Journal of Paleontology, 87(4), 2013, p. 537–549
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0022-3360/13/0087-537$03.00
DOI: 10.1666/11-104

OSTEOLOGICAL REDESCRIPTION OF THE SKULL OF *MICROCLEIDUS HOMALOSPONDYLUS* (SAUROPTERYGIA, PLESIOSAURIA) FROM THE LOWER JURASSIC OF ENGLAND

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Abstract—The plesiosaur specimen NHMUK 36184 from the Lower Jurassic of Whitby, Yorkshire and kept in the Natural History Museum of London, comprises an almost entire skeleton with nearly complete skull. It was described as one of two syntypes of *Plesiosaurus homalospondylus* by Owen, and selected as the lectotype by Lydekker. Extensive preparation of the skull has revealed it as one of the most complete and best-preserved Jurassic plesiosaurian skulls known, and its description adds much-needed data to our knowledge of the cranial osteology of the Plesiosauria. The three-dimensional preservation permits a relatively reliable reconstruction of its form. *Microcleidus homalospondylus* displays an interesting combination of cranial characters present in Jurassic plesiosauroids and Cretaceous Elasmosauridea. Its snout presents a very distinctive sculpture; the first pair of premaxillae teeth are extremely reduced; the frontal is partially overlain by the premaxillae, contacts the pineal foramen but does not contact the temporal fenestra; the jugal does not contact the orbit nor the temporal fenestra; the squamosal contacts the postorbital but not the maxilla and presents a bulb; the postfrontal contacts the posterolateral orbit margin; the anterior interpterygoid vacuity is absent; the pterygoids meet posterior to the posterior interpterygoid vacuities and are pierced by a foramen at this level; the quadrate ramus of the pterygoid presents a ventromedial flange; the parasphenoid is crested; the epipterygoid contacts the parietal; the paroccipital process is spatulate distally; the prootic presents an anteroventral process; the mandibular symphysis is keeled and bears four pairs of teeth. *Microcleidus* appears very similar to *Hydrorion* and *Occitanosaurus*, and the three taxa share a great number of plesiomorphic characters with basal plesiosaurians and pliosauroids.

INTRODUCTION

The plesiosaurians form a group of predatory marine reptiles whose stratigraphic range is Upper Triassic to uppermost Cretaceous (Bardet, 1992; Gasparini et al., 2003a; Benson et al., 2010; Sennikov and Arkhangelsky, 2010; Vincent et al., 2011). Most of the known Early Jurassic specimens were recovered from England and Germany during the nineteenth and early twentieth centuries (e.g., Owen, 1865; Dames, 1895). During recent decades, several of these specimens have been re-examined in detail in order to clarify their taxonomy and better constrain the phylogenetic relationships among Plesiosauria (e.g., Groβmann, 2007; Smith and Dyke, 2008; Benson et al., 2011a, 2011b; Vincent, 2011, 2012; Vincent and Benson, 2012). However, some specimens still need to be described in detail to complete our understanding of the early history of this group. Among them is the genus *Microcleidus* for which the phylogenetic position among Plesiosauria is still under debate. In recent phylogenetic analyses it is regarded as basal within Elasmosauridae (Brown, 1981, 1993; Carpenter, 1999; Smith, 2003; Vincent et al., 2011); as a sister-group of the Elasmosauridae (Bardet et al., 1999; O'Keefe, 2004; Gasparini et al., 2003b) or Cryptoclidia+Elasmosauridae (Ketchum and Benson, 2010); as a 'microcleidid elasmosaur' (Groβmann, 2007), equivalent to Plesiosauridae; as within Microcleididae (Benson et al., 2012) and as within Plesiosauroidea in the most recent phylogenetic analysis (Druckenmiller and Knutsen, 2012). These differences are mainly due to the different concepts for Elasmosauridae used by the authors, and the size of datasets used for phylogenetic analyses (the largest phylogenetic datasets [O'Keefe, 2001; Ketchum and Benson, 2010; Druckenmiller and Knutsen, 2012] do not recover *Microcleidus* as within Elasmosauridae); but also due to the lack of detailed description of *Microcleidus*. This work presents a restoration and detailed description of the recently-prepared skull NHMUK 36184. Comparison of this specimen with other plesiosaurs reveals morphological affinity with Liassic plesiosauroids and Cretaceous Elasmosauridae (sensu Ketchum and Benson, 2010).

SPECIMEN AND REPOSITORY

Repositories and institutional abbreviations for material discussed in this paper are: MANUM, Manchester Museum, Manchester, UK; NHMUK, Natural History Museum, London, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; YORYM, Yorkshire Museum, York, UK.

NHMUK 36184 kept in the collection of the Natural History Museum of London, was described and figured by Owen (1865) as *Plesiosaurus homalospondylus,* and is an adult (sensu Brown, 1981). It comprises the skull in association with the almost complete postcranial skeleton. The skull has been recently prepared (by DSB) and is stored separately and therefore easily accessible for study; the postcranial skeleton is exhibited under glass mounted with an old cast of the skull made prior to preparation. The skull, and especially the braincase, is preserved in three dimensions with minimal distortion, which is quite rare in plesiosaurs. The mandible is preserved in occlusion with maxillae and premaxillae, and thus a small part of the palate is hidden by the mandible; but otherwise, the palate is very well displayed in full articulation. Most of the teeth are missing, but the alveoli are uncrushed, permitting both a count of the teeth and estimation of their size, orientation and occlusion. The skull roof is only slightly disturbed and, having been previously protected by rock matrix, now shows good detail of the sutures between elements.

Watson (1909, p. 1) created the genus *Microcleidus* to which he referred the species *Plesiosaurus homalospondylus*, forming the new combination *M. homalospondylus*, and attributed a new species to this genus: *M. macropterus* in 1911 (Watson, 1911, p. 1–9). The species *M. homalospondylus* (Owen, 1865) is known from four sub-complete specimens and represents one of the most complete plesiosaur species recovered from the Lower Jurassic marine deposits. NHMUK 36184 and YORYM 502 are the two syntype specimens of Owen's species. NHMUK 36184 was regarded as the holotype of *M. homalospondylus* by Lydekker (1889), who thus acted as first reviser under article 74.6 of the International Code for Zoological Nomenclature (1999), selecting this specimen as the lectotype. NHMUK 36184 is the most complete specimen. Additional very incomplete and nondiagnostic NHMUK specimens were referred to this species by Lydekker (1889): NHMUK 1334, 40118, 32717, 1366 and 1367. In Manchester University, specimen MANUM 7077, comprises an almost complete post-cranial skeleton described by Watson (1909, p. 4–13), together with a dorsoventrally squashed and eroded skull. A second Manchester specimen, MANUM 7135, comprises the vertebral column and some girdle and propodial elements. Finally in York, specimen YORYM 502, briefly described by Owen (1865) and now designated the paralectotype, comprises part of the mandible and a substantially complete post-cranial skeleton.

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Gray, 1825 (Welles, 1943)
MICROCLEIDUS Watson, 1909
MICROCLEIDUS HOMALOSPONDYLUS (Owen, 1865)

1865 *Plesiosaurus homalospondylus* Owen, p. 12, pls. 5–8.

Diagnosis.—A plesiosauroid possessing the following unique combination of characters: snout presenting sculptures; first tooth alveoli on premaxillae small; frontal partially overlain by premaxillae; frontal-pineal foramen contact; no frontal-temporal fenestra contact; no maxilla-squamosal contact; no jugal-orbit contact; no jugal-temporal fenestra contact; postorbital-squamosal contact; postfrontal contacting the posterolateral orbit margin only; presence of a squamosal bulb; anterior interpterygoid vacuity absent; pterygoids meet posterior to the posterior interpterygoid vacuities; presence of a ventromedial flange of the quadrate ramus of the pterygoid; crested parasphenoid; ectopterygoid boss absent; presence of a foramen piercing the posterior part of the pterygoids; epipterygoid-parietal contact; paroccipital process long, slender and spatulate distally; presence of an anteroventral process of the prootic; dentary sculptured; presence of a keeled mandibular symphysis bearing four pairs of teeth; 38 elongated cervical vertebrae bearing lateral ridges; femur longer than humerus.

Description.—See complete description below.

Types.—Syntype NHMUK 36184 and YORYM 502; lectotype NHMUK 36184 (Lydekker 1889, acting as first reviser); and paralectotype YORYM 502.

Referred specimens MANUM 7077, 7135.

Occurrence.—The syntypes are from the upper Lias of Whitby, Yorkshire. According to Owen (1865), the specimen NHMUK 36184 was found in the Upper Alum Shale, *Hildoceras bifrons* Zone of Whitby, which is middle Toarcian in age. More recently, Benton and Taylor (1983) discussed its provenance and age, suggesting it was found in the cliffs of the Whitby-Saltwick section and could be referred to the Main Alum Shales (*commune* Subzone, lower part of the *bifrons* Zone), lower Toarcian. The specimen MANUM 7135 is from the upper Lias of Wellingborough, Northamptonshire.

