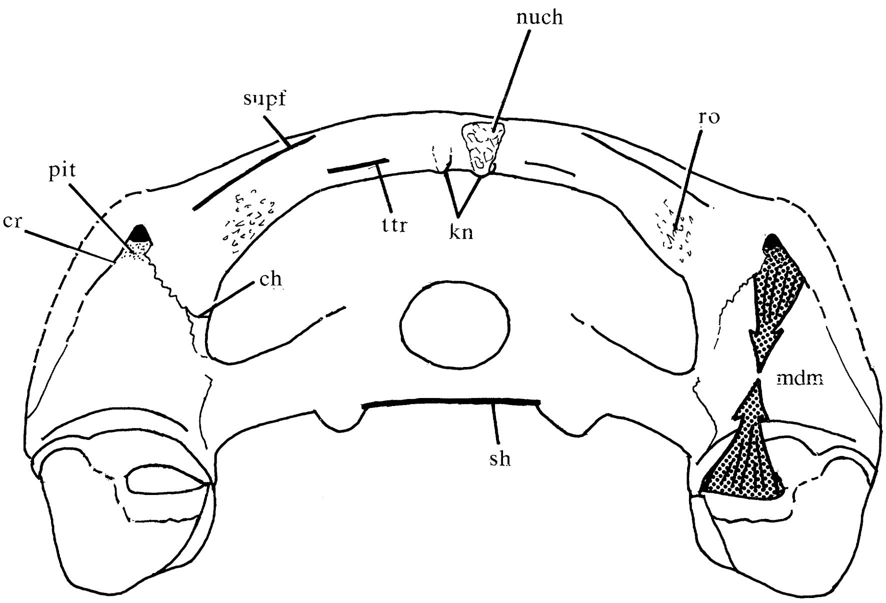

Figure 11. Reconstruction of mandibular depressor musculature and insertions of craniocervical musculature.

muscle would have run over this area, bulging outwards before running backwards and upwards to its insertion, and this smoothness would help its movement. The muscle may have had other fleshy insertions neighbouring its tendinous insertion.

A slight crest on the lateral face of the mandible runs along the angular–articular suture beneath the glenoid fossa, and there is coarse sculpture on the rim of the fossa and the adjacent bone. These are probably attachments for the ligaments and connective tissue of the joint capsule.

The intramandibularis is present in only some Recent reptiles. It originates in the adductor fossa and runs over its anterior edge dorsally to insert upon the pseudotemporalis tendon (Heaton 1979). However, this muscle cannot be verified in *Rhomaleosaurus*, as there is no trochlear groove visible at the anterior end of the adductor fossa.

(*c*) *Depressor mandibulae*

The depressor mandibulae (mdm, figures 10*b* and 11) appears to have had a tendinous origin from the posterior face of the squamosal and quadrate, on a heavily pitted area (pit) between the two sections of the squamosal–quadrate suture and below the squamosal–quadrate foramen. The suture medial to the foramen is heavily incised, and may have carried an extension of the tendinous origin. The channel (ch) running medially from this appears to have carried a blood vessel. There is no evidence that the origin extended dorsomedially beyond the pitted region; also, the squamosal is directed strongly inwards, taking such an extension of the origin away from its mechanically most efficient location above the jaw articulation. A crest (cr) running just above the squamosal–quadrate suture, ventrolateral to the squamosal–quadrate foramen, was probably an origin for the superficial fascia of the neck musculature, as the surface texture of the bone lateral to the crest suggests close attachment of the dermis here (§ 6*a*).

The depressor mandibulae presumably inserted onto the truncated posterior end of the retroarticular process, which contains two ill-defined shallow depressions, and is covered in a matt, very finely pitted surface which in plesiosaurs indicates the ends of bones extended and finished by cartilage (Robinson 1975). Such insertion of muscles into cartilage is known, for example, in Permian tetrapods (Bakker 1982). The depressor mandibulae may also have inserted in part on the dorsomedial portion of the knobbly region at the posterodorsal corner of the angular–articular suture ascribed above to the insertion of the posterior pterygoideus. In contrast, the entire dorsal surface of the retroarticular process (except for the glenoid rim) is covered in coarsely interwoven bone fibres. This texture does not match any other muscle insertions and is presumably related to the development of the articular as a bone replacing Meckel's cartilage.

(*d*) *Pharyngeal floor*

There is little direct evidence for the muscles forming the floor of the mouth and actuating the hyoid apparatus. The genioglossus probably originated on a knob on the ventromedial edge of each splenial behind the symphysis (kn, figure 7), and ran back to the hyoid bones. A chevron-shaped region of fine raised striae, posterodorsal to the knob (chv), may be the origin of the genioglossus or geniohyoideus. A rough, porous strip of bone (pst, figure 10*a*) runs along the ventral edge of the angular just posterior to the glenoid fossa, and may be the origin of a transverse muscle such as the geniohyoideus.

(*e*) *Functional analysis of adductor musculature*

The functional analysis presented here is a necessarily qualitative assessment of the torque exerted by each main muscle mass as the jaw opens and shuts. This torque is the product of the muscle's lever arm about the jaw joint and of the muscle's force. We can crudely assess the variation of the lever arm (also known as moment arm) with the angle at which the jaw is open, but not the simultaneous variation of the force exerted by the muscles, because of their complex pinnate structure.

The origin of the adductor mandibulae externus lies above and somewhat posterior to the insertion on and behind the coronoid eminence when the jaws are closed. The line of force is directed vertically upwards, inclined slightly posteromedially. When the jaws are open, the moment arm decreases although the muscle is directed less medially. The moment arm is longest when the jaws are closed, and longer than that of any other muscles except the pseudotemporalis. The muscle probably had the function of exerting static forces on prey held within the almost-closed jaws.

The origin of the adductor mandibulae posterior lies above the insertion when the jaws are closed, and the line of action is vertical. The moment arm is greatest when the jaws are shut, although it is still comparatively short. The muscle probably helped the adductor mandibulae externus to hold the jaws shut on prey.

The posterior portion of the origin of the pseudotemporalis lies anterodorsal and medial to its presumed insertions, with a line of action directed dorsally and somewhat anteromedially. When the jaws are open, the moment arm is longer and the muscle is directed more vertically. The muscle has a relatively long moment arm and probably had the function of closing the jaws when they were open.

When the jaws are closed, the line of action of the anterior pterygoideus is directed posteriorly and almost horizontally, with a short moment arm. The muscle has a small medial component of force which does not change significantly as the jaws open. When the jaws are closed, the moment arm is much longer but still relatively short. The muscle probably had the function of closing the jaws when they were open.

When the jaws are closed, a straight line from the origin of the posterior pterygoideus to its insertion passes close to the jaw joint, suggesting a very short moment arm. However, in life, the muscle would have deviated to curve under the mandible, probably bulging on either side of the glenoid region, as in crocodilians. It would therefore have acted to some extent as its own pulley, giving a longer effective moment arm along the radius from the jaw joint to some point on the ventral edge of the mandible anteroventral to the glenoid: the muscle then acts as an extension of the bony skeleton. It is hard to assess how this moment arm changed with the opening of the jaw, and I simply assume that it did not change. This muscle would then be equally effective when the jaws were open or closed.

Rhomaleosaurus thus appears to have had a dual-function muscle system, some muscles specialized to exert maximum force when the jaws were open, and others specialized to exert maximum force when the jaws were closed, with one muscle's role uncertain.

