A new reconstruction of the skull of the Callovian elasmosaurid plesiosaur *Muraenosaurus leedsii* Seeley

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Abstract: A new reconstruction of the skull of the elasmosaurid plesiosaur *Muraenosaurus leedsii* is presented, based on a partial but well preserved specimen. The bony labyrinth of the inner ear is used to orient the skull in the horizontal plane. In the new reconstruction, the skull is higher, with more anteriorly directed orbits and a more vertical suspensorium. This reconstruction suggests that *Muraenosaurus* had a more powerful jaw action than coeval cryptoclidid plesiosaurs.

Introduction

The skull of plesiosauroid plesiosaurs is generally a delicate structure which is easily damaged or lost in the processes leading to fossilisation and, ultimately, collection. This paper describes a skull from the Callovian (Middle Jurassic) Oxford Clay Formation of Peterborough, England. The specimen (LEICT G18.1996) was presented to Leicester Town Museum in 1902 by Mr. R. Swales of Peterborough. It seems probable that this is the Robert Swales listed in a local directory of the period (Anon, 1906; page 271) as a shopkeeper of Lincoln Road, Peterborough. The specimen, which includes most of the postcranial skeleton, is referable to the elasmosaurid genus *Muraenosaurus* Seeley, 1874 on the basis of the form and number of the cervical vertebrae (Brown, 1981). Taxonomically important skull characters shown in the specimen are: the number and ornament of the dentary teeth; the sagittal crest; and the form of the occipital condyle. Two species are recognised within *Muraenosaurus*, namely *M. leedsii* Seeley, 1874 and the much smaller *M. beloclis* Seeley, 1892. On the specimen described in this paper the right radius lacks the large facet for the intermedium diagnostic of *M. beloclis*. The specimen just falls within the size range of *M. leedsii*, although it is one of the smallest individuals of this species. The fused neural arches in the cervical vertebrae and fused coracoids and left scapula indicate that it was an "old adult" by the criteria of Brown (1981).

Although incomplete, the skull is largely uncrushed, allowing a new reconstruction to be produced. The only previously published skull reconstruction of *Muraenosaurus sp.* is that of Andrews (1910, reproduced here as Fig. 5c). This shows a relatively low skull with dorsally directed orbits and a sloping suspensorium. However, the specimens which Andrews (1910) described had all been subjected to dorsoventral crushing.

As the osteology of the species is well known, only additional points will be dealt with below. Besides Andrews' (1910) description, elements of the braincase and palate were described by v. Koken and Linder (1913). Their material consisted of four partial skulls curated in the Geological Institute in Tübingen. The prootic and exoccipital-opisthotic were accurately re-articulated, but the gross morphology of the skull was not reconstructed. More recently, Maisch (1998) has reviewed this material, providing detailed descriptions of the braincase and skull table. Brown (1981) commented upon Andrews' reconstruction, most notably on the relationship of the maxillae and jugals, but did not produce an updated reconstruction.

Description

Institution abbreviations: BMNH — Palaeontology Department, The Natural History Museum, Cromwell Road, London SW7 5BD, UK; LEICT — Natural Sciences Section, Leicester City Museums, New Walk Museum, Leicester LE1 7EA, UK.

Frontals and parietal. Portions of both frontals and parietals are preserved. There is some slight distortion in the area of the parietal foramen, so that the midline of the skull appears to be kinked. There is no fusion at the midline forward of the parietal foramen. The medial surface of the parietals and frontals can be seen as a result of a break in the right parietal. The frontal-parietal suture passes through the facet for the postfrontal and then traces a triangular path medially (Fig. 1a). On the ventral surface, the suture has an interdigitating structure before returning up the inner wall of the orbit (Fig. 1b). The ventral portions of the frontal-parietal suture were noted by Maisch (1998) as anterior processes of the parietals intruding between the frontals. Just anterior of the postfrontal facet, the right frontal shows a smooth edge which runs anterolaterally before turning more rostrally at a small boss. This edge forms part of the recess described by Maisch (1998), suggesting the possibility of an unpreserved "supraorbital" or prefrontal element. This recess and the anterior processes of the parietals have been highlighted as characters peculiar to one of the Tübingen skulls (Maisch, 1998).