Remarks.—Lydekker (1889) referred several other specimens to this species: NHMUK 1334, 40118, 32717, 1366, 1367. These specimens are isolated cervical or caudal vertebrae, or a few associated vertebrae. This material bears no diagnostic characters allowing its attribution to the species *Microcleidus homalospondylus*.

DESCRIPTION

Skull roof.—The premaxillae form the anterior part of the snout and produce posteromedial processes that extend posterodorsally along the midline and contact the frontals and prefrontals. Each premaxilla has five alveoli. The dorsal surface of the premaxilla exhibits a very distinctive sculpture of anteriorly and anterolaterally-oriented ridges and furrows, which are not artificial as it is possibly the case in *Plesiosaurus dolichodeirus* Conybeare, 1824 (Storrs, 1997). The presence of a distinctive sculpture on the snout was considered as a synapomorphy of the Early Jurassic taxa *M. homalospondylus*, *Hydrorion brachypterygius* (Huene, 1923) Groβmann, 2007, and *Occitanosaurus tournemirensis* (Sciau et al., 1990) Bardet et al., 1999, by Groβmann (2007). Nevertheless, some pliosauroids also exhibit distinctive sculpture on the snout (e.g., Gasparini, 1997). The premaxilla is of similar form to those described (Brown, 1981) for *Muraenosaurus* Seeley, 1874, *Cryptoclidus* Seeley, 1892 and *Tricleidus* Andrews, 1909 and the Early Jurassic taxa *Hydrorion* and *P. dolichodeirus*. A plaster-filled fracture (Figs. 1A, 2A, 2B) passes through the region of the nares. Part of the anterior border of the left naris may be preserved bordered by the left premaxilla. The right side is much damaged in this region, and the right maxilla is here much eroded. Behind the plaster repair, the dorsomedial processes of the premaxillae extend between the anterior one-third of the orbits and contact the anterior border of the frontal. The palatal contribution of the premaxilla to the palate cannot be seen, being covered by the mandible. The suture between the premaxilla and the maxilla extends posterodorsally from the dental margin between the 5th and 6th alveoli toward the external naris, although damage to the naris obscures its exact posterodorsal terminations.

The maxilla is long and forms most of the anterior and ventral margin of the orbit. It extends posteriorly just ventral to the edge of the supratemporal fenestra, but does not meet the squamosal. It contacts the jugal and postorbital anterior to the postorbital bar.

The anterior extremity of a suture between the maxilla and another skull roof element runs from the anterior orbital border to the external naris. This bone lying between the orbit, maxilla, naris and premaxilla is the prefrontal, as it has been interpreted in most plesiosauroids (e.g., *Plesiosaurus*: Storrs, 1997; *Thalassiodracon hawkinsii* [Owen, 1838]: Storrs and Taylor, 1996). Posterior to the fracture the prefrontal is plainly evident and lines the orbit anterodorsally. Its suture with the frontal is clearly

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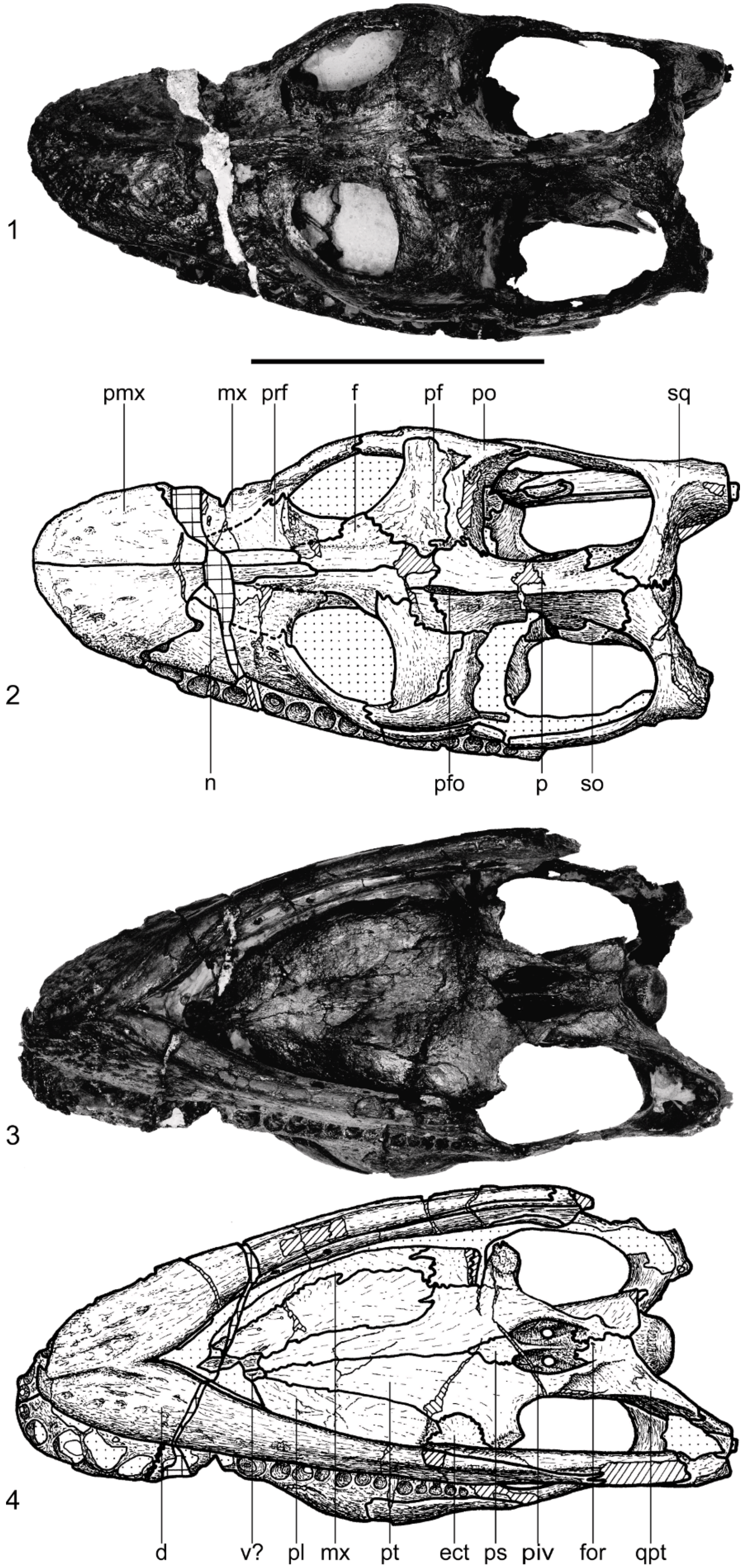
FIGURE 1—Skull of *Microcleidus homalospondylus*, NHMUK 36184. *1*, *2*, photograph and interpretation of the dorsal view; *3*, *4*, photograph and interpretation of the ventral view. The areas with dots correspond to areas filled with matrix. Scale bar=10 cm. Abbreviations: d=dentary; ect=ectopterygoid; f=frontal; for=foramen; mx=maxilla; n=external naris; p=parietal; piv=posterior interpterygoid vacuity; pl=palatine; pf=postfrontal; pfo=pineal foramen; pmx=premaxilla; po=postorbital; prf=prefrontal; ps=parasphenoid; pt=pterygoid; qpt=quadrate ramus for pterygoid; sq=squamosal; so=supraoccipital; v=vomer.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seen extending round the orbital border; and on the right side it can be traced on the deep orbital surface of the skull roof. Its extension anteriorly is not clear due to crushing and distortion in this region. Our interpretation is that the prefrontal meets the maxilla at the partly fused suture.

The frontal forms the roof of the orbit. It is overlain anteriorly by the premaxilla and borders the prefrontal anterolaterally. The frontals are in contact along the midline as in all Jurassic plesiosauroids (*Plesiosaurus*, *Hydrorion*, *Thalassiodracon*, *Occitanosaurus*, and *Seeleyosaurus guilelmiiperatoris* [Dames, 1895] Groβmann, 2007), and the Cretaceous taxa *Callawayasaurus colombiensis* (Welles, 1962) Carpenter, 1999; but differs from other Elasmosauridae in which the frontals are separated by the dorsal process of the premaxillae (Carpenter, 1997, 1999; Sato, 2003; Kear, 2005). The frontal extends posteriorly to meet the parietal at the margin of the pineal foramen, a condition observed in SMNS 16812 and *Hydrorion* (Groβmann, 2007), but differing from that observed in *Plesiosaurus* (Storrs, 1997) and *Thalassiodracon* (Storrs and Taylor, 1996). The widest part of the frontals is behind the prefrontals where they form part of the border of the orbits. The orbits are separated by 34 mm of bone at their closest approach. Posteriorly the frontal only just makes contact with the pineal foramen. The specimen is damaged in this region, and the pineal foramen and most posterior part of the frontal have been elevated and displaced about 6 mm to the left (Fig. 1A). Posterolaterally the frontal is overlain by the postfrontal, and posteriorly the frontal meets the parietal at a convoluted suture. It does not enter into the temporal fenestra, as is the case in a few Jurassic plesiosauroids: *Seeleyosaurus, Hydrorion* (Groβmann, 2007) and some Cretaceous plesiosauroids: *Callawayasaurus* (Druckenmiller and Russell, 2008; Sato, 2002).