Olson (1961) suggested that aquatic tetrapods tend to have large pterygoideus musculature to close the jaws rapidly from an open position, but relatively small adductor musculature to exert force on the jaws once these have been closed. He named this the 'kinetic inertial' system, suggesting that the pterygoideus musculature operates by conferring kinetic energy and momentum on the mandible which are expended when it hits the prey. He contrasted this with what he called the 'static pressure' system in terrestrial reptiles, which have relatively large adductor musculature to exert most force on the jaws when they are closed, for example when subduing or processing prey.

Olson's influential classification must now be qualified. Firstly, crocodilians do indeed have a 'kinetic inertial' system, dominated by the pterygoideus musculature (Sinclair & Alexander 1987), but a dual-function muscle system is now seen to be present in *Rhomaleosaurus* and in at least one nothosaur (Rieppel 1989; Taylor 1989). Secondly, it is not clear that the pterygoideus musculature of a 'kinetic inertial' system actually functions primarily to confer a high kinetic energy on the mandible. It is equally plausible that the pterygoideus accelerates the mandible quickly from rest and keeps it moving against the hydrodynamic drag which increases as the mandible's velocity increases (Beaumont 1977; Taylor 1987). Indeed, if inertia and drag are significant, then the mandible may not even have time to accelerate to a speed where kinetic energy is significant before the jaws shut. The relative importance of inertia, drag and kinetic energy can only be resolved by a quantitative study, which would be valuable in illuminating the functional adaptations of aquatic tetrapods.

(*f*) *Functional analysis of depressor musculature*

Rhomaleosaurus probably needed powerful depressor muscles to open the jaws quickly in water when seizing or manipulating prey. These muscles include the depressor mandibulae and the longitudinal muscles of the pharyngeal floor. The depressor mandibulae and (presumably) the genioglossus of *Rhomaleosaurus* had well-marked tendinous insertions. The stout hyoid bars suggest a strong hyoid musculature, which could, however, have been used when swallowing prey, or moving the tongue to act as a temporary secondary palate when breathing (but see Cruickshank *et al.* (1991)). The depressor mandibulae has a long moment arm provided by the long retroarticular process, a common feature in aquatic reptiles, including other plesiosaurs, crocodilians, ichthyosaurs and mosasaurs, and giving leverage to open the jaw against the drag of the water (Dodson 1975). Chernin (1974) suggested that crocodilians open their jaws by means of the drag of water within the opening gape, but this cannot apply when the animal is stationary, or when the moving animal is at such an angle to the water that the water tends to hold the jaw shut. Also, the mouth needs to be at least partly open. In contrast, terrestrial reptiles let the jaw fall under gravity and have much shorter processes.

The moment arm of the depressor mandibulae is shortest when the jaws are closed, because the origin is anterodorsal to the articulation. The muscle would only achieve its maximum moment arm when the jaws are opened through an angle of about 60 degrees. This may reflect the need for the largest possible gape. Also, the depressor mandibulae has classically been regarded as the main depressor muscle in tetrapods, but Bramble (1978; also Bramble & Wake 1985) suggest that its other, and sometimes primary, role is to stabilize the jaw articulation. He argues that the longitudinal musculature may cause initial depression of the mandible, and the depressor mandibulae only becomes active when the jaw is already open. This may well apply to *Rhomaleosaurus*.

(*g*) *Craniocervical musculature*

See figures 4 and 11. It is not possible to complete the reconstruction of the craniocervical musculature as the occipital aspect of the head is not fully known. Also, the anterior location of the occipital condyle relative to the jaw articulations implies extensive modification of the anterior cervical musculature compared with other reptiles. However, it is possible to trace several features which indicate insertions disposed around the occipital condyle to provide antagonistic pairs in all planes of flexion.

An obtuse crest (supf) along the posterodorsal edge of the dorsal ramus of the squamosal marks the posterior extent of the closely applied dermal connective tissue of the head (§ 6*a*) and the attachment point of the neck integument and perhaps also the superficial fascia. On the posterodorsal rim of the squamosals, on either side of the midline, is a small roughened knob (kn), elongate dorsoventrally. At the dorsal midline, an area of roughened bone appears to be the insertion of a heavy nuchal ligament (nuch). This is not surprising as the long head and neck would have had appreciable density in water and would have tended to sag. The scar is offset onto the right knob, apparently to insert into the connective tissue of the interparietal suture which is itself offset to the right. More laterally there are paired transverse troughs (ttr), each with a sharp ventral edge. Just ventrolateral to each transverse crest is an area (ro) which is heavily roughened with small knobs and brief crests. The ventral musculature would have inserted onto the basioccipital tubera and the posterior transverse shelf (sh) of the palate, as well as into the musculature of the floor of the mouth.

7. STRUCTURAL ANALYSIS

(*a*) *Introduction*

This section deals with the mechanical design of the skull and mandible (Warnock & Benham 1965; Wainwright *et al.* 1976; Gordon 1978; Alexander 1983; for aquatic tetrapods, see Bramble & Wake (1985) and Taylor (1987)).

The basic assumption of this analysis is that the head of *Rhomaleosaurus* was optimized to resist the forces involved in attacking and dismembering prey (Taylor 1987). Feeding involved sufficient force to disrupt prey tissues, while putting its own head at risk from these forces. The head was thus working close to its mechanical limits and the prevention of mechanical failure would then become a major determinant of its structure.

The failure of a loaded structure, such as the head of *Rhomaleosaurus*, occurs where the maximum working stress of the constituent material is first reached. The actual maximum working stress depends on the definition of failure (Lanyon & Rubin 1985). It could be limited by strength, so that the bone, muscle or tendon are not irreversibly and plastically deformed. Alternatively, it could be limited by stiffness, so that the head still remains the right shape for its function. Or it may be a subtle combination of the two in which, for example, displacement causes buckling and therefore incipient failure. A fourth alternative is fatigue failure. However, the head is a relatively stiff bony structure with small deflections under load, so that the optimal structures for maximum strength and for stiffness will not be markedly different for the purposes of this analysis.

The head of *Rhomaleosaurus* can therefore be assumed to maximize strength by concentrating material in regions of highest forces, and by optimizing the design of the jaw articulation and sutures between bones. A further assumption is that interdigitated sutures and oblique overlapping sutures are stronger in tension than plain sutures (Kemp 1972; Bolt 1974; Gans 1960; Herring 1972; Moore 1981; but see Buckland-Wright 1978). A third variable, the orientation of internal structures such as trabeculae and internal bone structures within the bone (Buckland-Wright 1978; Lanyon & Rubin 1985), can sometimes be examined by non-destructive computed tomography (Grine *et al.* 1989), but this is probably not possible in YORYM G503 because of dense pyrite mineralization.

A further, simplifying, assumption is that the forces on the head are bilaterally symmetrical. This is reasonable for much of the time spent in feeding, as the animal would often tend to hold prey in the front end of its jaws, and the rigidity of the skull and mandible restrict kinematic asymmetry (cf. Cundall *et al.* 1987). However, at other times, the food would have been asymmetrical or held asymmetrically, giving asymmetrical forces with implications for the optimal design of tooth rows and the possible induction of tension within a jaw joint (Druzhinsky & Greaves 1979). Also, the use of twist feeding to dismember prey (Taylor 1987) would have induced severe torsional loadings. These problems of bilaterally asymmetrical loadings are beyond the scope of the current paper.

The head comprises two rigid units, the skull and the mandible, orthally hinged at the jaw joint. This analysis considers first the bending forces, then the design of the mandible, skull and jaw joint in turn.