The frontals form a gentle dorsal arch over the orbit, in contrast to the flatter orbital margin seen in crushed specimens such as BMNH R.2421. Each frontal bears a trough running around the orbital margin towards the midline. Separating the troughs is a ridge formed by the anterior extension of the frontals (preserved only on the left side) which

amp	site of ampulla	mt	mature tooth
ang	angular	mx	maxilla
ar	articular	nfo	nutritive foramen
avsc	anterior vertical semicircular canal	p	parietal
bc	braincase	palv	primary alveolus
boc	basioccipital condyle	pmx	premaxilla
c	coronoid	pob	postorbital bar
d	dentary	ppr	paroccipital process
en	external naris	pt	pterygoid
eo-op	exoccipital-opisthotic	pvsc	posterior vertical semicircular canal
fbo	facet for basioccipital	q	quadrate
fc	facet for coronoid	rt	replacement tooth
fenov	position of fenestra ovalis	sa	surangular
fop	facet for opisthotic	salv	secondary alveolus
fpof	facet for postfrontal	so	supraoccipital
fpro	facet for prootic	sq	squamosal
fr	frontal	sut	suture between frontal and parietal
fso	facet for supraoccipital	ut	utricular recess
gl	glenoid fossa	wpfo	wall of parietal foramen
hsc	horizontal semicircular canal	XI	foramen for cranial nerve XI (accessorius)
j	jugal	XII	foramen for cranial nerve XII (hypoglossal)
jfo	jugular foramen	hatching	broken bone
lab	bony labyrinth	stipple	matrix
lag	approximate position of lagena		

Table 1. Key to abbreviations used in figures.

would have been overlapped by the facial processes of the premaxillae. The external nares would have lain in this trough, which may have played a role in the hydrodynamics of underwater olfaction (Cruickshank *et al.*, 1991).

Squamosals. Portions of both squamosals are present, and are free from each other and the parietals. These elements became disarticulated prior to burial. The squamosal facets of the parietals are preserved as dark brown bone, while the parietal facets of the squamosals are preserved as buff-coloured bone, probably demonstrating different burial histories (Martill, 1986). The posterior surfaces of the dorsal rami are roughened, presumably for the attachment of cervical musculature or ligaments. At the level of the anterior rami, the posterior surfaces form a keel, associated with a pair of ridges. Similar ridges in the pliosaur *Rhomaleosaurus megacephalus* (Stutchbury) have been interpreted as sites for the attachment of the skin and, possibly, musculature of the neck (Cruickshank, 1994), as seems to be the case here.

Each squamosal is broken approximately 3cm below the point where the anterior ramus sweeps forward to form the ventral border of the temporal fenestra. The break reveals a cavity containing a nub of bone, identified here as the head of the quadrate. Below this point, as in all specimens of *Muraenosaurus* described to date, the squamosal is crushed and "telescoped" and so remains poorly known. The dorsal edge of the anterior ramus is thicker than the ventral border, which is very thin. It is impossible to reconstruct the ventral extent of the squamosal due to the breakage of this edge. The thin bone in this region suggests that there was little direct transmission of force to the maxilla through the squamosal and jugal. This supports Brown's (1981) observation that the ectopterygoid provided the structural link between the maxilla and the jaw articulation. The thicker dorsal edge of the anterior ramus forms part of the rim of the temporal fenestra, and so would provide attachment for the temporalis musculature.