The parietals meet in the dorsal midline to form a thin sagittal crest between the temporal fossae, and suture posteriorly with the squamosals. Anteriorly the parietal sutures with the frontal and makes contact with both the postfrontal and the postorbital (Fig. 1A). They form almost the entire 16 mm long pineal foramen border, the frontals making only a very small anterior contact. The presence of the pineal foramen is consistent with Jurassic plesiosauroids (*Plesiosaurus*, *Seeleyosaurus, Hydrorion, Thalassiodracon*; Storrs, 1997, Groβmann, 2007; Storrs and Taylor, 1996), except *Occitanosaurus* (Bardet et al., 1999; contra Smith et al., 2012) and many Cretaceous Elasmosauridae (*Futabasaurus suzukii* Sato et al., 2006, *Libonectes morgani* [Welles, 1949] Carpenter, 1997, *Styxosaurus snowii* [Williston, 1890] Welles, 1943, *Terminonatator ponteixensis* Sato, 2003, *Tuarangisaurus keyesi* Wiffen and Moisley, 1986) in which the pineal foramen is absent. Its loss is considered as a synapomorphy of the Upper Cretaceous Elasmosauridea and polycotylids by Carpenter (1997) but recent phylogenetic data sets find that the pineal foramen is lost independently in some Cretaceous Elasmosauridae and some Polycotilidae (O'Keefe, 2001; Druckenmiller and Russell, 2008; Ketchum and Benson, 2010). Nevertheless, in *Hydrotherosaurus* Welles, 1943, the pineal foramen is anteroposteriorly long and slit-like. Such morphology could lead to misinterpreting its absence in transversely crushed skulls. A reexamination of some Cretaceous key taxa is thus needed, but is beyond the scope of this paper. The parietal extends deep to the temporal musculature and unites with braincase elements: anteroventrally it meets the dorsal end of the epipterygoid, posteroventrally it unites with the fused supraoccipital and prootic, and between these it forms a 7 mm upper border to a gap separating these elements (Fig. 3A). In occipital view (Fig. 3B) the suture of left and right parietals is visible ventral to the united squamosals and dorsal to the supraoccipital.

The postfrontal is sub-triangular in shape (Fig. 1A), forms the posterior border of the orbit, and overlies the frontal anteromedially. It sutures with the parietal posteromedially and overlies the postorbital posteriorly and laterally. Its contact with the orbit margin is as in other Jurassic plesiosaurs, and differs from some Cretaceous Elasmosauridae in which the postfrontal is excluded from the orbit margin by a postorbital-frontal contact. Druckenmiller and Russell (2008) observed that the postfrontal is excluded from the orbital margin in *Hydrotherosaurus alexandrae* only whereas Kear (2005) and O'Keefe (2001) found this character in *Callawayasaurus*, *Libonectes* and *Styxosaurus*, and Vincent et al. (2011) in *Zarafasaura oceanis*.

The postorbital is a relatively large triradiate element as in *Plesiosaurus* (Storrs, 1997), *Seeleyosaurus* (Groβmann, 2007) and *Thalassiodracon* (Storrs and Taylor, 1996). The anterior (orbital) process meets the maxilla forming part of the posterolateral border of the orbit, and ventrally is overlain by the jugal. It thus separates the maxilla and postfrontal on the orbital margin, and widely excludes the jugal from contact with the orbit. The posterolateral process is extensively overlain externally by the jugal and squamosal, and appears to exclude the jugal from the deep surface of the temporal bar. The anterior and posterolateral processes expand into an extensive posteromedial process which forms a deep anterior wall to the temporal fossa, and meets the ectopterygoid ventrolaterally (observable on the right side) and the parietal medially. It is thin in this region and has been damaged on both sides, but its extent is beyond question. Kear (2005; character 9) observed an absence of contact between squamosal and postorbital in *Callawayasaurus*, *Libonectes, Styxosaurus* and *Eromangasaurus australis* (Sachs, 2005) Kear, 2007 whereas Druckenmiller and Russell (2008; character 21) states that this contact is uncertain in *Callawayasaurus* and *Libonectes*. The postfrontal-postorbital complex of *Microcleidus* is close to that observed in *Plesiosaurus*, *Seeleyosaurus* and *Hydrorion* (Storrs, 1997; Groβmann, 2007). Nevertheless, in *Microcleidus*, the postorbital contacts the posterolateral orbit margins only; whereas in these three other species, the postorbital participates in the posterior border of the orbit.

The jugal is a quadrilateral element, 5 cm by 2 cm, overlapping the postorbital dorsally, the maxilla anteriorly and ventrally, and meeting the squamosal posteriorly at a convoluted suture. It narrowly separates the maxilla from the squamosal at the ventral cheek margin. Its undisturbed arrangement is best shown on the right side (Fig. 2B). It is excluded from the orbit margin by the maxilla and postorbital, as in *Occitanosaurus* and *Hydrorion*, thereby differing from most other Jurassic plesiosauroids and Cretaceous Elasmosauridae, in which the jugal forms the ventral margin of the orbit.

The squamosal has a triradiate structure. On the left side the quadrate ramus is missing, and the posterior part of the anterior ramus is damaged (Fig. 2A). The right anterior ramus is almost complete, slightly damaged, with a fracture hole through its