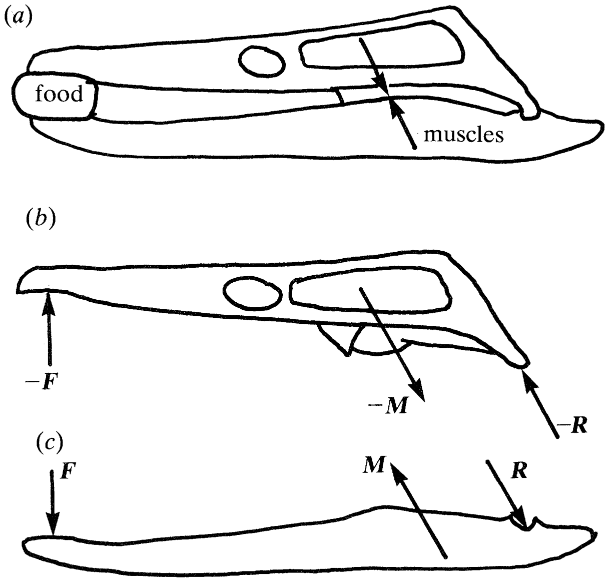

Figure 12. Major forces within head. (*a*) General, in static equilibrium, gripping food in the tips of the jaws while the adductor muscles contract; (*b*) forces acting on the skull; (*c*) forces acting on the mandible.

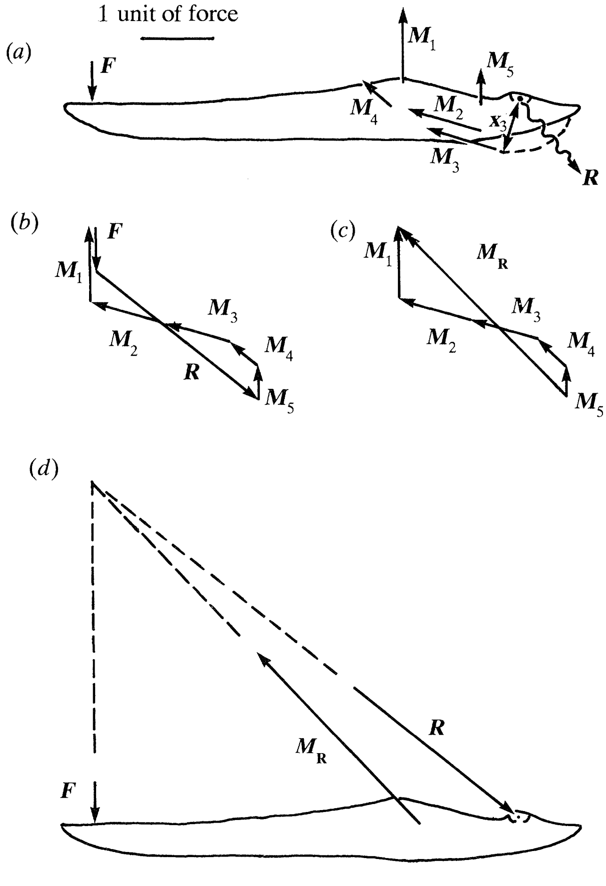

Figure 13. Forces on the mandible. (*a*) Forces as first given; (*b*) polygon of forces to show reaction at the joint; (*c*) polygon of forces to show resultant of all muscle forces; (*d*) forces on mandible.

(*b*) *Forces within the head*

When the animal is biting on food, the mouth is virtually closed, and there is no movement, the induced forces within the parasagittal plane include muscular forces $\boldsymbol{M}$ and $-\boldsymbol{M}$, reactions $\boldsymbol{F}$ and $-\boldsymbol{F}$ at the bite point, and reactions $\boldsymbol{R}$ and $-\boldsymbol{R}$ at the jaw joint (figure 12*a*–*c*; transverse components are considered later).

Consider the forces on the mandible (figure 13*a*). If the food is fleshy enough to deform readily, the bite point reaction $\boldsymbol{F}$ will be vertical. The muscle force vector $\boldsymbol{M}$ is estimated by arbitrarily assigning one unit of force each to the force vectors of the adductor mandibulae externus $\boldsymbol{M}_1$, anterior pterygoideus $\boldsymbol{M}_2$, and posterior pterygoideus $\boldsymbol{M}_3$, and half a unit to each of the smaller muscle masses, the pseudotemporalis $\boldsymbol{M}_4$ and the adductor mandibulae posterior $\boldsymbol{M}_5$, taking angles from the muscle reconstruction (§ 6). The magnitude of $\boldsymbol{F}$ is found by resolving moments about the jaw joint. $\boldsymbol{F}$ has moment arm y and exerts anticlockwise torque Fy. Muscles $\boldsymbol{M}_1 \ldots \boldsymbol{M}_5$ exert clockwise torques with moment arms $x_1 \ldots x_5$. At static equilibrium, moments about the jaw joint add to zero net torque:

$\boldsymbol{M}$(joint):

$$\boldsymbol{M}_1x_1+\boldsymbol{M}_2x_2+\boldsymbol{M}_3x_3+\boldsymbol{M}_4x_4+\boldsymbol{M}_5x_5-\boldsymbol{F}y=0. \qquad (1)$$

The estimated proportions of the muscles' moment arms are:

$$x_1{:}x_2{:}x_3{:}x_4{:}x_5{:}y=7.2{:}2.0{:}3.2{:}5.2{:}2.4{:}26.5. \qquad (2)$$

Substituting (2) into (1), $\boldsymbol{F}$ has a magnitude of approximately 0.6 units of force directed vertically, thus rather less than the force exerted by any one of the three main muscle masses. This shows the importance of strong musculature to obtain a forceful bite at the jaw tip when the mandible is elongated for catching mobile prey underwater.

At static equilibrium there is no net resultant force on the mandible, and the jaw joint reaction $\boldsymbol{R}$ is found by constructing a link polygon of forces (figure 13*b*). $\boldsymbol{R}$ has a magnitude of approximately 2.9 units of force directed posteroventrally. The strong musculature needed for forceful bites incurs great reaction forces and demands a strong jaw articulation.

It is convenient from now on to treat the forces produced by the muscles as a single resultant force vector $\boldsymbol{M}_{\mathbf{R}}$, from the link polygon of muscle forces $\boldsymbol{M}_1 \ldots \boldsymbol{M}_5$ (figure 13*c*). The principle of concurrence is that three forces acting on a body in equilibrium pass through the same point. The line of $\boldsymbol{M}_{\mathbf{R}}$ thus passes anterodorsally through the coronoid eminence (figure 13*d*).

The animal also generates large stresses dynamically when snapping its jaws shut underwater. This does not require a qualitatively different model. Rotational inertia and hydrodynamic drag can be treated as reaction forces directed tangential to the movement of the jaw, thus perpendicular to the jaw ramus, and located at the centres of inertia and drag respectively, which will lie rather more than half the length of the jaw from the joint.

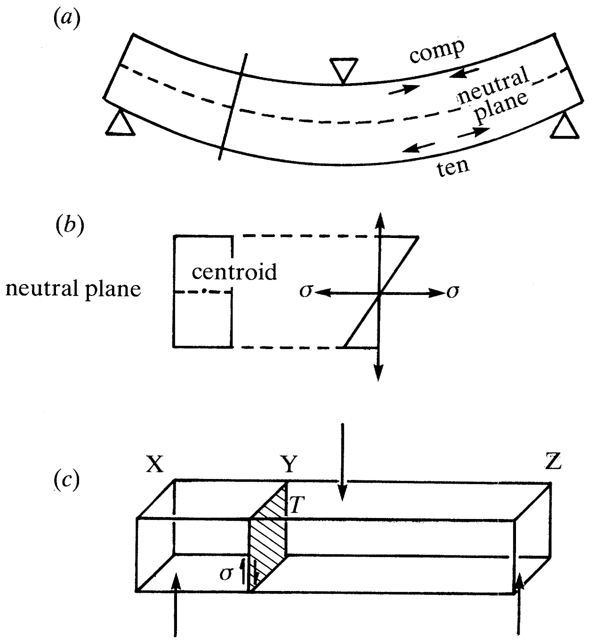

Figure 14. Beam theory. Beam under bending: (*a*) bending forces; (*b*) distribution of bending stresses; (*c*) shear forces.

