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RE-DESCRIPTION OF A BASAL PLESIOSAUR (REPTILIA, SAUROPTERYGIA) FROM THE LOWER JURASSIC OF ENGLAND

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ABSTRACT—The specimen NHMUK 39514 comprises the cranial remains of a plesiosaur found on the Dorset coast during the middle of the ninetieth century. It was partially described and figured by Owen and variously attributed to *Plesiosaurus rostratus* (Owen) and to *Plesiosaurus conybeari* (Sollas). NHMUK 39514 is a partial braincase and mandible. It differs from all other Early Jurassic plesiosaurs known including the two species to which it was originally referred. The mandible presents several pliosauromorph characters but the specimen is identified as Plesiosauria indet. because it has several plesiomorphic characters in its braincase anatomy. This assignment will prevent the introduction of a possible chimera in future phylogenetical analyses and paleobiogeographic reconstructions.

INTRODUCTION

THE PLESIOSAURIA form a group of predatory marine reptiles whose chronostratigraphical range is Late Triassic to latest Cretaceous (Bardet, 1992; Gasparini et al., 2003; Benson et al., 2010; Sennikov and Arkhangelsky, 2010; Vincent et al., 2011). They form a significant component of the Early Jurassic marine reptile faunas in Europe, where most of the known specimens were recovered during the ninetieth and early twentieth centuries (e.g., Owen, 1838, 1840; Carte and Baily, 1863; Dames, 1895; Fraas, 1910). Despite an increasing amount of redescriptions of Early Jurassic taxa during the last two decades (e.g., Bardet et al., 1999; Smith and Dyke, 2008; Vincent and Smith, 2009; Ketchum and Smith, 2010; Vincent, 2010; Benson et al., 2011a, 2011b), the taxonomy and anatomy of Liassic plesiosaurs are still poorly understood (Benson et al., 2011a), and efforts must be maintained to increase the number of detailed anatomical descriptions.

The Lower Jurassic strata (Hettangian–basal Pliensbachian) of the Dorset coast have yielded an impressive number of marine reptile remains for more than 200 years. Most of these remains have been collected during the beginning of the ninetieth century, partly thanks to the intensive fieldwork efforts of the most famous female fossil collector, Mary Anning (Torrens, 1995). Most of the specimens are ichthyosaurs but a large number of plesiosaurian specimens have also been discovered (Benton and Spencer, 1995). Most of these plesiosaurian remains were figured and described during the ninetieth century (e.g., Conybeare, 1822, 1824; Owen, 1865) and re-examined during the last two decades (e.g., *Plesiosaurus dolichodeirus* Conybeare, 1824: Storrs, 1997). Nevertheless, some specimens still require re-examination (e.g., NHMUK 1336: *Plesiosaurus macrocephalus* Owen, 1840, and NHMUK 49202 referred to the same species by Lydekker, 1889) in light of modern anatomical knowledge on this group. As part of this revision, a re-description is presented of the partial skull remains of an Early Jurassic specimen from England. The specimen, NHMUK 39514, was partially figured by Owen in 1865 but no complete illustration and description of this specimen have been available to date. The redescription of NHMUK 39514 adds further morphological information concerning its palate and braincase, and the first information concerning the mandible. This re-examination also corrects several misidentifications in the original description by Owen and permits a discussion of the taxonomic status of the specimen.

Repositories and institutional abbreviations for material discussed in this paper are: NHMUK, Natural History Museum, London, UK; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; GPIT, Geologisch-Paläontologisches Institut der Universität Tübingen, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; OUMNH, Oxford University Museum of Natural History, Oxford, U.K; ROM, Royal Ontario Museum, Toronto, ON, Canada; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

HISTORY OF THE SPECIMEN

NHMUK 39514 was found in 1863 between Charmouth and Lyme Regis, with the type specimen of *Plesiosaurus rostratus* Owen, 1865 (NHMUK 38525, now *Archaeonectrus rostratus* (Novozhilov, 1964)). It was initially referred to *Plesiosaurus rostratus* by Owen (1865) because it was found "in the same locality and formation with the skeleton above described" (Owen, 1865, p. 28). The two specimens were obtained by E. C. Hartsinck Day (1833–1895), a geologist, and a correspondent of the Geological Magazine (Jones and Woodward, 1864). Jones and Woodward (1864, p. 47) state that the type specimen of *Archaeonectrus rostratus* was "discovered in marls between two of the uppermost limestone beds of the Lower Lias Limestone," and consequently belongs to "the middle of the *Ammonites bucklandi* ammonite zone." It is therefore here assumed that this age assignment also applies to NHMUK 39514, which, according to current ammonite zonation, should be attributed to the *bucklandi* ammonite zone (lower Sinemurian; Page, 2003). Owen did not describe and figure the mandible found in association of the palatal and braincase remains of NHMUK 39514 (Owen, 1865, p. 28).

In 1889, Lydekker noted that NHMUK 39514 resembles R. 1338, a cast of the type specimen of '*Plesiosaurus*' *conybeari* Sollas, 1881 and thus referred it to that species (Lydekker, 1889, p. 269, 270). Lydekker noted that the previous attribution of NHMUK 39514 to '*P.*' *rostratus* by Owen in 1865 was not supported by the shortness of the mandibular symphysis compared to that of NHMUK 38525. Lydekker (1889) referred the following specimens to *Plesiosaurus conybeari* Sollas, 1881, which was later renamed *Attenborosaurus conybeari* by Bakker (1993; see also O'Keefe, 2001): 1) NHMUK R. 1370, a small portion of the dorsal part of the skull; 2) NHMUK 40140 (formerly R.1360), a partial skull and postcranial skeleton; and 3) NHMUK 39514, which is the partial skull re-examined here.

SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti, 1768
SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
Genus and species indeterminate

Material.—NHMUK 39514, a partial skull preserving part of the mandible, palate and braincase.