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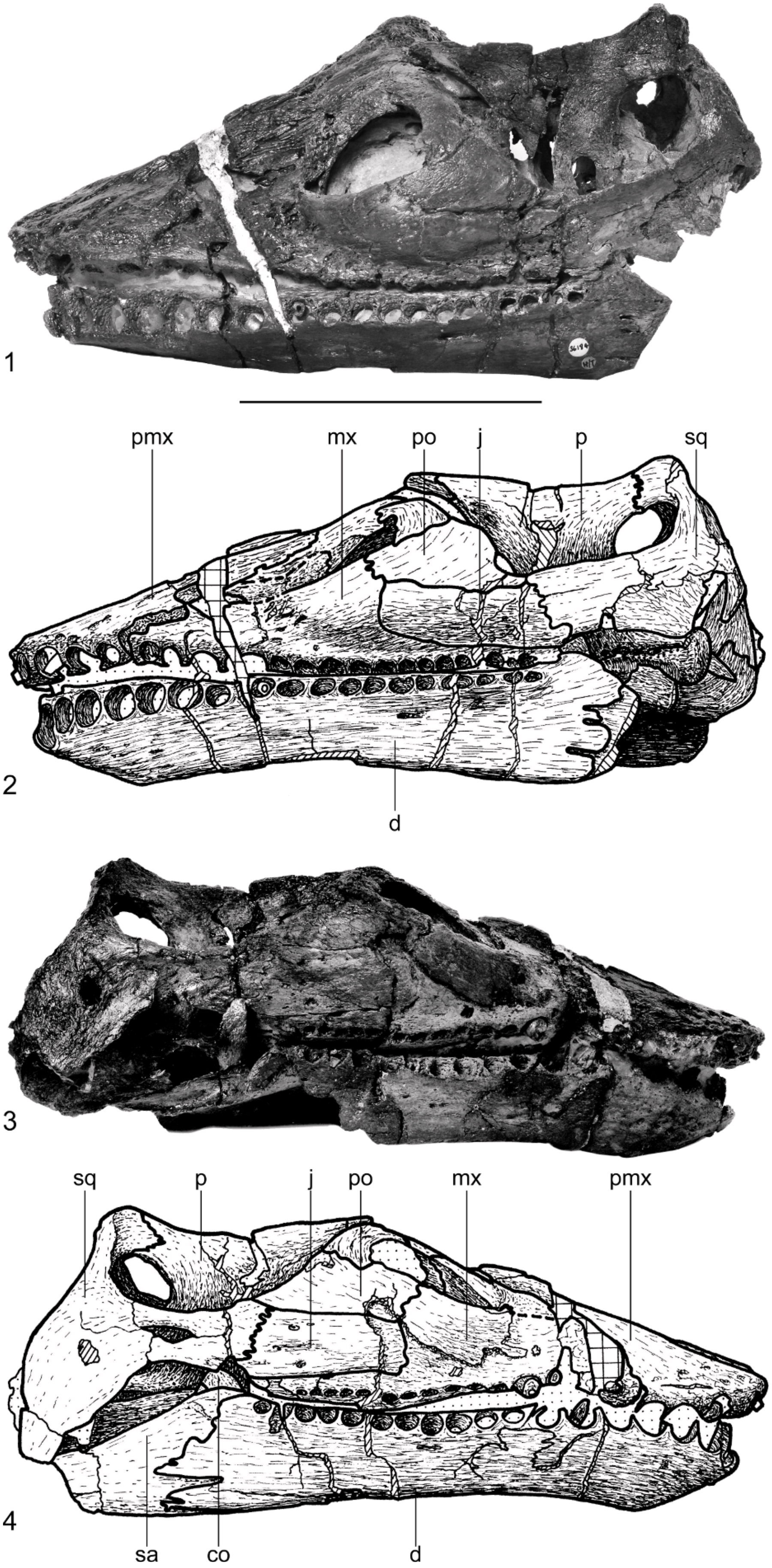
FIGURE 2—Skull of *Microcleidus homalospondylus*, NHMUK 36184. *1*, *2*, photograph and interpretation of the left lateral view; *3*, *4*, photograph and interpretation of the right lateral view. The areas with dots correspond to areas filled with matrix. Scale bar=10 cm. Abbreviations: co=coronoid; d=dentary; j=jugal; mx=maxilla; p=parietal; pmx=premaxilla; po=postorbital; sa=surangular; sq=squamosal.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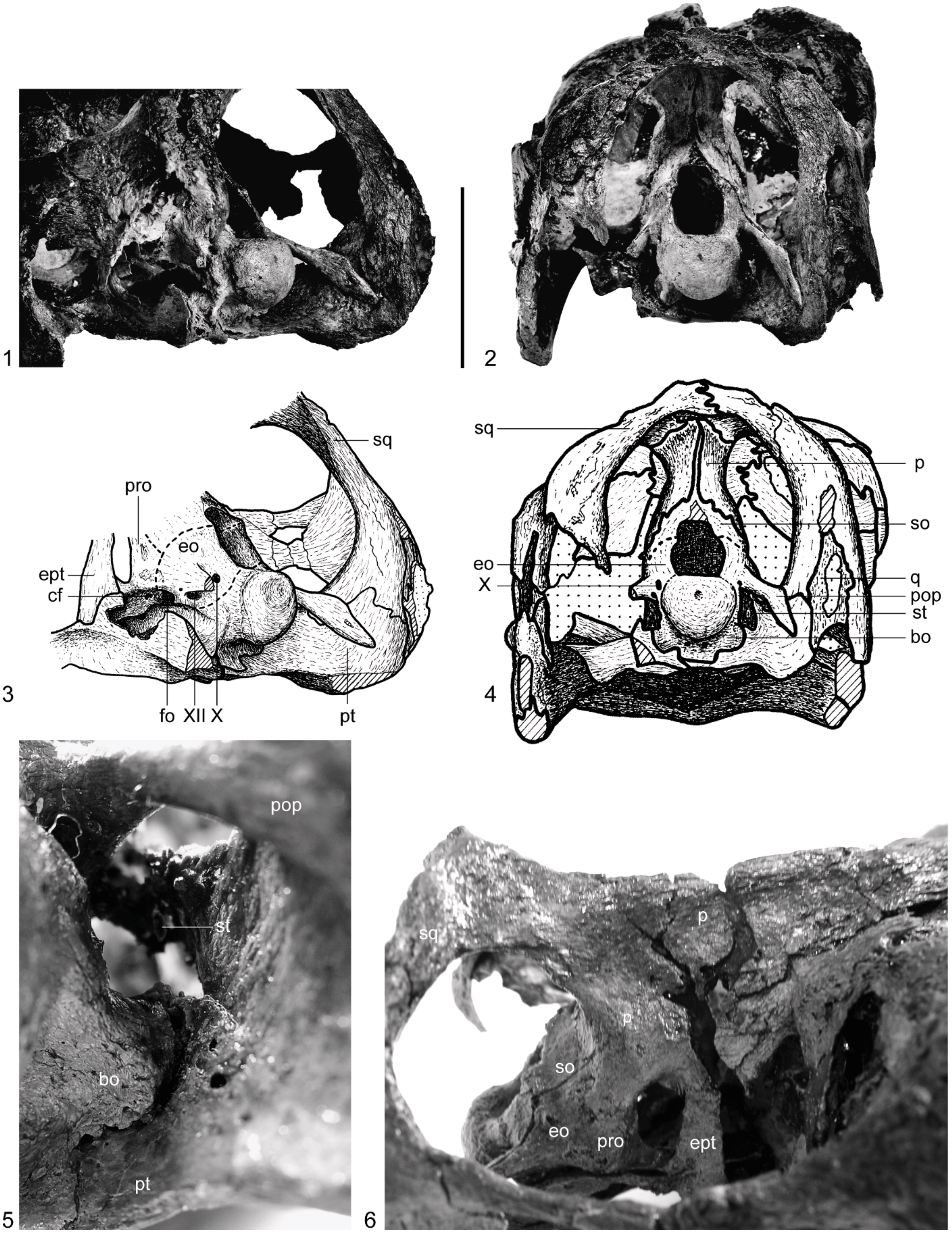

FIGURE 3—Skull of *Microcleidus homalospondylus*, NHMUK 36184. *1*, *3*, photograph and interpretation of the posterolateral view; *2*, *4*, photograph and interpretation of the occipital view; *5*, close-up photography of the stapes; *6*, close-up photography of the right side of the temporal region. The areas with dots

center. The left and right post-temporal bars of the squamosals meet at a dorsal midline suture which extends posteriorly onto the occiput. The squamosal sutures anteriorly with the parietal and posteriorly forms a bulb (see Druckenmiller and Russell, 2008; character 34) as in *Plesiosaurus*. The quadrate ramus on the right divides to enclose the quadrate, a fragment of which is visible posteriorly. Medial to the quadrate, the squamosal is overlain by the quadrate ramus of the pterygoid, and the paroccipital process of the fused exoccipital-opisthotic rests largely upon the pterygoid rather than the squamosal (Fig. 3A). The paroccipital process does not form an articular head, nor does the squamosal form a concave facet for articulation. Instead, the squamosal and pterygoid form an extensive posteromedial surface upon which lies the flattened attached paroccipital process. The posterior parts of the pterygoid and squamosal are missing, matrix remains between the dorsal and lateral flanges of the quadrate ramus of the squamosal, and only a thin fractured fragment of the right quadrate has been preserved; and so it is not possible to determine the morphology of meeting of the quadrate with the quadrate ramus of the pterygoid.

Despite the fact that the external nares are not observable because of the presence of a fracture running across the rostrum, their original location can be accurately estimated. They are close to each other and are only separated by the narrow dorsomedial processes of the premaxillae.

The orbits are well preserved, ovoid in shape and dorsolaterally orientated. Scleral ossicles are present: one is visible in the left orbit as prepared (Fig. 1A); and another was removed from an orbit during preparation of the specimen. Scleral ossicles are not preserved in the majority of plesiosauroid skulls, but are known from *Styxosaurus* (KUVP 1301; Williston, 1903; Sato, 2003) and *E. australis* (Kear, 2005).

The temporal fossa is proportionally large compared with the orbits and quadrangular in shape. The temporal fossa is estimated to have occupied about 25 percent (Sato [2002] proposed a ration of 32%) of the skull length (tip of the snout to the occipital condyle). A similar or lower ratio is observable in Jurassic taxa (close ratio: *Muraenosaurus*, *Occitanosaurus*, *Seeleyosaurus*; lower ratio: *Plesiosaurus* and *Hydrorion*). However, the temporal fossa of Upper Cretaceous plesiosauroids generally occupies more than 35 percent (Sato, 2002, 2003; Sato et al., 2006). Thus, Cretaceous Elasmosauridae may have possessed more powerful jaws than those of basal plesiosauroids. The comparative size of the temporal fenestra and skull length in Pistosauroidea resembles Elasmosauridae: e.g., in *Augustasaurus* the ratio is 38 percent (Sato, 2002), whereas that of Nothosauroidea resembles Jurassic plesiosaurians. A change in relative size of the temporal fenestra would lead to a reorganization of the bones surrounding this structure. Our hypothesis is that the morphology or relationships between skull roofing bones is being influenced by the relative size of the temporal fenestra (e.g., frontal-temporal fenestra contact present in Pistosauroidea and Cretaceous Elasmosauridae and absent in Nothosauroidea and Jurassic plesiosaurians; difference in the thickness of the postorbital bar between Jurassic forms and Cretaceous Elamosauridae).