(*c*) ***Structural analysis of the mandible***

The mandible is functionally a beam loaded in the middle against supports at each end. The engineering design for a beam is therefore the most suitable paradigm for functional analysis (Taylor 1987; Gans 1988; Hickman 1988; and references in § 7*a*). The stresses within a level beam supported at each end and loaded vertically in the middle are analysed by simple beam theory (figure 14; the following analysis makes several assumptions for simplicity, especially that the bone is isotropic and rigid). There are two types of force induced within the beam: bending moment and shearing force.

The bending moment arises from the fact that the ends of the beam are bent upwards relative to the centre (exaggerated in figure 14*a*). This causes tensile stresses in the lower part of the beam, and compressive stresses in the upper part. If the beam has a constant cross-section, the magnitude of the stress σ at any one point is proportional to the vertical distance from the centroid of the beam's cross-sectional shape (figure 14*b*). There is a neutral plane (figure 15*a*) with nil stress in the middle of the beam.

To maximize strength for mass and material used, a structure should concentrate material in the areas of highest stress, and along the lines of tensile and compressive stresses, suggesting a structure of two rods, one above and the other below the neutral plane. This structure is, however, prone to buckling of the upper rod under compressive stresses, so one solution is to spread material laterally and vertically to give the classic engineering I-beam, whose webs stabilize each other against buckling. When transverse loadings are also present, a good compromise structure is a box girder of hollow square or rectangular cross-section. If the loadings can come from any direction, the ideal structure is a tube.

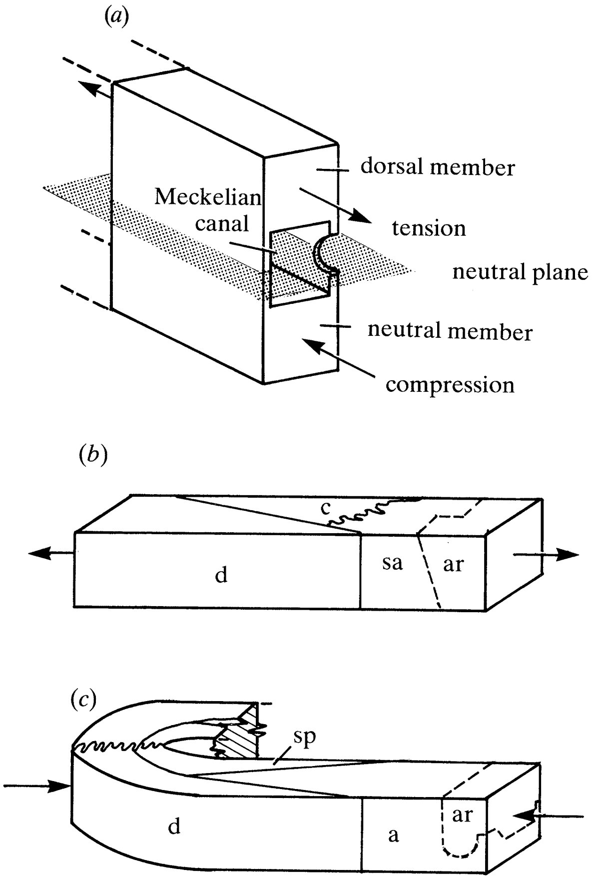

Figure 15. Mandible as a beam. (*a*) cross-section; (*b*), dorsal tensile member; (*c*) ventral compressive member.

The shearing force arises because the ends are being sheared vertically upwards relative to the middle. Consider a beam, XZ (figure 14*c*). The piece XY is sheared upwards relative to the piece YZ. The beam undergoes a shear stress, σ, with the plane of shear within the transverse plane T at Y, and the axis of shear directed vertically. For a simple centrally loaded beam of uniform cross-section, the magnitudes of the shear force and stress are constant throughout the beam. Maximum resistance to shear is simply provided by a sufficiently large cross-sectional area to carry the shear force at an acceptable level of shear stress. In practice, loaded beams fail by tensile or compressive failure rather than shear fracture, unless they are rather short and thick.

The forces on the mandible are mainly vertical and longitudinal with minor transverse components. This suggests an ideal structure of a box girder, rather higher than wide, to resist the predominantly vertical forces. The joints between the bony elements should be disposed to resist tension in the dorsal half, and compression in the ventral half, and shearing forces throughout. Finally, there should be a central mass- and material-saving vacuity in areas of minimum stress.

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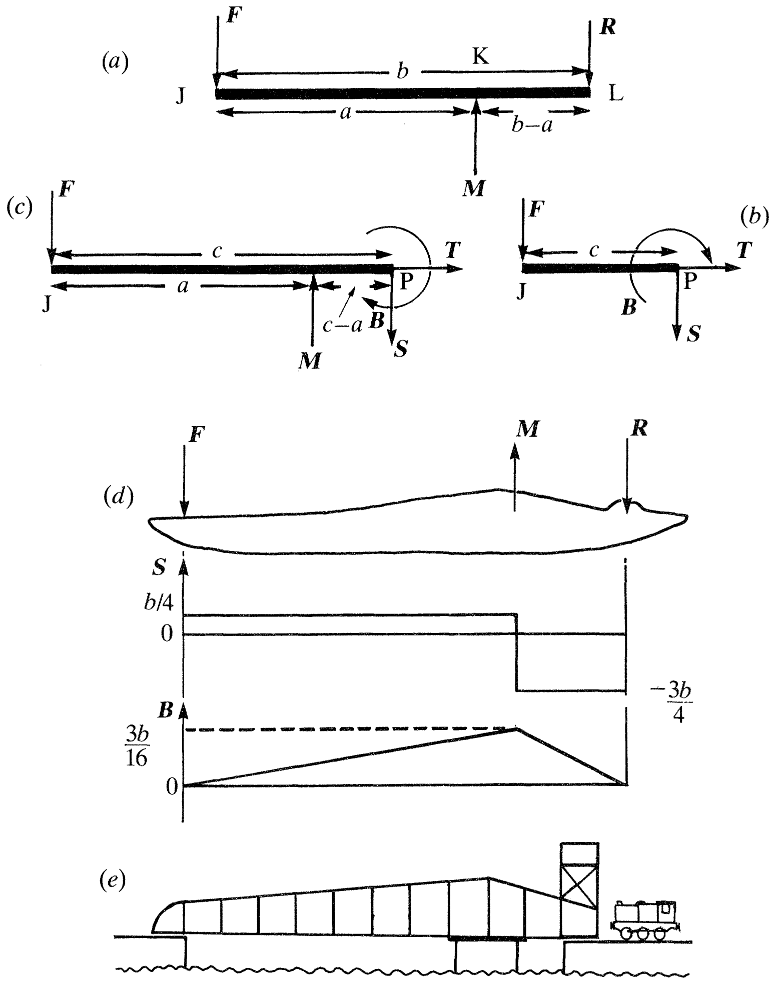

Figure 16. Bending moments within the mandible resulting from vertical components of force (see text for details). ***S***, shear force. ***B***, bending moment.