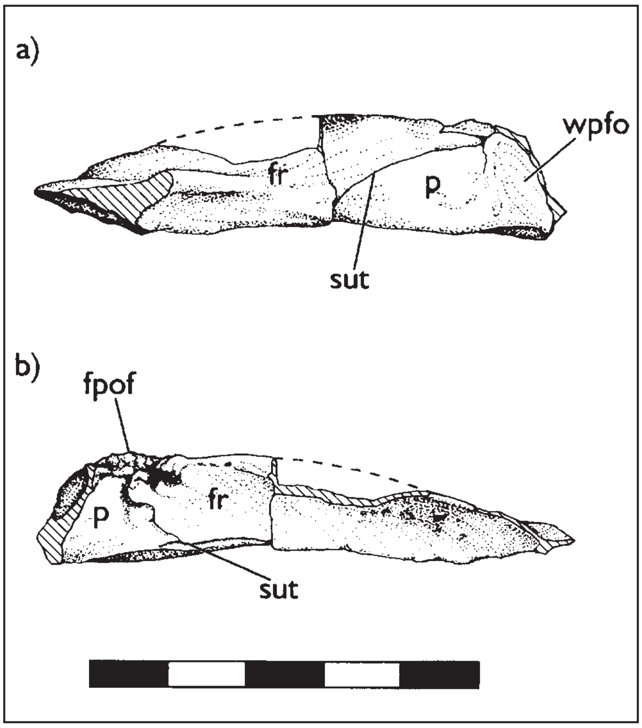

Fig. 1. *Muraenosaurus leedsii* (LEICT G18.1996). Partial right parietal and frontal, showing the suture and the arched dorsal margin, in (a) medial view and (b) lateral view. Scale bar = 50mm. For abbreviations see Table 1.