Geographic and stratigraphic occurrence.—NHMUK 39514 comes from the *bucklandi* ammonite zone, lower Sinemurian, Lower Jurassic of Charmouth, Dorset, England (Jones and Woodward, 1864; Owen, 1865).

DESCRIPTION

Material and repository.—The specimen, NHMUK 39514 comprises a few skull bones, incomplete palate, and mandible, with some teeth in situ. The floor of the braincase is observable dorsally but broken just in front of the pituitary fossa. The remains are preserved in several parts that can be connected except for the posterior left ramus of the mandible (Figs. 1, 2).

Skull roof.—The skull is poorly preserved. Only part of the premaxillae, maxillae, jugal?, squamosals and quadrate are recognizable (Figs. 1, 2). The crushed parts of the anterior portions of the premaxillae were displaced during fossilization. The premaxillae are massive bones forming the anterior part of the snout. Their surface preservation is so poor that the presence of foramina or grooves, which typically cover these bones, are not observable, except in ventral view where small foramina pierce the external ventral aspect of the left premaxilla. The tooth-bearing portion of the left premaxilla is incomplete but holds at least four alveoli and probably five; the presence of five premaxillary teeth is plesiomorphic for plesiosaurs (O'Keefe, 2001; Druckenmiller and Russell, 2008a; Ketchum and Benson, 2010). The left maxilla is only partially preserved on the left side, and is exposed in ventral view. Its surface preservation is also poor. It includes some teeth in situ. A fragment of a bone, lying dorsally and displaced from its natural position, is tentatively identified as the jugal. It is a flat, fan-shaped bone with a curved posterior end. It is ornamented by longitudinal striations that probably mirror the inner structure of the bone. The crushed left squamosal is partially preserved and only observable in lateral view. Its posterior preserved part lies near the posteriormost part of the left ramus of the mandible. It is massive and has a rugose, prominent ridge extending for most of its preserved length. This ridge is possibly similar to that in *Peloneustes philarchus* (Seeley, 1869) Lydekker, 1889 (Ketchum and Benson, 2011). The left quadrate is partially preserved. This massive bone occupies a nearly natural position because it lies on the glenoid fossa of the left ramus of the mandible. It appears to bulge but the poor preservation state of the specimen makes the structure of this bone unclear.

Palate and basicranium.—The anteriormost part of the palate is not preserved (Figs. 1, 2), and only the middle and posterior part of the pterygoids are observable. The pterygoids are partially separated from each other by the parasphenoid anterior to the posterior interpterygoid vacuities; they form the anterolateral margin of the latter. The pterygoids do not meet each other posterior to the posterior interpterygoid vacuities, being separated by the basisphenoid and the basioccipital. This interpretation differs from that proposed by Owen (1865) who stated that the pterygoids meet each other posterior to the posterior interpterygoid vacuities, covering the basioccipital. The right ectopterygoid reported by Owen is here reinterpreted as part of the right lateral ramus of the pterygoid. The quadrate rami of both pterygoids are long, mediolaterally compressed, and triangular in shape. Their ventral portions are slightly concave from side to side. They may have originally extended posterolaterally from the basicranium to the quadrate, but this part of the skull is not preserved.

The posterior interpterygoid vacuities are bordered laterally by the pterygoids and are separated on the midline by the parasphenoid anteriorly and by the basisphenoid posteriorly. They are anteroposteriorly elongated and kidney-shaped, with pointed posterior extremities. They are posterolaterally oriented as typical in plesiosaurians (e.g., Cruickshank, 1994a: '*Rhomaleosaurus*' *megacephalus* (Stutchbury, 1846); Taylor, 1992: *Rhomaleosaurus zetlandicus* (Phillips, 1854); Storrs and Taylor, 1996: *Thalassiodracon hawkinsii* (Owen, 1838); Storrs, 1997: *Plesiosaurus dolichodeirus*).

The parasphenoid was misidentified by Owen (1865) as the palatines. It is a large bone (Figs. 1, 2, 3c) that medially forms the anteromedial margins of the posterior interpterygoid vacuities. It extends anteriorly between the pterygoids, although its anterior terminus cannot be determined. Posteriorly, it contacts the basisphenoid along a well-defined suture; typically, this suture is fused in plesiosaurians (Bardet et al., 1999; Sato, 2005). As in *Macroplata tenuiceps* Swinton, 1930 (Ketchum and Smith, 2010) and NHMUK 49202, the parasphenoid is relatively broad, and its ventral surface is weakly concave mediolaterally. The ventral surface of the parasphenoid and basisphenoid between the posterior interpterygoid vacuities is not keeled.

The basisphenoid is exposed on the palatal surface of the cranium (Figs. 1, 2, 3c) as in *T. hawkinsii* (Storrs and Taylor, 1996; Benson et al., 2011b), OUMNH J.28585 (referred to *Eurycleidus* Andrews, 1922 by Cruickshank, 1994b; but see O'Keefe, 2004a; Ketchum and Benson, 2010), *Hauffiosaurus tomistomimus* Benson et al., 2011a, *Lusonectes sauvagei* Smith et al. (in press), and *Plesiosaurus dolichodeirus* (Storrs, 1997). It extends from the posterior end of the parasphenoid to the anterior margin of the ventral plate of the basioccipital medially and to the posterior margin of the palate laterally. The basisphenoid is bordered by the pterygoids posterolaterally, and posteriorly wraps around the basioccipital, forming a depression surrounding it. The dorsal aspect of the basisphenoid (Figs. 2a, 3a) resembles that in *Plesiopterys wildi* O'Keefe, 2004a (*Seeleyosaurus guilelmiimperatoris* (Dames, 1895) in Großmann, 2007). It forms the pituitary fossa (sella turcica) at its anterior end, which houses the pituitary (hypophysis). Dorsally, it forms a convex elevation of bone recognized as the presphenoid by Owen (1865). The pituitary fossa possesses a flat floor and is open anteriorly (Fig. 3a); its anterior extent is not observable probably owing to a lack of ossification or the loss of the enclosing bones. The fossa occupies about one-third of the braincase floor in NHMUK 39514, comparable to *Tricleidus* Andrews, 1909, *Plesiopterys,* and *Rhomaleosaurus* (see Sato et al., 2011). The sella turcica posteriorly terminates with the poorly developed dorsum sellae, which is usually poorly developed in plesiosaurians (O'Keefe, 2006). The basisphenoid is deeply incised by a narrow triangular notch in its posterior margin, surrounded by the two basal articulations with the basioccipital, as in *P. wildi* O'Keefe, 2004a.