The actual mandible conforms well to this ideal form (figure 15*a*). The bone is concentrated at the dorsal and ventral edges, with a web on either side of the Meckelian canal which contains the neutral plane. The dorsal elements are strongly joined to resist tension (figure 15*b*). The coronoid has an interdigitating suture with the surangular and a long, tapering overlap over the dentary, which overlaps the surangular, which is itself fused to the articular. The ventral elements are disposed to resist compression (figure 15*c*). The articular is fused to the angular whose long anterior tongue is wedged between the dentary and the splenial, which are themselves held together by long overlaps with the angular and the rigid symphyseal joint with the other dentary and splenial. This is a close functional analogue to the postdentary bones in whaitsiid therocephalians (Kemp 1972, but see Bramble 1978). The dorsal elements of *Rhomaleosaurus* are proportionately rather thicker, partly to contain the dental alveoli, and perhaps also to resist torsion (Taylor 1983).

The variation of bending moments and shear stresses along the mandible can be estimated by treating the mandible as a beam JL of uniform cross-section loaded at K by an upwards force ***M***, and downwards reactions ***F*** and ***R*** at supports at J and L (figure 16*a*), taking upwards forces and clockwise moments as positive:

$$\text{moments about L: } \boldsymbol{F}b+\boldsymbol{M}(b-a)=0, \tag{4}$$

$$\boldsymbol{F}=-\boldsymbol{M}(b-a)/b. \tag{5}$$

Consider the forces on a portion of the beam JP, length c, when $c<a$, i.e. P is between J and K (figure 16*b*), letting ***B*** be the bending moment and ***S*** the shearing force. Resolving horizontally and vertically:

$$\text{R}(\rightarrow)\text{: } \boldsymbol{T}=0, \tag{6}$$

$$\text{R}(\uparrow)\text{: } \boldsymbol{F}+\boldsymbol{S}=0, \tag{7}$$

$$\text{and } \boldsymbol{S}=-\boldsymbol{F}. \tag{8}$$

$$\text{Substituting (5) in (8): } \boldsymbol{S}=\boldsymbol{M}(b-a)/b. \tag{9}$$

$$\text{Moments about P: } \boldsymbol{B}+\boldsymbol{F}c=0, \tag{10}$$

$$\text{and } \boldsymbol{B}=-\boldsymbol{F}c. \tag{11}$$

$$\text{Substituting (4) in (11): } \boldsymbol{B}=\boldsymbol{M}c(b-a)/b. \tag{12}$$

For the case when $c>a$, i.e. P is between K and L (figure 16*c*):

$$\text{R}(\rightarrow)\text{: } \boldsymbol{T}=0, \tag{13}$$

$$\mathrm{R}(\uparrow)\colon \boldsymbol{F}+\boldsymbol{S}+\boldsymbol{M}=0, \tag{14}$$

$$\boldsymbol{S}=-\boldsymbol{M}-\boldsymbol{F}. \tag{15}$$

Substituting (5) in (15): $\boldsymbol{S}=-\boldsymbol{M}+\boldsymbol{M}(b-a)/b$, (16)

$$\boldsymbol{S}=-\boldsymbol{M}a/b. \tag{17}$$

Moments about P: $\boldsymbol{B}+\boldsymbol{F}c+\boldsymbol{M}(c-a)=0$, (18)

$$\boldsymbol{B}=-\boldsymbol{M}(c-a)-\boldsymbol{F}c. \tag{19}$$

Substituting (5) in (19):

$$\boldsymbol{B}=-\boldsymbol{M}(c-a)+\boldsymbol{M}c(b-a)/b \tag{20}$$

$$=\boldsymbol{M}(b-c)a/b. \tag{21}$$

For *Rhomaleosaurus*, $a{:}b$ is about 3:4.

The bending moments are nil at each end of the mandible, increasing towards the coronoid eminence (figure 16*d*). One factor determining the resistance of a beam to vertical bending is I, the second moment of area for bending of the cross-section. I is equal to $4e^3f/3$ for a beam of rectangular cross-section, height $2e$ and width $2f$. Ignoring the Meckelian canal, which lies around the neutral plane and makes relatively little difference, the jaw ramus is approximately rectangular in cross-section. The mandible widens anterior and posterior to the coronoid eminence, so it can be very approximately treated as of constant cross-sectional area A; f then approximates $A/4e$, and I at any one point becomes approximately proportional to $e^2A/3$, thus the square of the height of the mandibular ramus for constant A. Thus the coronoid eminence has an important strengthening function against the bending moments which are greatest at that point, as well as providing an area of insertion for the jaw musculature and a butt for the pterygoid flange. A good mechanical analogy for the mandible is a swing bridge which is loaded by its own weight when it is open (figure 16*e*).

The shearing forces are constant from the bite point back to the muscle insertion, and also from the muscle insertion to the joint, with the forces behind the muscle insertion about three times as great as the forces in front (figure 16). If shear resistance is important, then one would expect the mandible to have a constant cross-sectional area on either side, with the posterior cross-section markedly greater than the anterior one. The anterior ramus is very roughly of constant cross-sectional area, but the posterior ramus is not markedly greater in cross-sectional area, and is heavily modified by the joint and muscle insertions. However, the sutures appear disposed to resist shear arising from the upwards pull of the muscle insertions. The posterior portion of the jaw is effectively continuous because of fusion and the manner in which the angular embraces the articular. The sutures between the anterior elements (dentary, coronoid and splenial) and posterior elements (surangular, angular) are irregular in transverse section, so that vertical shear stresses tending to displace the bones are borne by compressive loadings across at least part of the sutures.

The muscles also exert an anteriorly directed longitudinal component of force on the jaw, which sustains a backwards directed reaction. The main muscle involved is the anterior pterygoideus, which inserts on the angular. The articular is wrapped below and behind by the angular, and the tensile forces are borne within the angular and by the fused articular–angular suture. The posterior pterygoideus inserts behind the articulation, and simply compresses the angular onto the articular. Overall, the longitudinal component of the muscular force acts along the line of the jaw, approximately along the neutral plane, or just ventral to it. The tensile force resulting from the anterior pterygoideus will therefore act along the neutral plane or within the compressive member, acting to balance the compressive stresses from the bending moment. However, there is no general tendency for the longitudinal component of the muscle force to balance the bending moment (cf. therapsid mandibles (Kemp 1972)).

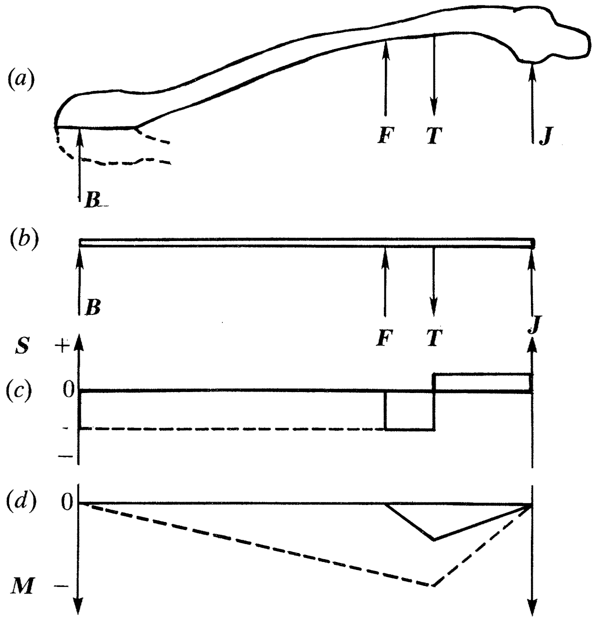

Figure 17. Bending moments and shear forces within the mandible resulting from transverse components of force. (a) and (b), transverse forces on mandible and model of mandible as straight beam. ***B***, reaction at bite point; ***F***, reaction at pterygoid flange–mandible contact; ***J***, reaction at jaw joint; ***T***, transverse component of muscle force. (*c*) Variation of shear force ***S*** along length of model beam. Solid line, force with pterygoid flange contacting mandible. Dotted line, force with pterygoid flange not contacting mandible. (*d*) Variation of bending moment ***M*** along length of model beam. Solid line, moment with pterygoid flange contacting mandible. Dotted line, moment with pterygoid flange not contacting mandible.