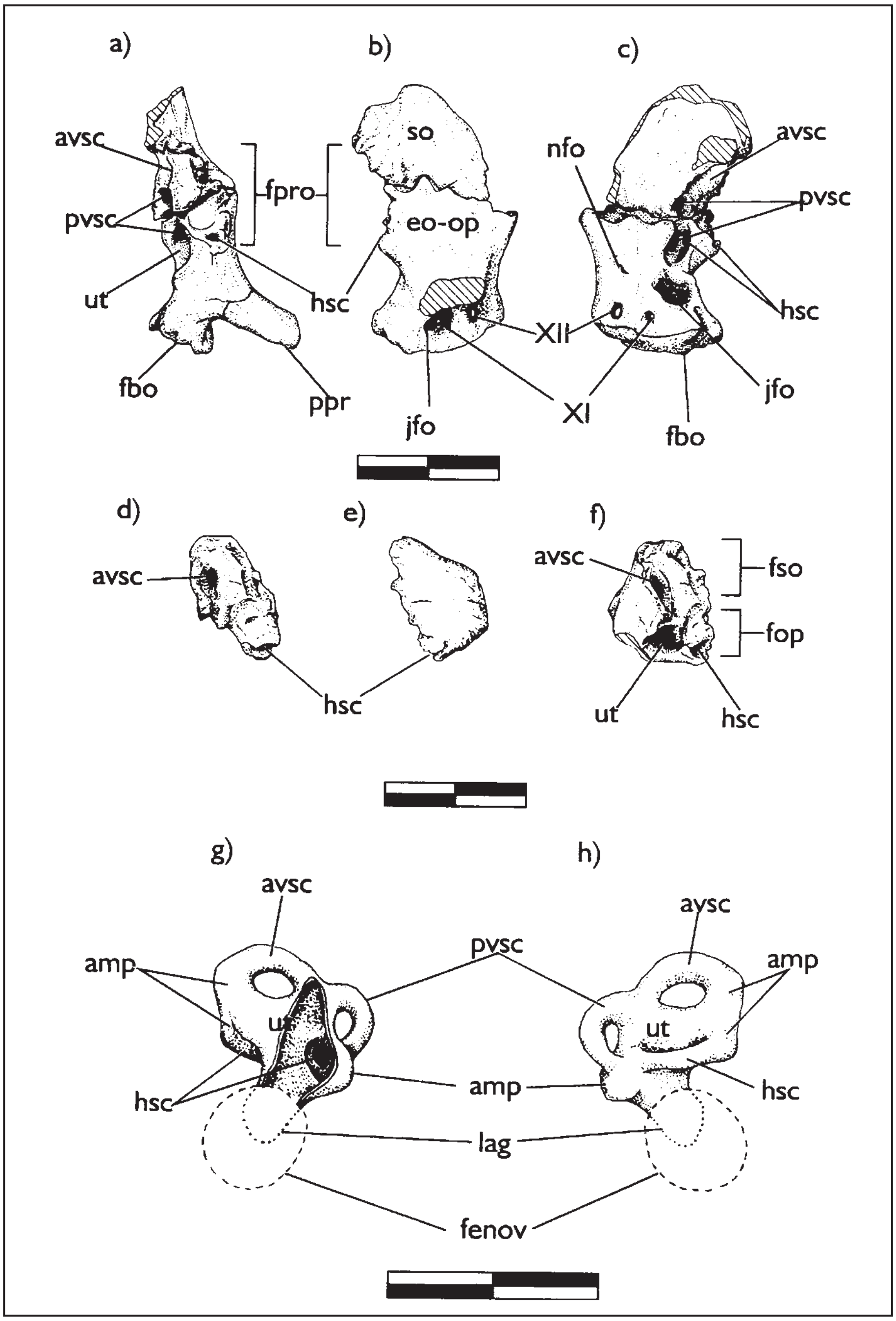

Fig. 2. *Muraenosaurus leedsii* (LEICT G18.1996). Left exoccipital-opisthotic with partial supraoccipital in (a) anterior, (b) lateral, and (c) medial view. Paroccipital process omitted for clarity in (b). Right prootic in (d) posterior, (e) lateral and (f) medial view. Reconstruction of bony labyrinth of right inner ear in (g) medial and (h) lateral view. The medial wall in (g) is rendered transparent. Scale bar = 20mm in all cases. For abbreviations see Table 1.

Braincase. The braincase is represented by the basioccipital, basisphenoid, parasphenoid, partial right prootic, and left exoccipital-opisthotic with attached partial supraoccipital. The occipital condyle is separated from the body of the basioccipital by a groove, and the pedicels of the exoccipitals take no part in its formation. This confirms the identification of this specimen as a small adult. The basicranium agrees with existing descriptions (Andrews, 1910; v. Koken and Linder, 1913; Maisch, 1998).

The medial surface of the exoccipital-opisthotic (Fig. 2a, b and c) bears a relatively large rectangular slit, the jugular foramen (the metotic foramen of Maisch, 1998) and two smaller foramina. At first sight, the lateral surface bears only one smaller foramen. Close inspection shows that the more anterior foramen opens within the jugular foramen. Maisch (1998) suggested that this would be the case, and identified the foramen as that of the accessorius nerve (XI). The lateral wall of the prootic (Fig. 2d, e and f) shows no foramina, unlike those described in BMNH R.2422 by Brown (1981). Inspection of that specimen confirms the presence of at least one foramen, which may have been a nutritive foramen rather than the opening for the facial nerve (VII).

The bony labyrinth of the inner ear can be reconstructed using data from the right prootic, left exoccipital-opisthotic and supraoccipital (Fig. 2g and h). The horizontal and posterior vertical semicircular canals run from a deep excavation for