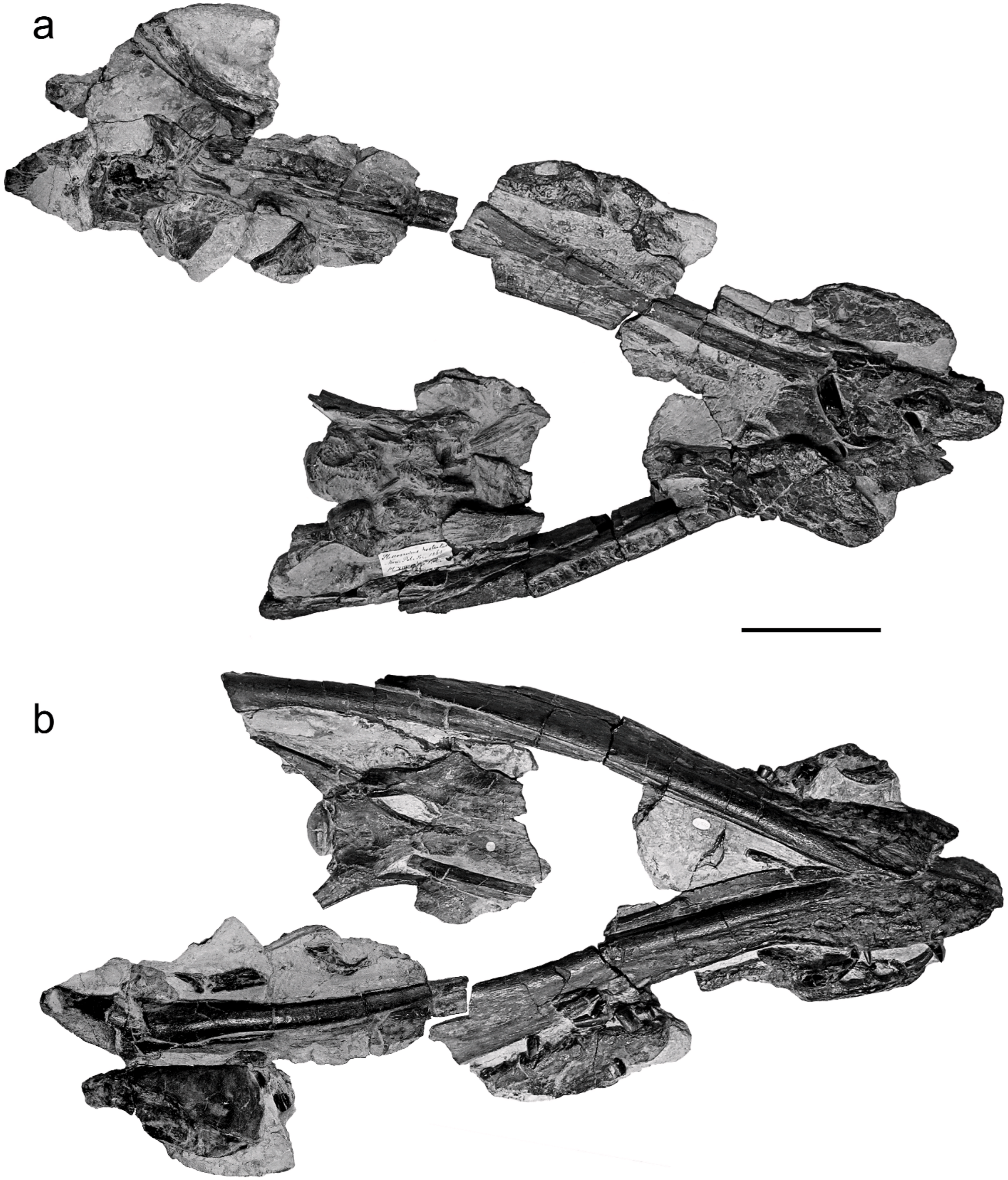

FIGURE 1—Photograph of NHMUK 39514 from the Lower Jurassic of England: *a*, the ventral aspect; *b*, the dorsal aspect of the preserved skull remains. Scale bar=10 cm.

The sulci for the internal carotid arteries (Fig. 2a), recognized as the neuropophysial ridges by Owen (1865), extend in an anteroposterior direction on the dorsal surface of the basisphenoid and basioccipital as in *P. wildi* O'Keefe, 2004a. From the point of their entry, which is not observable, into the cranial cavity, the internal carotids continue their anterior course within a distinct groove following the suture between the basioccipital and the quadrate ramus for the