Struggling prey will exert forceful forwards and backwards loadings on the loaded mandible, which is already under tension dorsally and compression ventrally. The dorsal tensile member can thus take substantial compressive loads without undergoing net compression, and the ventral compressive member can absorb tensile loads, providing an important reserve of tensile strength.

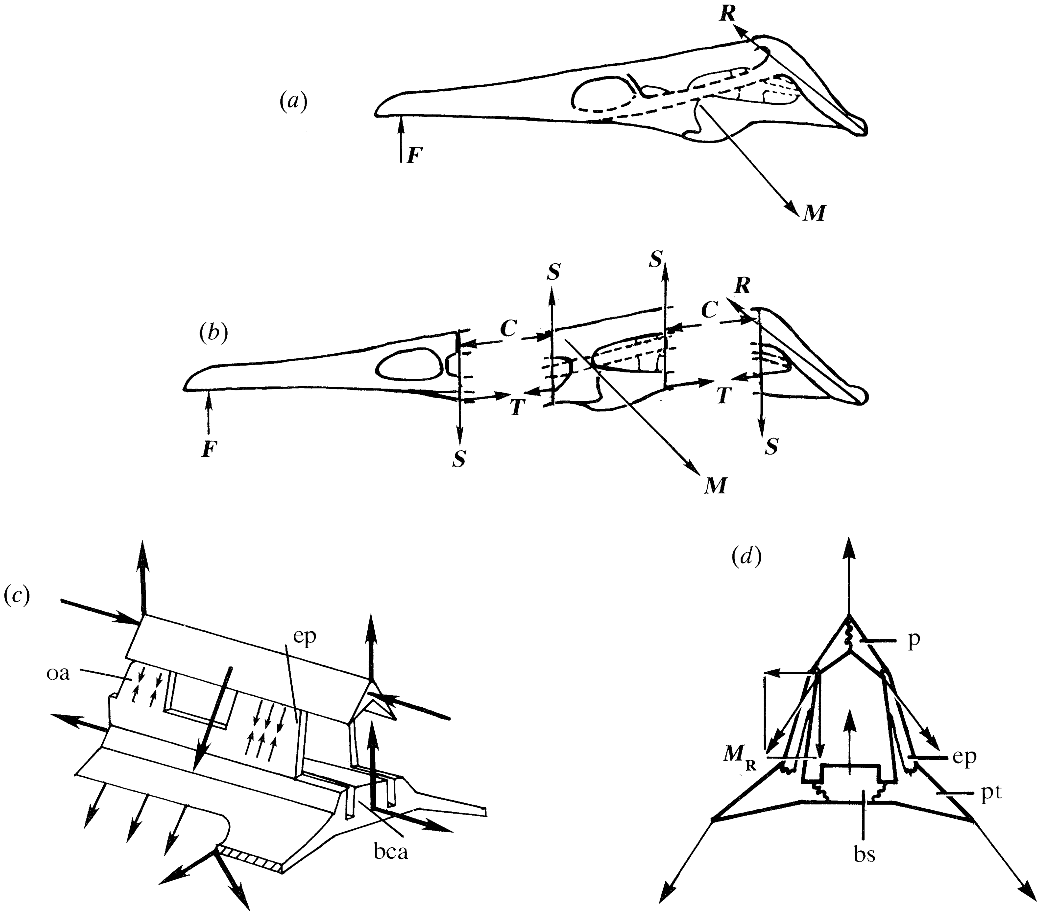

Figure 18. Forces within the skull. (*a*) External loadings, forces as figure 12; (*b*) division into snout and orbits, middle portion, and rear skull; (*c*) middle portion of skull with pterygoid flanges and marginal bones removed; (*d*) section through middle portion of skull.

The transverse components of the muscle forces are greatest when the jaws are closed, and the pterygoid flange supports the ramus against medial loadings. The jaw ramus can then be treated as a beam supported at three points and loaded at one point (figure 17). If the beam is rigid, the reaction at the symphysis is nil or small compared with the reactions at the pterygoid flange and jaw joint. An analysis similar to that of the vertical components of force above shows that the presence of the pterygoid flange eliminates transverse bending and shearing forces from the jaw ramus anterior to the flange, and markedly reduces forces between the flange and the articulation (figure 17). Opening the jaws reduces the support given by the pterygoid flange. However, this loss of support is delayed because the pterygoid boss continues to abut the highest part of the mandible, and is compensated by the more vertical orientation of the muscles at greater angles of opening, with a reduction in transverse components of force.

The analysis is complicated by local modification of the mandible. The anterior and dorsal portions of the dentary are swollen to take the teeth, and the articular region is swollen to accommodate the glenoid. The primarily tensile stresses induced at the muscle insertions are sustained by extensive interdigitation and fusion of sutures between the coronoid eminence and the articulation. Also, the plane of each suture, such as the surangular–angular suture, is usually oblique to the main stresses.

(*d*) *Functional analysis of the skull*

The skull is loaded equally and oppositely to the mandible, assuming that no forces are being transmitted through the neck. Again, a suitable paradigm is a beam, this time a Warren truss or lattice girder, because the skull is pierced by openings for the eyes and muscle attachments. The skull can only be partly evaluated here, as the important marginal bones are missing. Also, little is known about strengthening internal structures such as the box girders suggested by section 1, or the deep structure of the sutures.

For analysis, the skull can be divided into anterior, middle and posterior portions (figure 18*a*, *b*). Biting prey or closing the jaws quickly in water involves forces equal and opposite to those on the mandible. The middle portion, with the muscle origins, is pulled downwards relative to the snout and the articular region, which each carry reaction forces.

The snout (including the orbits) sustains an upwards reaction ***B*** at the bite point, a compressive reaction ***C*** through the dorsomedian bar, and a tensile reaction ***T*** through the basicranium and palate. A vertical shearing force $\boldsymbol{S}$ tends to shear the anterior snout upwards relative to the posterior portion. The compressive forces are borne by the dorsal compressive member comprising the premaxillae, frontals and parietals, with ventral flanges or box-like structures, and extensive overlap, increasing resistance to buckling and vertical shearing. The tensile forces are transmitted by the palate, basicranium, and perhaps the lateral temporal bars, which are longitudinally oriented, and have some overlapped or interdigitating sutures. The anteroposteriorly elongate suborbital fenestrae do not weaken them. The snout is deeper posteriorly, increasing resistance to the higher bending moments near the muscle origins.

The posterior skull bears an anterodorsally and somewhat medially directed reaction along the length of the squamosal–quadrate unit which is U-shaped in section to prevent buckling under the compressive load which wedges the quadrate firmly into the V-shaped socket on the squamosal. These forces are then transferred to the lateral temporal bars and the dorsal rami of the squamosals. The paroccipital processes brace the quadrates against the anteromedial component of force. The quadrate ramus of the pterygoid is part of the ventral tensile member, with an interdigitated suture with the quadrate. The orientation of the squamosal–quadrate unit along the main axis of compressive force is typical in non-mammalian tetrapods (Bramble 1978) although in plesiosaurs the quadrate is complemented by the squamosal.