Palate.—Preparation of the specimen in ventral view has revealed the palatines, ectopterygoids and pterygoids, but the vomers and internal nares are still largely hidden by matrix (Fig. 1B). The palatines are large, elongated elements, almost all of the left element being visible (the right is obscured laterally since the mandible has been left in situ as preserved). Laterally it overlaps the maxilla, medially overlies the lateral part of the anterior process of pterygoid, anteriorly it is seen meeting the posterior border of the vomers (the only part of the latter that is visible), and posteriorly it contacts the ectopterygoid. The internal nares being hidden by matrix in palatal view, the presence of a contact between the palatines and the internal nares cannot be attested.

The ectopterygoids appear as small component elements, each suturing anteriorly with the maxilla, anteromedially with the palatine and medially and posteriorly with a thickened part of the anterior process of the pterygoid. It does not present any prominent, ventrally projecting structure (ectopterygoid boss) as it is the case in *Plesiosaurus* and Triassic sauropterygians (e.g., *Cymatosaurus* Fritsch, 1894, *Augustasaurus* Sander et al., 1997; Druckenmiller and Russell, 2008).

The pterygoids are large and complex bones forming about half the palatal area and extending backwards beneath and lateral to the braincase. The right element is largely complete whereas the left is missing the dorsal margin lateral to the braincase and the posterior region of the quadrate ramus. The long anterior (palatal) ramus forms a dorsoventrally flattened plate which meets its opposite in the palatal midline and is overlain squamously by the palatine, behind which it sutures with the ectopterygoid. At the posterior edge of the palate (which is level with the pituitary fossa of the basisphenoid above) the pterygoids are separated in the midline by the parasphenoid. Laterally each pterygoid forms the thickened anterior margin of the subtemporal fossa and wraps around the medial and posterior margins of the ectopterygoid. Moving posteriorly, the pterygoid develops dorsally into a vertically-orientated flange, curved in shape, which runs posteriorly, forming the medial boundary of the subtemporal fossa and becoming the quadrate ramus. It is not possible to determine the relationship of this ramus to the quadrate, since the quadrate is missing and there remains much matrix within the right quadrate ramus of squamosal where it was housed. The union of pterygoid and quadrate was probably hidden by the extensive overgrowth of this area by the squamosal. The quadrate ramus of the pterygoid produces a ventromedial flange which extends beneath the basioccipital and sutures with its opposite in the midline (Fig. 1B). This structure has been observed in pistosauroids (e.g., *Yunguisaurus liae* Sato et al., 2010), few plesiosauroids (*Occitanosaurus* and probably *Hydrorion*), and pliosauroids (e.g., *Liopleurodon* Sauvage, 1873; Noè, 2001; *Peloneustes*, Ketchum and Benson, 2011; figures by Andrews, 1913; see also Druckenmiller and Russell, 2008; Ketchum and Benson, 2010). Posteriorly to the posterior interpterygoid vacuities, there is a small foramen that pierced the posterior part of the pterygoids at the level where they meet each other in a serrated medial suture. This foramen is also observable in some Lower Jurassic taxa (e.g., *Occitanosaurus*; Bardet et al., 1999), some species of *Hauffiosaurus* (Benson et al., 2011a; see Smith et al., 2012). In *Muraenosaurus*, this foramen lies at the level of the suture between the basioccipital and basisphenoid and is considered as a remnant of the embryonic fenestra basicranialis posterior (Maisch, 1998).

The epipterygoid is a thin and flat element with the appearance of being entirely of intramembranous development. It forms a bar anterior to the prootic from which it is separated by a gap (Fig. 3A). Dorsally it sutures with the ventral surface of the parietal.

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correspond to areas filled with matrix. Scale bar=5 cm. Abbreviations: bo=basioccipital process; cf=*canalis falopii*; eo=exoccipital-opisthotic; ept=epipterygoid; fo=fenestra ovalis; p=parietal; pop=paroccipital process; pro=prootic; pt=pterygoid; sq=squamosal; so=supraoccipital; st=stapes; X=jugular foramen; XII=foramen for branches of hypoglossal nerve.

Ventrally it is associated with the basal process of basisphenoid and the pterygoid. Both pterygoid and epipterygoid are thin at this site, and it is not clear how they met the basal process. Above the basal process the epipterygoid is separated from the anteroventral process of the prootic by a space, the cavum epiptericum, for the trigeminal (V) cranial nerve and ganglion.

Braincase.—The basioccipital, exoccipital-opisthotics, supraoccipital, prootics, basisphenoid and parasphenoid are all fused together, which probably indicates that this specimen was an old individual (sensu Brown, 1981); but evidence remains for the sites of fusion of these elements. Additionally, the pterygoids and epipterygoids are well preserved with sutures traceable; and the proximal half of the right stapes is preserved in situ outside the fenestra ovalis (fenestra vestibuli).

The basioccipital appears to form the entire occipital condyle. The condyle is not spherical but is flattened dorsally and slightly pointed ventrally (Fig. 3B). The surface of the occipital condyle is pitted, suggesting that it was covered by cartilage (Maisch, 1998). The stout processus pterygoideus of the basioccipital faces ventrally and unites with the pterygoids. This process corresponds to a modified basioccipital tuber identical in shape to that of *Muraenosaurus* (Maisch, 1998), but probably formed by both basioccipital and basisphenoid in *Microcleidus*, whereas it is formed by the basioccipital only in *Muraenosaurus* (Maisch, 1998). The ventral aspect of the basioccipital is of unusual appearance: instead of resembling a cervical vertebra with midventral ridge between paired nutritive foramina then forming the basioccipital tubera laterally, this region is entirely covered by the pterygoids, which hide the basioccipital in palatal view (Fig. 1B). The contact between the pterygoids and the processus pterygoideus seems to be un-sutured and as proposed by Maisch (1998) for *Muraenosaurus,* possibly permitting relative movement between these two bones. In occipital view (Fig. 3A, 3B) the ventral area of the basioccipital is produced into a posteriorly-extending flange for union with the two pterygoids beneath. Thus, beneath the occipital condyle a concave posteriorly-orientated surface is formed, bounded above by the condyle, laterally by the basipterygoid processes and ventrally by this median pterygoid flange. The concave surface is pierced by two nutritive foramina, the left being slightly larger than the right. The occipital condyle appears to be well developed differing from those of *Thalassiodracon* (Benson et al., 2011b, fig. 4) or *Plesiosaurus*, in which the occipital condyle is a shallow dome with no groove between the condyle and the body of the basioccipital (O'Keefe, 2006).

The exoccipital-opisthotic elements are fused and show the usual quadrilateral structure. They define the lateral margin of the foramen magnum. There is a large jugular foramen beneath the base of the paroccipital process (for nerves IX, X and XI in addition to the jugular vein) with behind it a smaller hypoglossal foramen (for XII). Plesiosauroidea usually exhibit two foramina whereas Pliosauroidea have only a single foramen in the lateral surface of the exoccipital-opisthotic (Benson et al., 2011b). In front of the jugular foramen is another much smaller foramen, presumably a nutritive foramen. Anteriorly the opisthotic forms the posterior margin of the fenestra ovalis. This character differs from the hypothesis proposed for *Muraenosaurus* by Maisch (1998) for which the opisthotic did not contribute to the fenestra ovalis. On the left side this region is clear of rock matrix, and the entire structure of the fenestra ovalis can be seen, whereas on the right side the broken very thin shaft of the right stapes became revealed in situ during preparation (Fig. 3B, 3E), and so the rock supporting this fragile bone was preserved. The paroccipital process is long and slender (length 35mm on the right, incomplete on the left), and becomes spatulate distally, as in some pliosauroids (Andrews, 1913; Smith and Dyke, 2008) and is applied to the medial surface of the squamosal rather than forming a head and fossa articulation with the squamosal or quadrate (Fig. 3A).

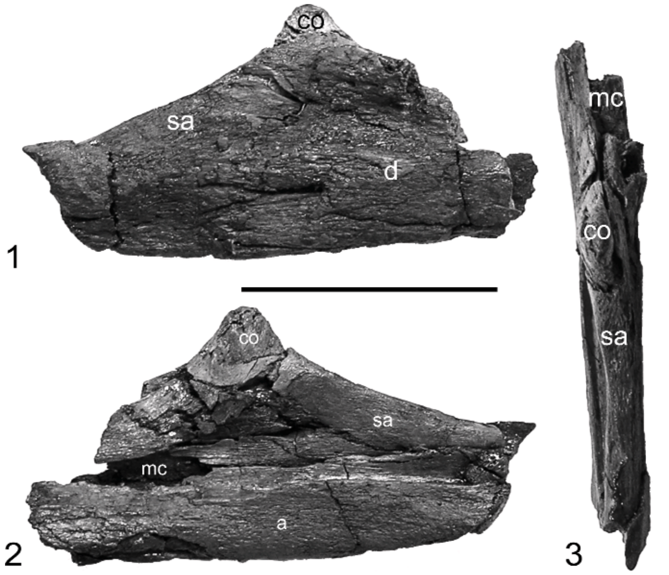

FIGURE *4*—Mandible of *Microcleidus homalospondylus*, NHMUK 36184. *1–3*, photographs of the lateral, lingual and dorsal surfaces, respectively. Scale bar=5 cm. Abbreviations: a=angular; co=coronoid; d=dentary; mc=Meckelian canal; sa=surangular.