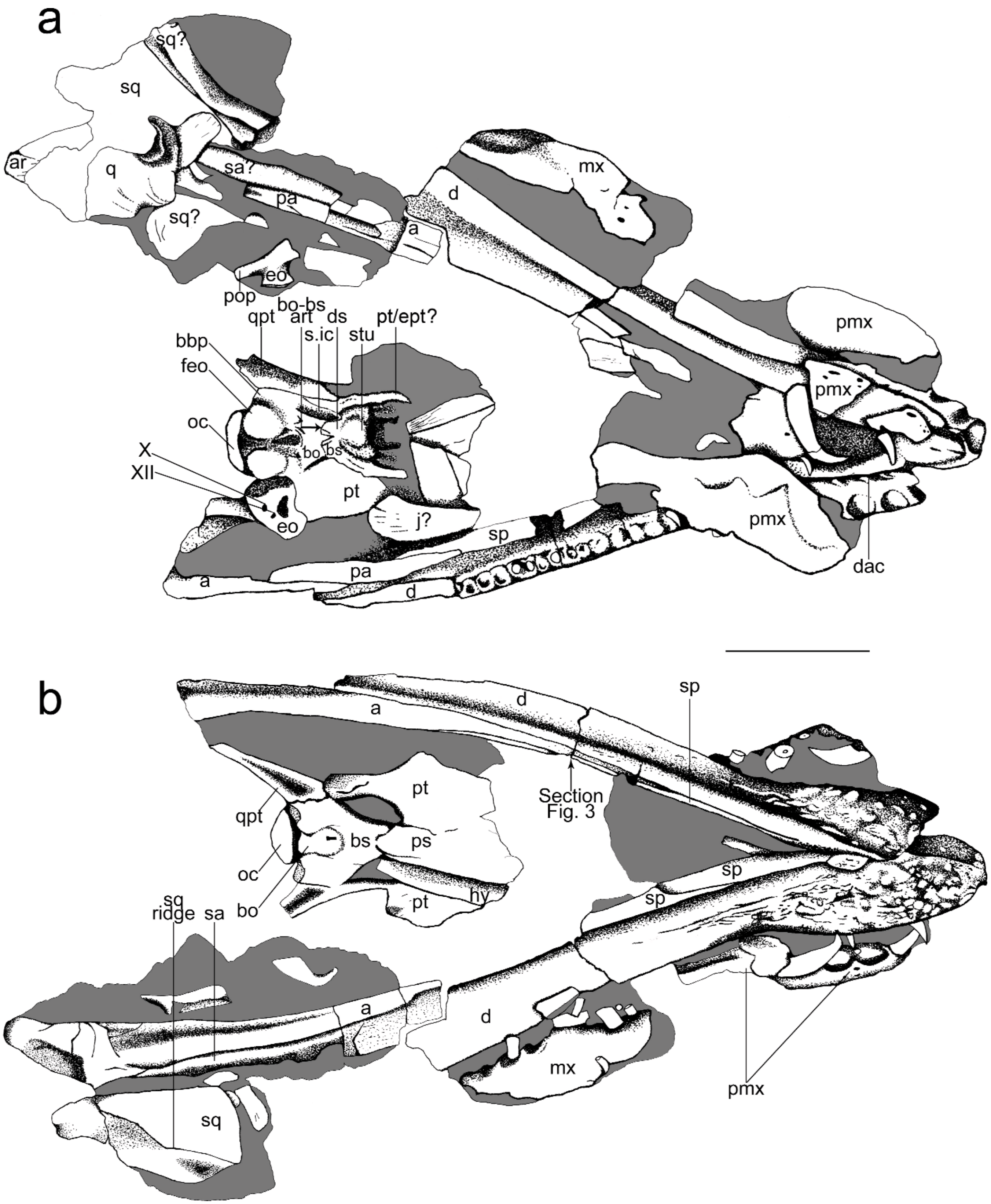

FIGURE 2—Interpretative drawing of NHMUK 39514 from the Lower Jurassic of England: *a*, the ventral aspect; *b*, the dorsal aspect of the preserved skull remains. Scale bar=10 cm. Anatomical abbreviations: a=angular; ar=articular; bbp=basioccipital basipterygoid process; bo=basioccipital; bo-bs art=basioccipital-basisphenoid articulation; boc art=basioccipital articulation; bs=basisphenoid; co=coronoid; d=dentary; dac=dentary alveolar channel for tooth replacement; ds=dorsum sella; eo=exoccipital-opisthotic; ept=epipterygoid; feo=facet for exoccipital-opisthotic; hy=hyoid element; j?=jugal; mx=maxilla; nc=neural canal; oc=occipital condyle; pa=prearticular; piv=posterior interpterygoid vacuity; pmx=premaxilla; pop=paroccipital process; ps=parasphenoid; pt=pterygoid; pu.f=pituitary fossa; q=quadrate; qpt=quadrate ramus for pterygoid; s.ic=sulcus for the internal carotid; sa=surangular; sp=splenial; sq=squamosal; stu=sella turcica; X?=jugular foramen; XII?=foramen for branches of hypoglossal nerve.