The middle skull (figures 18*b*, *c*, *d*) bears most of the musculature. It acts as two beams, one above the other, both heavily loaded downwards along their length by the muscle forces and supported at either end by the shearing forces. The epipterygoids and occipital arch (oa) join them into a single girder. The dorsal beam, the intertemporal bar, is in section an inverted V to resist buckling while providing ridges for muscle origins. It is braced by the epipterygoids and occipital arch. The outward pull of the muscles $\boldsymbol{M}_{\mathbf{R}}$ is resisted by interdigitation of the interparietal suture, and by the inwards lean of the epipterygoids transferring some of this force to the ventral bar via the interdigitated epipterygoid–pterygoid sutures. The location of the occipital arch anterior to the jaw articulations is probably a consequence of the posterolateral movement of the jaw articulations for maximum gape, but it also provides a good location for support of the dorsal bar.

The complex ventral bar comprises the basicranium (bca) and pterygoids which are markedly strengthened against bending by vertical flanges. Transverse tensile loads from the muscles are resisted by interdigitated sutures. The pterygoid flange is heavily loaded by the strong posteroventral pull of the pterygoideus musculature. To resist this, the ectopterygoid lies in a broad socket facing anterolaterally, so that the ectopterygoid–pterygoid suture is loaded mainly in compression against the muscles as well as any medially directed transverse forces arising from contact with the mandible. The outwards transverse component of the posterior pterygoideus is met by interdigitation of the suture.

The middle skull is a close functional and structural analogue to that of whaitsiid therocephalians (Kemp 1972). It also highlights the expansion of the epipterygoids into strong blades, unlike the weaker pole- or leaf-like epipterygoids of smaller and perhaps more primitive plesiosaurs such as '*Plesiosaurus*' *hawkinsi* (Owen 1840). This expansion may be a derived character functionally correlated with the development of powerful adductor musculature, particularly the adductor mandibulae externus, to clamp the jaws shut on prey while dismembering it.

(*e*) *Jaw joint*

The jaw joint is assumed to have been a simple orthal hinge with a double-condyle structure, with the medial condyle of the quadrate larger than the lateral condyle, and two glenoids separated by an approximately longitudinal sulcus. The structure inherently resists vertical compressive loadings. The sulcus butts against either condyle to stabilize the joint against transverse forces caused, for example, by struggling prey. Laterad displacement of the mandible is also resisted by the medially directed component of the muscular force. Vertical tensile loadings would not normally have occurred. The anteriorly directed longitudinal component of muscular force, as well as anteriorly and posteriorly directed forces arising from struggling prey, are strongly resisted by the anterior and posterior transverse ridges of the glenoid fossa when the jaws are shut. When the jaws are open, the posterior ridge becomes even more effective, and the anterior ridge remains effective as its high lateral portion still engages the quadrate. The joint is thus highly stabilized by bony structures acting in concert with the muscles. Unlike that of cynodonts (Bramble 1978), the joint is not modified to minimize reaction forces; in those circumstances the design of the joint should optimize its strength. The strongest biological compressive joints are of the ball-and-socket type, and the jaw joint can be interpreted as two ball-and-socket joints side by side, to restrict movement to one degree of rotational freedom, thus maximizing strength. This structure is common to primitive reptiles such as pelycosaurs (Kemp 1982), and is permitted because of the simple caniniform dentition which does not require complex mandibular movements.

8. HEARING IN PLESIOSAURS

The stapes (§ 3*c*) is long, recurved, and thin, with a pointed distal end apparently ending in a cartilaginous extrastapes. In modern reptiles the extrastapes is distally anchored in one or more of three ways (Wever 1978): to the medial face of the quadrate, to the hyoid apparatus (as in crocodilians), or to a post-quadrate tympanum (as in chelonians, lacertilians and crocodilians). However, *Rhomaleosaurus* bears no otic notch or other structure forming the rim of a tympanum. Also, any tympanum would have been located level with or below the squamosal–quadrate foramen, in the region apparently occupied by the depressor mandibulae muscle (§ 6*c*; figures 4 and 11). Most probably there was simply no tympanum, and the stapes–extrastapes attached directly to the quadrate, and perhaps also to the hyoid by a cartilaginous or ligamentous branch, as in *Sphenodon*.

Primitive tetrapods and reptiles lacked a tympanic ear; instead, the stapes braced the jaw articulation against the braincase (McGowan 1973; Lombard & Bolt 1979; Carroll 1980; Smithson 1982; Clack 1983; Bolt & Lombard 1985). The plesiosaurian middle ear can be interpreted as a modification of this plesiomorphic state, but with a more delicate stapes. The stapes' bracing function has been taken over by the pterygoids which form a novel articulation with the basicranium behind the posterior interpterygoid vacuities.

Alternatively, plesiosaurs evolved from animals with tympanic ears that were secondarily lost, as has occurred in some lizards (Wever 1978). The tympanum is an adaptation to hearing airborne sound, by matching the different impedances of air and water, and a primarily aquatic animal has less need for a tympanum as it can hear by direct conduction from the water. This may also allow the loss of an air-filled middle ear, eliminating problems of hydrostatic pressure during diving. The retention of eardrums in pinnipeds, penguins and crocodilians is probably a reflection of their amphibious lifestyle, which involves communication on land by means of airborne sound.

The large orbits and sclerotic plates of plesiosaurs (Andrews 1913; Linder 1913) suggest that they were primarily visual hunters, although underwater olfaction is suggested by the location of the nostrils of *Rhomaleosaurus zetlandicus* and a functional analysis of the closely similar *R. megacephalus* (Cruickshank *et al.* 1991). Plesiosaurs probably did not use sound echolocation (biosonar), as odontocete whales do (Fleischer 1978; Moore 1981; Nachtigall 1989). If plesiosaurs' ears were typical of reptiles, they were comparatively insensitive to the sound frequencies at and above 10 kHz required for biosonar. Their otic capsules are not acoustically isolated from the braincase and each other, and indeed form part of the load-bearing structure (§ 7*d*). Finally, the skull lacks bony structures for focusing and transmitting sound comparable to the concave frontal region and mandibular fat tract of odontocetes. Similar arguments have been used to rule out echolocation in ichthyosaurs (McGowan 1973) and the primitive cetacean *Pakicetus* (Gingerich *et al.* 1983).

The plesiosaurian ear was thus a passive organ without a tympanum, comparatively non-directional under water, with direct conduction from the water to the ear through the lower jaw, quadrate, and perhaps hyoid apparatus, all used in substrate conduction by terrestrial tetrapods. The ear could also have heard airborne sound (cf. snakes and *Sphenodon* (Wever 1978)), perhaps with some directional sensitivity (cf. amphisbaenians (Wever 1978)). Presumably the plesiosaur used its ears as modern reptiles do, to alert itself to nearby occurrences (Wever 1978): prey, predators and, perhaps most importantly, the signals of conspecifics, as in crocodilians (Lang 1989).

9. CONCLUSIONS

Comparison of *Rhomaleosaurus* with other predatory tetrapods, both terrestrial and aquatic, suggests the key functional conflicts and resulting compromise solutions to the problems of predation in water.

The skull and mandible combine strength with economy of material. The mandible is a box beam highest in the middle, and the skull is a girder lattice posteriorly and flange-reinforced shell anteriorly, all classic designs to maximize strength for mass while providing the necessary openings to the Meckelian canal, orbits, and fenestrae for muscles. Bone is about twice as dense as water (Wainwright *et al.* 1976) with an appreciable weight when submerged. Any unnecessary mass in the head adds to the downwards pitching moment caused by the head's location on a long neck, and reduces the acceleration of the head and neck, and the animal as a whole, when pursuing prey (cf. fish (Webb 1982)).