The supraoccipital meets the parietals anterodorsally, the prootics anteroventrally and the exoccipital-opisthotics posteroventrally. There is no foramen between supraoccipital and parietals, the specimen differing in this respect from all English Upper Jurassic skulls previously studied by Brown (1981, p. 260). It is not slightly keyhole shaped as in *Libonectes* (Druckenmiller and Russell, 2008). Moreover, it probably does not present a process on the midline projecting ventrally into the foramen magnum as *Thalassiodracon* (Storrs and Taylor, 1996) does, but this area is abraded in *Microcleidus* precluding any conclusion.

The prootic is visible in oblique occipital view (Fig. 3A, 3C, 3F) and is fused with the supraoccipital and the exoccipital-opisthotic; but the suture dorsally with the parietal can still be traced. It is also partially fused anteroventrally with the basisphenoid. The foramen for VII is close to the border of the fenestra ovalis; there is an anteroventral process (see below); and a suture with the parietal was not envisaged in *Muraenosaurus* (Brown, 1981). The prootic forms the dorsal anterolateral margin of the fenestra ovalis, only the lateral surface of which could be examined. The foramen for VII (canalis fallopii or canalis nervi facialis) lies just anterior to the fenestra ovalis and is of similar size to the hypoglossal foramen. The anterior margin of the prootic forms a narrow ridge from which the meninges were reflected forwards; and additional support was given by an anteroventral process of the prootic resting upon the lateral margin of the basisphenoid. This arrangement of prootic and basisphenoid can be seen by looking between the left prootic and epipterygoid at the inner ventral end of the right prootic, where the line of union between prootic and sphenoid is clearly demonstrated. The tab-like anteroventral process of the prootic observed in *Microcleidus* is absent in derived plesiosauroids (e.g., Brown, 1981; Maisch 1998: *Muraenosaurus*; Wegner, 1914: *Brancasaurus*; Carpenter, 1997: *Libonectes*) and Polycotylidea (Sato et al., 2011: *Dolichorhynchops osborni* Williston, 1902, *Georgiasaurus* [Otschev, 1976], Otschev, 1977). It is present in pliosauroids, some basal plesiosauroids and Triassic sauropterygians (see Ketchum and Benson, 2011; Sato et al., 2011) and likely represents the primitive condition. The right prootic is fused to the basisphenoid only in its midpoint, being separated from it by once cartilage-filled fissures running posteriorly to the fenestra ovalis and anteriorly beneath the anteroventral process. This anterolateral process is as long as the main body of the prootic is wide, and the element therefore differs significantly from that described (Brown, 1981) for *Muraenosaurus*.

The basisphenoid and the braincase floor can be seen in the specimen through the various gaps between elements and also from the palatal aspect. The line of the partially-fused spheno-occipital synchondrosis lies exactly level with the center of the fenestra ovalis, and both basioccipital and basisphenoid contribute to the foramen's margins. Anterior to the fenestra ovalis the basisphenoid unites with the prootic. The paired carotid foramina perforate the cranial base medial to the anterior edge of the body of the prootic (the right is patent, the left blocked with matrix), and the pituitary fossa lies in front of these. The lamellar bone of the cranial cortical plate under and behind the pituitary fossa forms a very thin forward-projecting shelf, with a large space beneath it: this space may be a post mortem defect due to breakdown of cancellous bone rather than a sphenoidal sinus. The floor of the pituitary fossa is shallowly concave from left to right. Behind it the posterior clinoid processes are very poorly developed; but in front a well developed delicate and slender anterior clinoid process is preserved on the right side, tapering to 1 mm wide at its posterior tip. The left side is still obscured by rock matrix. Below this region, anterior to the carotid foramina, the basal processes of the basisphenoid extend ventrolaterally to give support to the pterygoids in the region of the anterior quarter of the interpterygoid vacuities. The bone here is thin-walled and highly cancellous, with some damage.

In ventral view, the suture between the parasphenoid and the basisphenoid is not visible. Nevertheless, in ventrolateral view, at the level of the posterior interpterygoid vacuities, the presence of a sub-horizontal furrow could be interpreted as the suture between the parasphenoid (the keeled bone ventrally exposed) and the basisphenoid (situated dorsally). The parasphenoid sutures anteriorly with the left and right pterygoids, between which it forms part of the palatal surface. Behind this suture it narrows to a crest of bone which separates the two interpterygoid vacuities, and is fused to the ventral surface of the basioccipital between the carotid canals. The crested parasphenoid is usually found in pliosaurids (e.g., Taylor and Cruickshank, 1993), leptocleidids (e.g., Druckenmiller and Russell, 2008), polycotylids (Druckenmiller, 2002), elasmosaurids (*Eromangasaurus, T. keyesi*, *Libonectes* and *Callawayasaurus*) whereas the ventral surface of this bone is flat in Jurassic plesiosaurs (*Lusonectes* Smith et al., 2012, *Hydrorion*, *Plesiosaurus*, *Seeleyosaurus* and *Muraenosaurus*) except for *Occitanosaurus*. This central ridge of the parasphenoid dissipates posteriorly, becoming enlarged and rounded, a condition not observed in other plesiosaurians. Behind this it again sutures with left and right pterygoids where they cover the ventral surface of the basioccipital.

The course of the internal carotid artery and its anterior, ophthalmic or orbital branch, are clearly shown by grooves on the braincase elements (Figs. 1B, 3A). The internal carotid artery courses forwards and upwards between the basioccipital and pterygoid into the infratemporal fossa, grooving the dorsal surface of the basipterygoid process of basioccipital and the ventral part of the opisthotic until coming to lie below and medial to the fenestra ovalis. It continues forwards and slightly downwards, grooving the basioccipital medially and the prootic dorsally until it reaches and passes through the carotid canal. It divides to give the ophthalmic branch immediately external to the carotid canal, and this branch continues forwards lateral to the parasphenoid and above the pterygoid. It grooves the basisphenoid dorsally, the region of union of basisphenoid and parasphenoid medially and the basal process of basisphenoid laterally, then disappears dorsal to the palate above the anterior sutures of parasphenoid and pterygoid.

Mandible.—The general shape is similar to that of *Muraenosaurus* (Andrews, 1910; Brown, 1981; Evans, 1999) or *Seeleyosaurus* (Groβmann, 2007). Posterior parts (articular and retroarticular processes) are missing (Fig. 2A, 2B) and the surangular is incomplete.

The dentary sutures against the surangular by a squamous overlap (Figs. 2A, 2B, 4A). It is shallowest under the ninth and tenth teeth, and becomes gradually higher dorsoventrally in both anterior and posterior directions. There is neurovascular foramina ornament anteriorly on the external surface. The mandibular symphysis is 3.9 cm long on the anteroventral surface and comprises probably only the dentaries. The symphysis is long relative to the overall length of the skull (17%), as in *E. australis* (23% of skull length), *Libonectes* (18.1%), *Plesiosaurus* (18.4%) whereas others specimens have a symphysis equal or shorter than that of NHMUK 36184: *Hydrotherosaurus* (16%), *Terminonatator* (15%), *T. keyesi* (6%) (Druckenmiller and Russell, 2008; Kear, 2007). Kear (2005) considers the mandibular symphysis of *M. homalospondylus* enforced as for *Callawayasaurus*, *E. australis*, *Libonectes*, *Styxosaurus* and *Terminonatator*. There is no lateral expansion at the symphysis, and there are four pairs of dentary teeth above the symphysis, resembling other Jurassic and Cretaceous taxa which bear less than 8 mandibular symphysial teeth: *Hydrotherosaurus* (3), *Libonectes* (4), *Muraenosaurus* (4 to 5), *Plesiosaurus* (4), *Terminonatator* (3 to 4) (Druckenmiller and Russell, 2008). The dentary exhibits a very distinctive sculpture of anterior ridges and furrows, and bear a keel on the ventral surface of the mandibular symphysis.