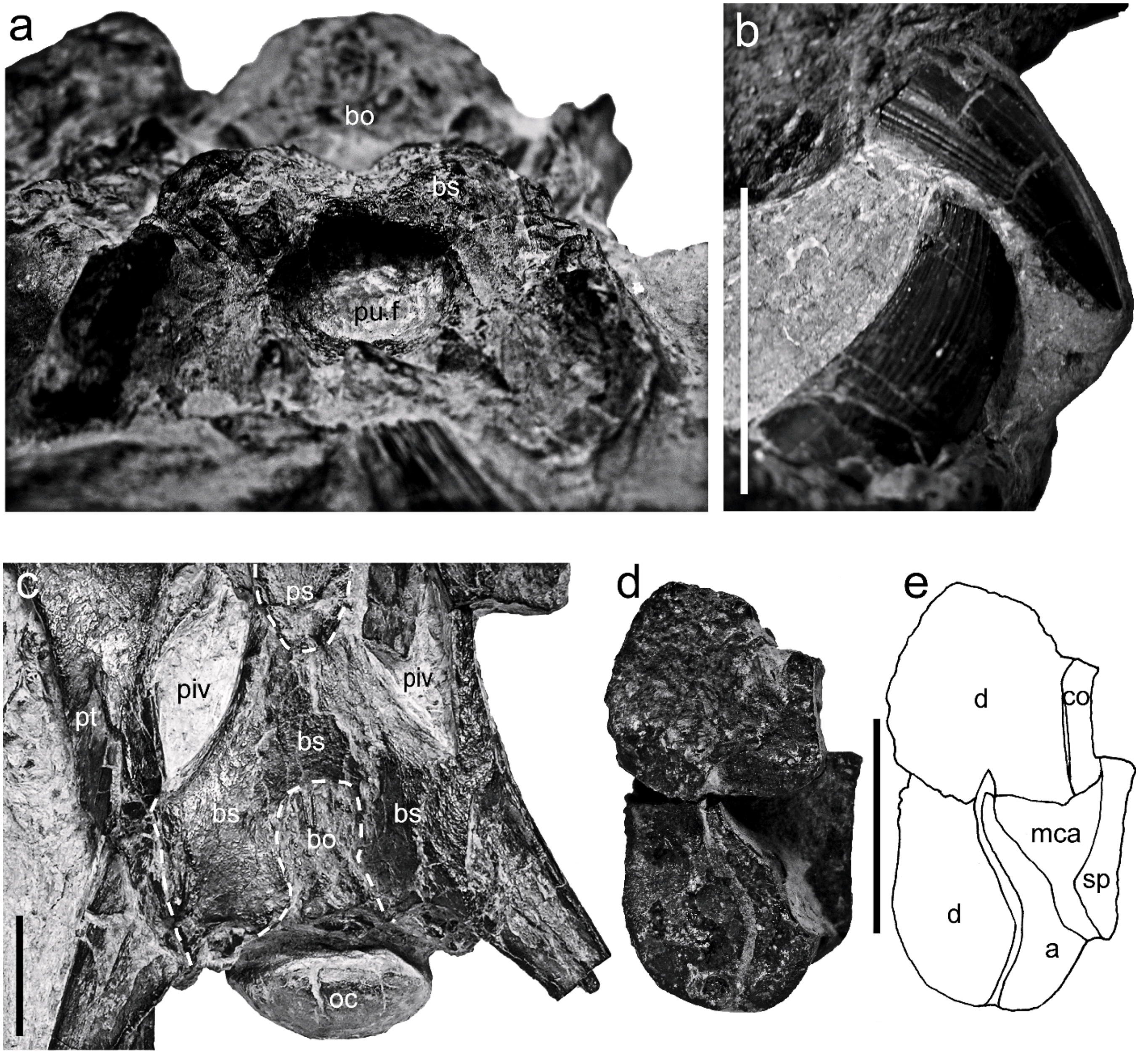

FIGURE *3*—NHMUK 39514 from the Lower Jurassic of England: *a*, braincase in anterior view; *b*, teeth; *c*, close-up view of the ventral surface of posterior basicranium; *d*, *e*, mandibular cross-section. Scale bars=2 cm. Anatomical abbreviations: a=angular; bo=basioccipital; bs=basisphenoid; co=coronoid; d=dentary; mca=meckelian canal; oc=occipital condyle; piv=posterior interpterygoid vacuity; ps=parasphenoid; pt=pterygoid; pu.f=pituitary fossa; sp=splenial.

pterygoid laterally. The foramen present in the body of the basisphenoid posterior to the basal articulation in *Thalassiodracon* and *Eurycleidus* and interpreted as the entrance for the internal carotid artery by O'Keefe (2006), is not observable here.

The basioccipital (Figs. 1, 2, 3c) forms the posteroventral portion of the braincase and is visible in palatal view as in other plesiosaurians in which the pterygoids do not meet posterior to the posterior interpterygoid vacuities (e.g., Storrs and Taylor, 1996: *T. hawkinsii*; Storrs, 1997: *P. dolichodeirus*; Ketchum and Smith, 2010: *Macroplata tenuiceps*). It is visible through the rounded depression surrounded by the basisphenoid, which covers it partially. Dorsally, the basioccipital is delimited anteriorly by the basisphenoid and laterally by the sulci for the internal carotids. The anteriormost part of the basioccipital is obscured by the matrix near its junction with the basisphenoid. The two large lateral facets of the exoccipital-opisthotic occupy most of the dorsal surface of the basioccipital, between which lies the narrow median concave floor of the braincase; this was recognized as the neurapophysial surface by Owen (1865). The floor of the foramen magnum is elevated above the level of the facets for the exoccipital-opisthotic, which are slightly concave and inclined ventrolaterally. Anterior to the exoccipital-opisthotic facets, the midline of the basioccipital floor bears a shallow concavity as in the polycotylid ROM 29010 (Sato et al., 2011). The occipital condyle is spherical, slightly flattened dorsally, and marked by a notochordal pit that is situated largely above the center. It is an anteroposteriorly compressed hemisphere and slightly wider than high. A groove extends around the base on the ventral and lateral sides, and is less marked dorsally. Both basioccipital tubera are moderately developed, as in *Eurycleidus arcuatus* (O'Keefe, 2006), *T. hawkinsii* (Storrs and Taylor, 1996), and NHMUK 49202, but less than that observed in *Meyerasaurus victor* (Fraas, 1910) Smith and Vincent, 2010.

Two long flanges of bone lateral to the sella turcica are slightly convex (Figs. 2, 3a). They probably correspond to the pterygoids or epipterygoids. They contact the basisphenoid at the basipterygoid process.

Both exoccipital-opisthotics are preserved and observable from the dorsal view but are displaced from their natural positions (Fig. 2). The exoccipitals are fully sutured with the opisthotics as in other plesiosaurians (Brown, 1981). The two anterior facets for the prootic and the basioccipital are visible in the right element. In medial view, two foramina are distinguishable, which likely correspond to the jugular foramina and one of the foramina for branches of hypoglossal nerve. The paroccipital processes are probably incompletely preserved.

A probable hyoid element is preserved on the palatal surface, overlaying the parts of the left pterygoid and left posterior interpterygoid vacuity (Figs. 1, 2). This bone was identified as such by Owen (1865). It is only partially preserved, and does not preserve either of the two extremities. It forms a long piece of bone but does not have the typical rod-like shape usually observed in plesiosaurians (e.g., Kear, 2005; Smith and Vincent, 2010). A longitudinal ridge extends anteroposteriorlly along its length but the state of preservation of this badly crushed bone precludes any conclusion.