The long, snapping snout or 'pincers jaw' of many aquatic predators catches mobile prey relatively easily (Taylor 1987). However, shortening the snout increases the bite force on prey held at the tips of the jaws (§ 7*b*) and reduces the bending moment acting on the skull. Gharials (*Gavialis*) have a long, narrow snout and feed on relatively small fish which do not require much force to subdue, but durophagous animals such as placodonts have heavy crushing teeth and short jaws (Sues 1987*b*).

The jaw shape and teeth of *Rhomaleosaurus* suggest a mixed sarcophagous diet similar to that of the Nile crocodile (*Crocodylus niloticus*), including large prey forcibly subdued and dismembered (Taylor 1987; Pooley 1989). There is a long jaw to capture prey in water, especially the smaller prey which still forms a significant portion of the diet (Massare 1987; Pooley 1989). The tapering mandible is triangular or ogival (like a Gothic arch) in plan view to brace the tip against transverse loadings during prey struggles and to help swallow large prey by maximizing posterior gape. The skull is triangular for the same reasons as the mandible, and also to house a powerful jaw adductor musculature firmly attached within enormous temporal fenestrae, strong pterygoid flanges, and suborbital fenestrae (§ 7*b*).

The long snout, however, requires increased adductor muscle masses and thus loadings for a given bite force at the tip, and functionally specialized muscles to close the jaws quickly or to clamp them shut. The increased bending stresses require strengthening adaptations such as the layout and nature of the sutures, the overlapped and flanged bones forming the girder-like longitudinal dorsomedian bar, the pterygoid flange, the orientation of the squamosal–quadrate unit, and the coronoid eminence. Langston (1973) has documented the evolution of analogous features in the long, low head of crocodilians.

The need to move the head rapidly underwater, for streamlining and snapping sideways at prey, implies a dorsoventrally compressed skull and mandible (Taylor 1987; Pooley 1989). However, this decreases the resistance to bending loads during feeding by reducing the cross-sectional height. There is thus a compromise between structural strength and efficiency in predation. This is probably why most theropod dinosaurs and the aberrant terrestrial sebecosuchid crocodilians have markedly higher skulls than aquatic crocodilians and the aberrant, possibly aquatic, theropod *Baryonyx* (Charig & Milner 1986; Taylor 1987). In *Rhomaleosaurus* the weakening effect of dorsoventral compression has been countered by adaptations to maximize skull and mandible strength. Also, the reduced height of the snout has probably led to the extension of the tooth roots into almost the full depth of the premaxillae and maxillae, thereby crowding the external nares posteromedially.

Like many aquatic predatory tetrapods, *Rhomaleosaurus* shows adaptations to maximize the transverse gape, and therefore the size of food which can be swallowed without having to be dismembered. The jaw articulations are cantilevered outwards and backwards, and the pterygoid flange and pterygoideus musculature are disposed laterally, leaving the median palate clear for swallowing large pieces of prey.

Rhomaleosaurus was primarily a visual predator with large eyes located about halfway along the skull, where the widening gape allowed ample room. It may have been able to use underwater olfaction. It did not use biosonar, so there was no functional compromise between mechanical requirements and the need to provide sound tracts for outgoing and returning sound.

The overall shape and detail construction of the skull and mandible of *Rhomaleosaurus* can thus be explained as adaptations for resistance to the forces involved in capturing and dismembering prey. This conclusion must, however, be tentative, until more complete material is described and compared with other forms (Gans 1985, 1986), particularly plesiosaurs feeding on smaller prey, as well as aquatic and terrestrial predators in other groups, such as crocodilians and theropods. Finally, a full analysis of *Rhomaleosaurus* will need to include any scaling factors and the torsional stresses during twist feeding (Taylor 1983).

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LIST OF ABBREVIATIONS AND CONVENTIONS USED

a	angular
adc	anterodorsal crest
addfo	adductor fossa
aiv	anterior interpterygoid vacuity
aof	antorbital flange
ap	origin of aponeurosis
ar	articular
ars	anterior ramus of squamosal
arpt	anterior ramus of pterygoid
atrc	anterior transverse crest of glenoid fossa
bar	broken base of anterior ramus of squamosal
bca	basicranial axis
bo	basioccipital
boden	bodenaponeurosis
bs	basisphenoid
c	coronoid
can	canal between alveoli
cap	bone cap over replacement tooth
cc	central cavity
ce	coronoid eminence
ch	channel
chv	chevron of striae
cl	cleft
con	concavity
cr	crest
d	dentary
dep	depression
df	dorsal flange
dist	distal end
dlc	dorsolateral crest
dlf	dorsolateral flange
dmc	dorsomedian crest
dmf	dorsomedial flange
dmfo	dorsomedian foramen
dms	dorsomedial shelf
dmt	dorsomedial trough
dr	dorsal ramus
ec	ectopterygoid
en	external naris
ep	epipterygoid
fac	facial process of premaxilla
fo	foramen
fr	frontal
fra	fragment
gl	glenoid fossa
gr	grooves
imf	intermandibular foramen
in	internal naris
kn	knob
kns	knobs
l	lacrimal
lc	lateral condyle
ldmc	longitudinal dorsomedial crest
lflr	lateral flare under glenoid fossa
lgr	longitudinal groove on dentary
lmc	longitudinal medial crest
lrpt	lateral ramus of pterygoid
mame	m. adductor mandibulae externus
mamp	m. adductor mandibulae posterior
mapt	m. anterior pterygoideus
mc	medial condyle of articulation
mca	Meckelian canal
mcr	median crest
mdm	m. depressor mandibulae
mflr	medial flare under glenoid fossa
mppt	m. posterior pterygoideus
mpst	m. pseudotemporalis
mto	mature tooth
mx	maxilla
mxc	maxillary cavity
no	notch
nop	notochordal pit
nuch	scar of nuchal ligament
oa	occipital arch
oc	occipital condyle
omc	ossified Meckel's cartilage
orb	orbit
p	parietal
pa	pre-articular
pal	palatine
palv	primary alveolus
pap	pit of primary alveolus
pfo	parietal foramen
pit	pitted area
piv	posterior interpterygoid vacuities
pl	squamosal–parietal plate
pmc	cavity in premaxilla
pmx	premaxilla
po	postorbital
pof	postfrontal
por	porous area
ppr	paroccipital process
pr	process
prf	prefrontal
prox	proximal end
prpt	posterior ramus of pterygoid
ps	parasphenoid
psc	parasagittal crest
pss	parasagittal sulcus
pst	porous strip on angular
pt	pterygoid
ptb	pterygoid boss
ptrc	posterior transverse crest
ptf	pterygoid flange
q	quadrate
qrpt	quadrate ramus of pterygoid
r	ridge
rap	retroarticular process
ro	roughened area
rto	developing replacement tooth
sa	surangular
salv	secondary alveolus
sc	sculpturing
sh	transverse shelf
sof	suborbital fenestra
sp	splenial
sq	squamosal
sqf	squamosal–quadrate foramen
ssc	spiral sculpture
st	step in bone surface
stf	subtemporal fenestra
supf	origin of superficial fascia
tf	temporal fenestra
ttr	transverse trough
v	vomer
vc	ventral crest
vlf	ventrolateral flange
vlfc	ventrolateral flange of coronoid
vme	ventromedial edge
vmf	ventromedial flange
vx	vertex