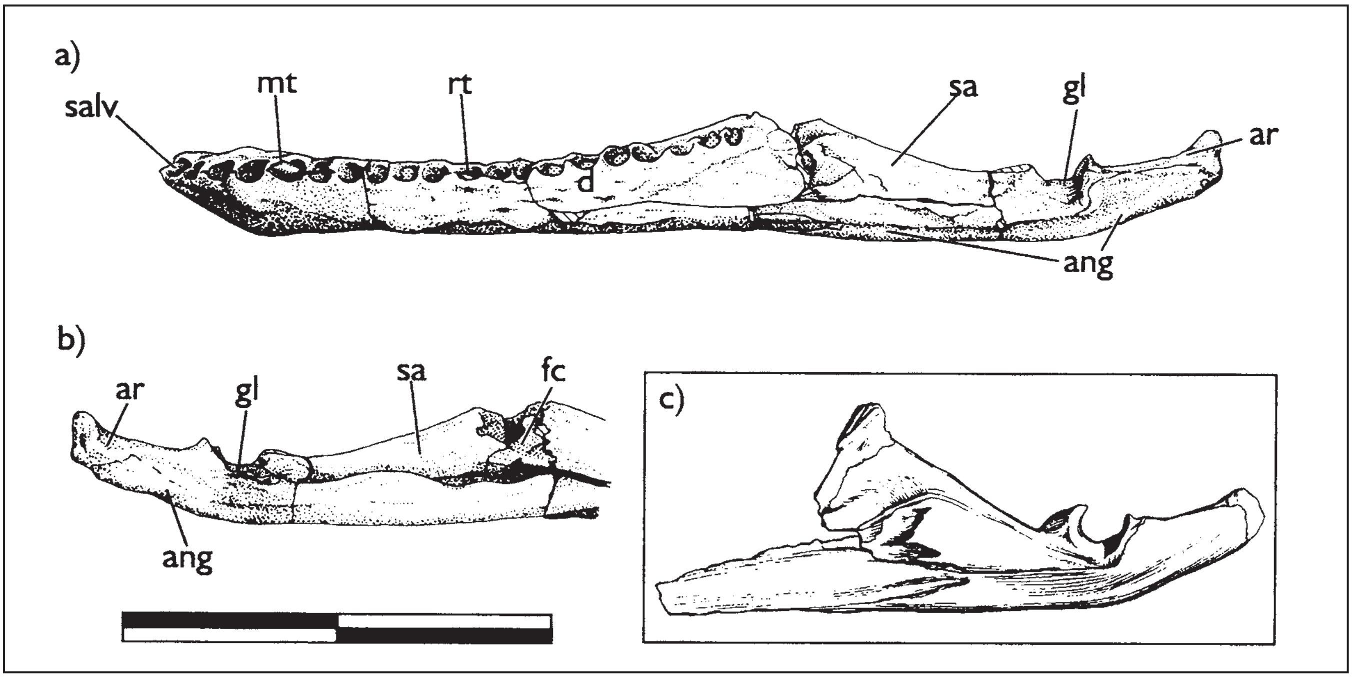

Fig. 3. *Muraenosaurus leedsii* (LEICT G18.1996). Lower jaw in (a) lateral and (b) medial view. Scale bar = 100mm. (c) Articular region of BMNH R.2678, not to scale (from Andrews, 1910). For abbreviations see Table 1.

the utriculus, while the anterior vertical semicircular canal runs up a groove on the sutural surface of the supraoccipital, confirming Maisch's (1998) suggestion. Corresponding passages in the prootic for the anterior vertical and horizontal canals lead to the anterior part of the utricular cavity. The horizontal semicircular canal can be used to reconstruct the horizontal orientation of the skull (Fig. 5).

Jaws and dentition. The lower jaw is complete on the left side (Fig. 3), except for the coronoid. This element in BMNH R.2678 was identified as the splenial by Andrews (1910), and as part of the dentary by Brown (1981), but the distinct concave facet formed by both the dentary and surangular indicates the presence of a separate coronoid. The coronoid eminence does not appear to have been as high and steep as in larger, but ontogenetically younger, specimens such as the "adult" BMNH R.2678 (Fig. 3c) and "juvenile" BMNH R.2863. The proportionally taller coronoid eminence of these larger animals indicates that animals of different sizes were not geometrically similar. In other words, this area of the skeleton displays allometry. A relatively higher coronoid eminence would bring the insertions of the jaw adductor musculature closer to their points of origin around the temporal fenestra, resulting in a smaller muscle mass than otherwise expected. Muscle mass, being dependent on volume, would be expected to increase as the cube of any linear scaling factor. However, the advantages gained by reducing body weight would have been less important in an aquatic animal.

A fragment of upper jaw containing a small replacement tooth is also preserved, and is identified as premaxilla on the basis of the surface ornament and angle of the dental alveoli. The left dentary carries 20 tooth positions. No fully erupted teeth are preserved, apart from broken stubs. The largest complete replacement tooth (Fig. 4) agrees with the description of the dentition of *Muraenosaurus leedsii* given by Brown (1981), although the ridges appear sparser and the tooth blunter. These are size-related differences associated with the small size of both the tooth and the animal. The teeth would have penetrated and held the prey, which would have been mainly soft-bodied (Massare, 1987).