Mandible.—The mandible is damaged but almost complete (Figs. 1, 2). The posterior left end is preserved, and is separated from the rest of the mandibular ramus. The right mandibular ramus lacks only the distal portion. The mandible is approximately 60 cm long.

The dentaries are the largest bones of the mandible and bear the lower dentition. They form the anterior portion of the mandible and over three-quarters of its total length. The dentaries extend from the tip of the snout anteriorly, to the coronoid eminence posteriorly. The mandibular rami meet in an elongated, spatulate symphysis without a prominent ridge. Their surfaces are covered with numerous vascular foramina and deep sockets. The length of the mandibular symphysis cannot be given with certainty but can be estimated as between 7 and 8 cm, which is approximately 13% of the total mandible length. Several pliosauroids show an elongated mandibular symphysis but this character is also present among few plesiosauroids (e.g., *Libonectes morgani* (Welles, 1949): 18%; *P. dolichodeirus*: 18.4%; *Hydrotherosaurus alexandrae* Welles, 1943: 16%; *Terminonatator ponteixensis* Sato, 2003: 15%; Druckenmiller and Russell, 2008a). The number of symphysial teeth is four or five on each side. The lateral margins of the dentaries at the posterior end of the mandibular symphysis are strongly indented laterally to form a constriction. The dental groove can be seen on the two mandibular rami. The splenials take part in the symphysis. Posteriorly, the dentaries and splenials are separated by the angulars ventrally and the coronoids dorsally. The mandible being partially obscured by matrix, it cannot be determined whether a longitudinal trough similar to that observed in *Hauffiosaurus tomistomimus* (Benson et al., 2011a) and most of the rhomaleosaurids (e.g., *Meyerasaurus victor*, Smith and Vincent, 2010) occupies the lateral surfaces of the dentaries in NHMUK 39514.

The splenials are long and transversely compressed bones, which take part in the symphysis (Figs. 2, 3d, 3e), although the extent of this participation cannot be determined. They form the ventral portion of the medial face of the mandibular rami. The splenials extend from the posterior portion of the mandibular symphysis to at least the level of the coronoid eminence. In the anterior part of the mandible, the splenials form the medial border of the Meckelian canals and contact the coronoids dorsomedially (Fig. 3d, 3e). Posteriorly, the splenials form the ventromedial border of the mandibular rami. The posterior part of the splenials are squeezed between the prearticulars medially, the coronoids, and the angulars.

The Meckelian canal is observable through the cross-section of the right mandibular ramus in the anterior portion of the mandible (Fig. 3d, 3e). At this level, it is transversely triangular in outline. It is bordered by the coronoid and dentary dorsally, the splenial lingually and the articular ventrolaterally.

The prearticulars are narrow bones, only partially observable on the two mandibular rami. They extend from the posterior part of the splenials to the beginning of the articulars and are bordered laterally by the coronoids.

The coronoids are only partially visible. They are long and thin plates of bone between the dentaries laterally and the splenials ventrolingually (Fig. 3d, 3e). Their anterior extensions are not exposed.

The surangular is partially preserved on the left ramus of the mandible. Ventrolaterally, it unites with the angular in a long straight suture.

The angulars form the posteroventral portions of the mandibular rami. They are preserved at least partially on both sides. Anteriorly, they are elongated as narrow processes within a few centimeters of the symphysis, between the dentaries laterally, the splenials medially and the Meckelian canals dorsally (Fig. 3d, 3e). In their posterior part, they extend beneath the retroarticular processes.

Teeth.—The partially preserved left premaxillae bear four tooth positions with two teeth in situ (Fig. 1). The right dentary bears 18 alveoli (Fig. 2). This is a minimum estimate, because much of the right dentary is hidden by the right premaxilla and is damaged anteriorly and at the level of the coronoid eminence. At least ten further alveoli may have been present. The number of mandibular symphysial teeth cannot be determined with certainty but is likely comprised four or five on each side. The teeth present a range in size, with the largest teeth occurring in the premaxillae and the anterior part of the dentary, then decreasing in size posteriorly. The largest tooth of the left dentary probably corresponds to the third alveolus (1.7 cm in diameter). The dentition is severely damaged, most of the teeth were lost before fossilisation and few teeth have been preserved in situ. The teeth are curved and circular in cross-section, and lack carinae (Fig. 3b). The base is large and bulbous and the apex is pointed. They are lingually ornamented by longitudinal enamel ridges.

COMPARISONS

NHMUK 39514 was originally referred to *Plesiosaurus rostratus* by Owen (1865). The type specimen (NHMUK 38525) of what is now *Archaeonectrus rostratus* preserves the skull roof and a partial mandible, thus limiting comparisons as the two specimens preserve few corresponding cranial portions. Both specimens possess anterior parts of the dentaries, which are pierced by numerous vascular foramina and deep sockets, and have robust, curved and lingually ornamented teeth. Nevertheless, the mandibular symphysis of *A. rostratus* is much longer than that of NHMUK 39514 and has seven teeth on each ramus. Moreover, the skull of *A. rostratus* is proportionally long and narrow, unlike NHMUK 39514.