Some fragments of splenials adhere to the medial surface of the dentary lingually and in the middle. The angular is of the usual form and extends on the left side to 5 cm behind the posterior cleft of mandible, adhering to the dentary (as in *Cryptoclidus*). An unusual feature is the coronoid process, present on the right side (Figs. 2B, 4). The coronoid is about 13 mm long mesiodistally, and about 4 mm bucco-lingually. Its top edge thus forms the rounded summit of the coronoid process which is distinctly high and pointed. Cruickshank (1994a) states that absence of the coronoid is a character of plesiosauroids; but his hypothesis is not supported with the present observation. O'Keefe (2001) states that the coronoid is present in all taxa but *Kimmerosaurus*, but probably very thin and often lost. This hypothesis seems to be confirmed here as the coronoid of *Microcleidus homalospondylus* is reduced. The Eusauropterygia *Simosaurus gaillardoti* Meyer, 1842, the pachypleurosaurs *Serpianosaurus mirigiolensis* Rieppel, 1989 and *Neusticosaurus pusillus* Seeley, 1882 and the Pistosauroidea *Yunguisaurus liae* possess a coronoid (Rieppel 1989, 1994; Sander, 1989; Cheng et al., 2006; Druckenmiller and Russell, 2008), so that the presence of a coronoid is probably plesiomorphic within Plesiosauria. The surangular or prearticular wraps around the lingual surface of the dorsal part of the coronoid process (Fig. 4B, 4C), and the small coronoid element is sandwiched between it and the angular at the highest point. Posterior parts of the mandible (articulation and retroarticular proc) are missing from both sides.

The surangular is only partially preserved. It is a thin bone forming the dorsal surface of the mandible anterior to the coronoid eminence. Anteriorly, it contacts the dentary laterally

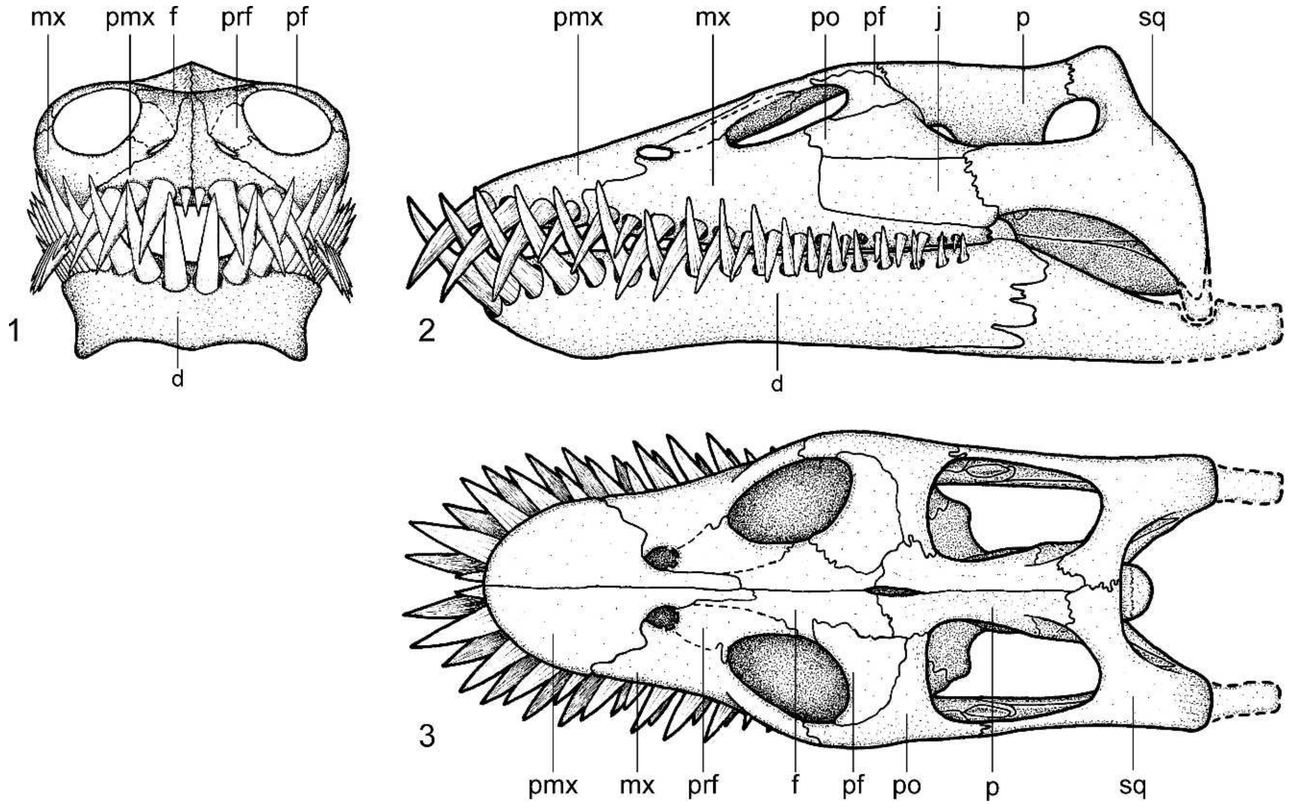

FIGURE 5—Skull of *Microcleidus homalospondylus*, NHMUK 36184. *1–3*, reconstructions of the anterior, lateral, and dorsal views, respectively. Abbreviations: d=dentary; f=frontal; mx=maxilla; p=parietal; pf=postfrontal; pmx=premaxilla; po=postorbital; prf=prefrontal; sq=squamosals.

and the coronoid medially. Posteriorly, it deepens over the Meckelian canal, forming its roof.

The angular forms the bulk of the ventral part of the posterior area of the mandible. Anteriorly, it is prolonged as a narrowing process, forming the ventral surface of the coronoid eminence, and joins the dentary on the lateral side of the mandible.

Dentition.—Except for a few tooth fragments remaining in the alveoli, there are no well-preserved teeth. The premaxilla contains sockets for five teeth. Jurassic plesiosaurs usually bear five pairs of premaxillary teeth. This number is variable in Cretaceous Elasmosauridae, ranging from five pairs in *Callawayasaurus* (Welles, 1962), *Hydrotherosaurus* (Welles, 1943), *Libonectes* (Carpenter, 1997) and *T. keyesi* (Wiffen and Moisley, 1986), to nine or seven premaxillae teeth in *Terminonatator* and *E. australis*, and up to 10–13 in each premaxilla for *Aristonectes parvidens* Cabrera, 1941. The first premaxillary alveolus of *Microcleidus* is very small compared to the others but the tooth size difference between the first premaxillary alveolus and the following ones is greater than that observed in *Plesiosaurus* (Storrs, 1997). The first is very small (diameter 4 mm), the second to the fourth are large with the third and the fourth as large as equivalent teeth in the lower jaw, then the fifth is much smaller (diameter 7 mm) (restored in Fig. 5A). The first premaxillary tooth lies medially to the first dentary tooth as in *Plesiosaurus* (Storrs, 1997; Owen, 1865, pl. 3, fig. 3). The same variation of size is observable in *Occitanosaurus* and *Seeleyosaurus*, for which the first teeth are the smallest, the fourth the largest and the fifth small. In *Hydrorion* and *Plesiosaurus*, similar variation is observable but the third is the largest.

Behind the suture there are 15 or 16 sockets for maxillary teeth on the left (the last one or two are an enlarged broken hole, we cannot be certain if one tooth or two were present here), and there appear to have been 16 maxillary teeth on the right. Therefore, there are 20 or 21 teeth in the upper dental arch, as in *Hydrorion*, *Seeleyosaurus* and *Muraenosaurus*. Socket size distribution in maxillary teeth is best seen in the left side: the first maxillary tooth socket is 6 mm in diameter, the second, 7 mm, the third, 9 mm, the fourth, similar or slightly smaller (spoilt by a plaster repair), the fifth, 7–8 mm, then reducing to 5 mm by the twelfth; and finally using the better-preserved posterior sockets of the right side, they reduce down to 3.5 mm diameter in the sixteenth maxillary tooth socket. The distribution is similar to *Muraenosaurus*, *Seeleyosaurus* and *Hydrorion*. Posteriorly, the thin maxilla bone rests squamously on the ectopterygoid and the jugal for support. There are 18 alveoli on each side of the dentary, though nearly all teeth are missing. The specimen YM 502, which preserves only the dentary, possesses 19 teeth. Socket size grades very evenly from 10 mm diameter anteriorly to 7 mm at 11th to 4 mm at 18th. Anterior sockets are oval, being 13 mm vertical (labio-lingual) height.