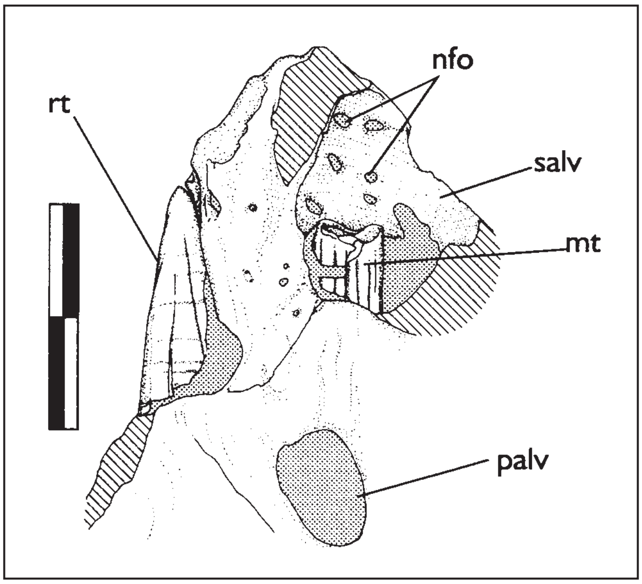

Fig. 4. *Muraenosaurus leedsii* (LEICT G18.1996). Camera lucida drawing of first and second left dentary alveoli, showing tooth ornament. Scale bar = 10mm. For abbreviations see Table 1.