NHMUK 39514 has subsequently been referred to the species *Attenborosaurus conybeari* by O'Keefe (2001). Unfortunately the type specimen of *A. conybeari* (BRSMG Cb 2479) was destroyed along with some other plesiosaurian specimens (*Rhomaleosaurus megacephalus*) during World War II (Swinton, 1948), so direct comparisons are no longer possible. Casts of BRSMG Cb 2479 show that the skull had been compressed laterally during fossilization and the palate is not visible on existing casts. The description of BRSMG Cb 2479 by Sollas (1881) provides relatively little information concerning the mandible, palate, braincase and teeth. The drawing of a section across the skull of BRSMG Cb 2479 by Sollas (1881, fig. 1) shows the posterior region of the skull. The channel noted by Sollas in the middle of this structure likely corresponds to the floor of the foramen magnum. Sollas (1881) stated that *A. conybeari* possesses teeth with longitudinal ridges but did not mention which part of the crown is striated, hence precluding further comparisons with NHMUK 39514. *A. conybeari* has an elongated mandibular symphysis bearing five or six teeth on each side (Smith, 2007; character 54 and 58), whereas NHMUK 39514 has a short mandibular symphysis (sensu Smith, 2007; character 54), bearing four or five teeth on each side. These differences in mandibular characters, though relatively slight, suggest that NHMUK 39514 does not belong to *A. conybeari*.

Few characters are available on NHMUK 39514 to establish precise comparisons with other plesiosaurian taxa. Only palatal and mandibular characters can be used for comparisons at present. Indeed, the rarity of specimens preserving braincase structures precludes determination of whether a particular feature of the braincase is diagnostic to a lower taxonomic level or shared within a higher taxonomic rank in plesiosaurians (Sato et al., 2011). Nevertheless, the available palatal and mandibular characters strongly suggest that NHMUK 39514 differs from other known Early Jurassic plesiosaurs. A bowed mandible (sensu Druckenmiller and Russell, 2008a) is present in NHMUK 39514 and many rhomaleosaurids and is an unambiguous synapomorphy of the clade Rhomaleosauridae of Ketchum and Benson (2010). However, the mandible of rhomaleosaurids is much more strongly bowed than in NHMUK 39514. Moreover, NHMUK 39514 differs markedly from almost all rhomaleosaurids, which have a closed palate with the pterygoids meeting posterior to the posterior interpterygoid vacuities and with a keeled parasphenoid (Smith and Dyke, 2008: *R. cramptoni* [Carte & Baily, 1863]; Taylor, 1992: *R. zetlandicus*; Smith and Vincent, 2010: *M. victor*). Nevertheless, the pterygoids are not in contact posterior to the posterior interpterygoid vacuities in *Macroplata tenuiceps* (a taxon recovered in the clade Rhomaleosauridae by Smith and Dyke [2008], contra Ketchum and Benson [2010]), and the parasphenoid is not keeled in *M. tenuiceps* and *R. megacephalus* (Cruickshank, 1994a; Ketchum and Smith, 2010). *M. tenuiceps* possesses enamel ridging on the labial and lingual crown surfaces of the teeth and seven or eight teeth along the mandibular symphysis (Ketchum and Smith, 2010); this is not the case in NHMUK 39514. NHMUK 39514 differs from *Hauffiosaurus tomistomimus* Benson et al., 2011a, *Hauffiosaurus zanoni* O'Keefe, 2001 (see Vincent, 2011) and *Hauffiosaurus longirostris* Benson et al., 2011a (*Macroplata* in White, 1940), which have a long, unexpanded snout tip and longitudinal ridges on all sides of the tooth crowns. NHMUK 39514 differs from NHMUK 49202, which has a basioccipital more extensively exposed on the palate, not laterally surrounding by the basisphenoid and a short mandibular symphysis with three tooth positions. NHMUK 39514 shares many morphological traits with *Thalassiodracon hawkinsii* (Storrs and Taylor, 1996; Benson et al., 2011b): the mandible has a long, spatulate symphysis, the parasphenoid is not keeled, and the pterygoids are not in contact posterior to the posterior interpterygoid vacuity. Nevertheless they differ with regards to the number of symphyseal teeth, which is lower in *Thalassiodracon* (two or three on each side), as well as to their respective teeth ornamentations, which is present at least labially in *Thalassiodracon* (Benson et al., 2011b).

The general outline of the mandible of NHMUK 39514 (elongate, spatulate symphysis with several tooth positions) is typically pliosauromorph (e.g., Noè, 2001: *Simolestes* Andrews, 1909, *Liopleurodon* Sauvage, 1873; Smith and Dyke, 2008 and Smith and Vincent, 2010: Rhomaleosauridae; Ketchum and Benson, 2011: *Peloneustes*; *Borealonectes* Sato and Wu, 2008) and absent in all plesiosauroids (e.g., Andrews, 1910: *Muraenosaurus* Seeley, 1874; *Cryptoclidus* Seeley, 1892; *Kimmerosaurus* Brown, 1981; *Libonectes* Carpenter 1997; Storrs, 1997: *P. dolichodeirus*; O'Keefe, 2004b: *Dolichorhynchops* Williston, 1903; *Nichollssaura* Druckenmiller and Russell, 2008b; *Zarafasaura* Vincent et al., 2011; *M. homalospondylus* (Owen, 1865): NHMUK 36184). Moreover, NHMUK 39514 possesses an elongated lingual coronoid process, a synapomorphy of Pliosauridae sensu Ketchum and Benson (2010). By contrast, the morphology of the braincase of NHMUK 39514 differs from that in known pliosoromorph taxa and resembles that in plesiosauroids and basal plesiosaurians. Among Early Jurassic taxa, NHMUK 39514 shares an almost flat parasphenoid-basisphenoid surface between the posterior interpterygoid vacuities with NHMUK 49202, *Thalassiodracon*, *Hydrorion*, *M. tenuiceps*, and *Lusonectes*. Nevertheless, this character also varies slightly among these taxa: the surface of parasphenoid-basisphenoid is gently convex transversely in *Thalassiodracon* (Benson et al., 2011b) and *Lusonectes* (Smith et al., in press), weakly concave in NHMUK 39514, NHMUK 49202 and *M. tenuiceps* (Ketchum and Smith, 2010), and flat in *Hydrorion* (Maisch and Rücklin, 2000). The absence of contact between pterygoids posterior to the posterior interpterygoid vacuities is considered to be plesiomorphic by O'Keefe (2001), and is observed in NHMUK 39514. Among Plesiosauria, only plesiosauroids and basal plesiosaurians show this character: *P. wildi* (O'Keefe, 2004a), *P. dolichodeirus* (Storrs, 1997), *Occitanosaurus tournemirensis* (Bardet et al., 1999), *Muraenosaurus leedsii* (Ketchum and Benson, 2010, fig. A6), *T. hawkinsii* (O'Keefe, 2006), *H. tomistomimus* Benson et al., 2011a and NHMUK 49202. This character is observable in Pistosauroidea such as *Yunguisaurus liae* Cheng et al., 2006, or *Augustasaurus hagdorni* Sander et al., 1997 (see Rieppel et al., 2002). O'Keefe (2006) stated that basal plesiosaurians are neotenic in their pterygoid ossification, and that the secondary closure of the palate represents an evolutionary trend within Plesiosauria.