DISCUSSION

Comparisons.—Comparison with basal Sauropterygia and Jurassic and Cretaceous plesiosaurians indicates that *Microcleidus homalospondylus* (NHMUK 36184) presents many plesiomorphic characters (frontal midline contact, postfrontals-orbit margin contact, postorbitals-squamosal contact, presence of a pineal foramen) shared with the Jurassic forms (except *Occitanosaurus*, which does not possess a pineal foramen [Bardet et al., 1999] but see Smith et al., 2012), with basal Sauropterygians such as *Augustasaurus* (Rieppel et al., 2002), *Pistosaurus* (Sues, 1987), *Yunguisaurus* (Cheng et al., 2006), *Corosaurus* (Storrs, 1991) and *Simosaurus* (Rieppel, 1994) and with most of the pliosauroids (e.g., *R. cramptoni*, *R. zetlandicus*, *Simolestes*, *Pliosaurus, Peloneustes*; Smith and Dyke, 2008, Vincent and Smith, 2009, Noè, 2001, Taylor and Cruickshank, 1993, Andrews, 1910, Ketchum and Benson 2011; except for the first character cited).

In contrast to the skull roof, the palatal aspect of *M. homalospondylus* is close to that of Cretaceous Elasmosauridae. *Microcleidus homalospondylus* does not present an anterior interpterygoid vacuity, as in Cretaceous Elasmosauridae and the Jurassic form *Hydrorion*. The parasphenoid is keeled, a character observed in Cretaceous Elasmosauridae and *Occitanosaurus* but absent in other Jurassic forms. The pterygoids meet behind the posterior interpterygoid vacuities in *M. homalospondylus* and in Cretaceous Elasmosauridae, but not in Jurassic plesiosauroids except *Hydrorion*. A contact of the pterygoids posteriorly is also present in some Leptocleidia (e.g., *Umoonasaurus demoscyllus*, *Leptocleidus capensis*; Kear et al., 2006, Cruickshank and Fordyce, 2002) and most of pliosauroids (e.g., *Meyerasaurus*; Smith and Vincent, 2010). The plesiomorphic condition for the plesiosaurian palate is shown by OUMNH J.10337 (*Thalassiodracon* in O'Keefe, 2006 but see Benson et al., 2011b) and *Plesiosaurus*: both taxa possess open palate (O'Keefe, 2001), a character probably derived from the plesiomorphic condition (closed palate of basal pistosaurians like *Augustasaurus* and *Pistosaurus*). In some plesiosaurian taxa the closure of the palate should therefore be reversal (O'Keefe, 2001). *Microcleidus homalospondylus* possesses a closed palate, reversal character, as in Cretaceous Elasmosauridae: the anterior interpterygoid vacuity is absent and the pterygoids meet behind the posterior interpterygoid vacuities. The ventromedial flange of the quadrate ramus of the pterygoid present in *Microcleidus* is not observed in other plesiosauroids. This character is nevertheless present in pliosaurids (e.g., Andrews, 1910; Noè, 2001) and some pistosauroids, and has been used as a phylogenetic character (e.g., O'Keefe, 2001; Ketchum and Benson, 2010). In this regard, this character could be interpreted as plesiomorphic.

Among Jurassic forms, *Microcleidus*, *Occitanosaurus* and *Hydrorion* present a mix of both Jurassic plesiosaurian (including pliosauroid) and Cretaceous elasmosaurid characters. All three genera form a monophyletic clade in the more recent phylogenetical analyses (Benson et al., 2012; Groβmann, 2007; Ketchum and Benson, 2010) except that of Druckenmiller and Knutsen (2012). The uncertain phylogenetic position of *M. homalospondylus* is only one example amongst other early Jurassic plesiosaurians. In this context, the growing number of redescriptions of known Early Jurassic taxa such as '*Microcleidus*' *macropterus* (Seeley, 1865) Watson, 1911, will most probably contribute to clarify the phylogenetical relationships and early evolution of Plesiosauria. It should be noted that these three taxa have been found in three European Toarcian basins, showing that at this time the plesiosaur faunas at least were rather homogeneous.

Braincase anatomy.—The braincase structure of sauropterygians is poorly known so far. The anatomy of the nothosaurian braincase has been described in detail (Rieppel, 1994) but only a limited number of studies on the plesiosaur braincase are available: the first plesiosaur braincase description was made by Andrews (1913) for *Peloneustes*; Wegner (1914) described the braincase elements of *Brancasaurus*, Carpenter (1997) discussed the endocast of *Libonectes* and *Dolichorhynchops,* Maisch (1998) and Evans (1999) gave a detailed description of disarticulated components of the braincase of *Muraenosaurus*; Noè (2001) described the braincase organization in *Liopleurodon* and *Simolestes*, and O'Keefe (2006) described the morphology of the braincase of *Thalassiodracon*, OUMNH J.28585 ('*Eurycleidus*') and *P. wildi*; Ketchum and Benson (2011) reexamined and added valuable details of the braincase organization of *Peloneustes*; Benson et al. (2011a, 2011b) gave detailed descriptions of the braincases of *Thalassiodracon* and *Hauffiosaurus*; and Sato et al. (2011) detailed the basicranium of polycotylids. Specimen NHMUK 36184 extends our knowledge of the plesiosauroid braincase since, for the first time in an Early Jurassic specimen, it is preserved in three-dimensional articulation and is now largely free of matrix.

The exoccipital-opisthotic and prootic of the specimen are preserved in situ and reveal for the first time the relationships and positioning of these bones in the skull. Maisch (1998) suggested that in *Muraenosaurus* there was probably a thin cartilaginous layer—even in old adults—between the sutural surfaces of the exoccipital-opisthotic and the prootic. However, NHMUK 36184 shows no gap between the two bones, but instead a large connection between them. The specimen also shows the correct positioning of the prootic, which was previously considered as problematic (Maisch, 1998): his reconstruction of *Muraenosaurus* shows this bone misorientated by approximately 45°, with the contact surface for the exoccipital-opisthotic including the border of the fenestra ovalis being misinterpreted as the dorsal surface. The figure of the prootic in *Muraenosaurus* given by Brown (1981, fig. 20) is correctly orientated but the border of the fenestra ovalis misinterpreted. The border of the fenestra ovalis shared by the prootic now faces ventrally.

The epipterygoid varies in shape between the species for which it is known. In *Libonectes* (Carpenter, 1997) and *Thalassiodracon* (Druckenmiller and Russell, 2008) it is triangular whereas it is laterally compressed and rod-like in *Dolichorhynchops* (Carpenter, 1997) and NHMUK 36184. The relationships between the epipterygoid and surrounding bones can also vary substantially among the different species: in contrast to NHMUK 36184, the epipterygoids of *Libonectes* and *Dolichorhynchops* do not seem to be in contact with the parietal dorsally (Carpenter, 1997). In *Nothosaurus* the structure is very similar to that of NHMUK 36184, as the epipterygoid contacts the parietal dorsally; but this contact is broad (Rieppel, 1994) in contrast to the very thin one in NHMUK 36184.

The course of the carotid arteries in NHMUK 36184 is similar to that observed in *Muraenosaurus* (Maisch, 1998) and thereby gives support to his hypothesis concerning the emergence of the artery through the posterior interpterygoid vacuities. This structure is also observable in OUMNH J.28585 ('*Eurycleidus*') and *Thalassiodracon* (O'Keefe, 2006).

Hearing in plesiosaurs.—Welles (1962) considered absence of the fenestra ovalis and stapes as a character of the Plesiosauria. However, the presence of a fenestra ovalis has been clearly demonstrated over a range of plesiosaurian taxa (Brown, 1981; Carpenter, 1997), and a stapes in plesiosaurians has been reported for *R. zetlandicus, R. megacephalus*, *Eurycleidus, Thalassiodracon* and *Plesiosaurus* (Taylor, 1992; Cruickshank, 1994a, 1994b; Benson et al., 2011a; Storrs, 1997). Williston (1907) described a stapes in a fourth plesiosaur, *Brachauchenius* but Taylor (1992) doubted the association of the bone with the specimen. The present study thus reports one of the few undoubted plesiosaurian stapes, being the first for a plesiosauroid taxon, and which moreover is preserved in situ clearly associated at its proximal end with the fenestra ovalis. It is thin and fragile, and its distal end is missing. The presence of a stapes in the exceptionally well preserved NHMUK 36184 specimen and a range of other taxa, suggests that the supposed absence of these thin and free bones for some plesiosaur taxa might only be due to the poor preservation of the fossils. Its structure and position indicate that it could be likely functional, transmitting vibration from a superficial tympanum to the inner ear. Unfortunately, it is here only partially preserved, its posteriormost part missing, so that it is not possible to know if it reached the lateral surface of the exoccipital and sutured with it as in *Thalassiodracon* (Storrs and Taylor, 1996).

ACKNOWLEDGMENTS

We thank S. Chapman (NHM, London) for providing access to the collections within the NHM. P. Vincent's research was partly supported by the Alexander-von-Humboldt-foundation and the SYNTHESYS Project http://www.synthesys.info/ which is financed by European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area" Programme. This paper benefited from the valuable comments of R. B. Benson and A. S. Smith.

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Accepted 23 January 2013