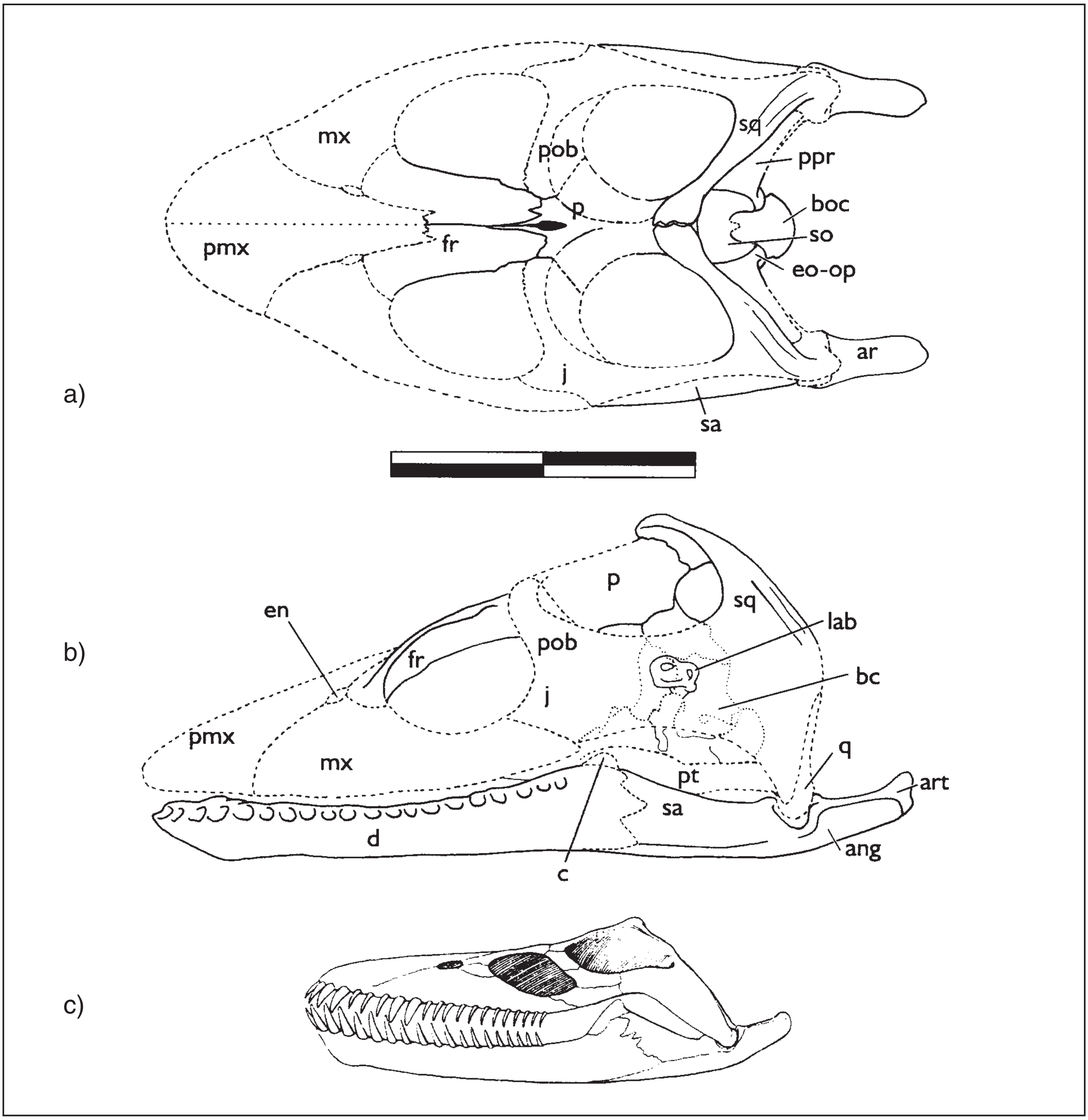

Fig. 5. *Muraenosaurus leedsii*. Reconstruction of skull in (a) dorsal, and (b) lateral view with cheek rendered partially transparent. Based on LEICT G18.1996, with additional data from Andrews (1910) and BMNH R.2861. (c) Andrews' 1910 reconstruction, not to scale. Scale bar = 100mm. For abbreviations see Table 1.

Reconstruction

A new reconstruction of the skull of *Muraenosaurus leedsii* is presented (Fig. 5), based on this specimen. There are three main sections to this skull as preserved, the skull roof, the braincase and occiput, and the lower jaw. The reconstructed skull needs to be high to accommodate the occipital plate, while the lower jaw gives the snout to quadrate length. Comparisons with other specimens indicate that the premaxillae would have extended for approximately 5cm anterior to the end of the frontal.

Unfortunately, the taxonomically important area around the cheek still remains poorly known; here the cheek has been reconstructed as being dorsoventrally deep. The reconstructed horizontal orientation of the skull, as indicated by the semicircular canals, gives the orbits a more anteriorly directed view with the possibility of stereoscopic vision.

The suspensorium is significantly more vertical than has been previously reconstructed (Andrews, 1910; see also Fig. 5). In this respect, it resembles the skulls of the coeval cryptoclidid plesiosaurs (Brown, 1981; Brown and Cruickshank, 1995) more than has been previously thought. However, the temporal fenestra and coronoid eminence are situated more anteriorly. This arrangement results in a longer lever arm for the action of the temporalis musculature, and therefore a more powerful bite. By comparison the shorter coronoid to glenoid distance in the cryptoclidids would result in a faster, snapping bite. This indicates that *Muraenosaurus* could have taken more substantial prey than the cryptoclidids, and supports the niche-partitioning demonstrated by the difference in dentition.

Acknowledgements

Thanks are due to Dr. Arthur Cruickshank, Mr John Martin and Mr. Richard Forrest for bringing me on to the project and for the many discussions on the mechanics of plesiosaurian skills. I would also like to thank the above, along with Dr. Andrew Milner and an anonymous referee, for reading drafts of this manuscript and for their comments. Richard Forrest also kindly provided translations of German references where needed. Sandra Chapman (Natural History Museum, London) provided access to specimens in her care. This paper is based on a poster presented at the 45th Symposium of Vertebrate Palaeontology and Comparative Anatomy (SVPCA) held at the University of Derby in 1997, and I would like to thank SVPCA delegates, especially Dr. Michael Taylor and Dr. David Brown, for their comments. I would also like to acknowledge an award from the Jones-Fenleigh Memorial Fund which allowed me to attend the SVPCA.

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