Dorsal braincase structure remains poorly documented within Plesiosauria, as the preservation of most plesiosaurian skulls precludes detailed observations. Even in specimens with three-dimensional preservation, those structures are only partially observable without removal of the skull roof (e.g., *M. homalospondylus* NHMUK 36184). In some rare cases, the skull roof is partially crushed and hence allows observation of these structures (e.g., MCZ 1033: White, 1940; SMNS 16812: O'Keefe, 2004a; OXFUM J.28585: Cruickshank, 1994b; NHMUK R3536, GPIT 3). Recent improvements of scanning techniques and their growing use on plesiosaurians skulls (e.g., Carpenter, 1997; Druckenmiller and Russell, 2008b; Sato et al., 2011) will undoubtedly contribute to increase our knowledge of these structure among the group. Meanwhile, preliminary comparisons of the braincase structure of NHMUK 39514 with that of other available specimens reveal some interesting similarities and differences. The dorsal braincase is comparable to that observed in SMNS 16812 (*Plesiopterys* of O'Keefe, 2004a). In both specimens, the basioccipital contacts the basisphenoid at the level of the two basal articulations with the basioccipital, which surround a narrow triangular notch. This condition is comparable in MCZ 1033 but the latter shows a notch forming a more obtuse angle, a reduced basioccipital articulation, and a very short basioccipital (White, 1940). According to Cruickshank (1994b), OXFUM J.28585 (juvenile of *Eurycleidus*) presents a reduced dorsal basioccipital exposure, forming the floor of the foramen magnum and anteriorly contacting the dorsum sellae. O'Keefe (2006) interpreted a possible facet for prootic identified by Cruickshank (1994b; labeled "?fpro") as the basioccipital articulation, and the recess enclosed by the basiphenoid (Cruickshank, 1994b; labeled "bs") as the sella turcica. If this interpretation is correct, the morphology of the braincase of OXFUM J.28585 would be very close to that observed in SMNS 16812 and NHMUK 39514. Interestingly, the braincase structure of NHMUK 39514, SMNS 16812, OUMNH J.28585 and MCZ 1033 differs substantially from that in stratigraphically younger specimens. Neither the basal basisphenoid-basioccipital articulations surrounding a narrow triangular notch nor the shallow basin-shaped basioccipital area posterior to the dorsum sellae are present in the polycotylid ROM 29010 (Sato et al., 2011), in *Simolestes* and *Liopleurodon* (Noè, 2001: NHMUK R3536 and GPIT 3) and probably in *Libonectes* (Carpenter, 1997). In *Simolestes* and *Liopleurodon* the basioccipital is not as long as in NHMUK 39514. The small pit for the internal foramen of cranial nerve VI recovered on the anterodorsal part of the basisphenoid in the polycotylid ROM 29010 (Sato et al., 2011) and *Libonectes* (Carpenter, 1997), is not observed in NHMUK 39514. The dorsal braincase of NHMUK 39514, SMNS 16812 (O'Keefe, 2004a), OUMNH J.28585 (Cruickshank, 1994b), and MCZ 1033 (White, 1940) is very similar to that of *Nothosaurus* (Rieppel, 1994, fig. 10). NHMUK 39514, OXFUM J.28585 and *Nothosaurus* have a similar shallow, basin-shaped basioccipital area anterior to the exoccipital-opisthotic. The high lateral edges of the dorsum sellae are common to all these specimens but the triangular notch present on this bone in the Liassic specimens is absent in *Nothosaurus*. The course of the internal carotid arteries appears to be the similar in all known Early Jurassic plesiosaurian taxa and *Nothosaurus*.

In summary, these preliminary comparisons of the dorsal braincase morphology confirm that its general outline has a large range of variation among Plesiosauria as stated by Sato et al. (2011). The dorsal braincase morphology of Early Jurassic taxa, however, appears rather conservative and retains some plesiomorphic characters also observed in *Nothosaurus*. Therefore, NHMUK 39514 presents plesiomorphic braincase characters associated with pliosauromorph mandibular characters, suggesting that it likely occupies a rather basal position among Plesiosauria. The dorsal braincase being still poorly documented among Plesiosauria and basal Sauropterygia, additional work is required to increase the number of detailed descriptions of this region and hence provide potentially useful phylogenetic signals that could help better constraining the evolutionary trends of the plesiosaurian skull.

CONCLUSION

NHMUK 39514 presents morphological characters that exclude it from the species to which it was previously attributed, *A. rostratus* and *A. conybeari*. It differs from all other known Early Jurassic taxa and shows some plesiomorphic characters. Because the specimen lacks much diagnostic anatomical information, it is here proposed to classify NHMUK 39514 as Plesiosauria indet. Previous attempts to reconstruct phylogenetic relationships among Plesiosauria (e.g., O'Keefe, 2001) have referred NHMUK 39514 to *Attenborosaurus* and hence used its braincase anatomical characters to complete those missing in *Attenborosaurus*. Considering NHMUK 39514 Plesiosauria indet. implies that its braincase anatomy cannot be used to add data missing in the type specimen of *A. conybeari* (or any other Early Jurassic plesiosaurian) in future phylogenetical analyses.

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