



NEW INFORMATION ON *HAUFFIOSAURUS* (REPTILIA, PLESIOSAURIA) BASED ON A NEW SPECIES FROM THE ALUM SHALE MEMBER (LOWER TOARCICAN: LOWER JURASSIC) OF YORKSHIRE, UK

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Abstract: An almost complete, three-dimensionally preserved plesiosaurian from the *Hildoceras bifrons* Zone of the Alum Shale Member (Whitby Limestone Formation; Lower Toarcian) of Yorkshire, UK, is described in detail. This represents a new species of *Hauffiosaurus*, *H. tomistomimus*, distinguished from *H. zanoni* (*Harpoceras serpentinum* Zone, Lower Toarcian, Germany) by the proportionally shorter neck and strongly concave preaxial margin of the tibia. It differs from *H. longirostris* (previously ‘*Macroplata*’ *longirostris*; *Har. serpentinum* Zone, Yorkshire) by the absence of prominent midline ridges on the dorsal surface of the premaxillae and ventral surface of the mandibular symphysis, and the absence of midline pterygoid contact ventral to the basioccipital. Several synapomorphies support a monophyletic *Hauffiosaurus*: broad longitudinal troughs occupy the dorsolateral surface of the maxilla and the posterior half of the lateral surface of the dentary; basicranial fontanelle bounded laterally by postero-

laterally elongate projections of an undetermined ossification; and the neural arch contacts the rib facet in all postaxial cervical vertebrae. However, the systematic position of *Hauffiosaurus*, as a pliosauroid or basal plesiosauroid, remains uncertain. There is little evidence for geographic differentiation of Lower Toarcian plesiosaurian faunas in the United Kingdom and Germany as minor differences between abundant taxa may arise from temporal offset of fossils from these regions, and marked taxonomic differences are confined to rare taxa whose absence in one or other area may be attributable to incomplete sampling. Lack of consensus on the relationships of Lower Jurassic plesiosaurians requires further detailed description of Lower Jurassic taxa.

Key words: Plesiosauria, *Hauffiosaurus tomistomimus*, Toarcian, Whitby Mudstone Formation, Alum Shale Member, Posidonia Shale.

THE uppermost Triassic and Lower Jurassic marine deposits of Western Europe have yielded numerous articulated plesiosaur specimens. Most are from the United Kingdom, where numerous horizons yield abundant remains from almost every stage of the interval. These include the Rhaetian–Hettangian Pre-*Planorbis* and *Planorbis* beds, which yield the stratigraphically earliest plesiosaurians (Storrs and Taylor 1996), the Pliensbachian–Sinemurian Lower Lias Group (e.g. Storrs 1997) and the Toarcian Whitby Mudstone Formation of Yorkshire (Benton and Taylor 1984). Together, these provide abundant data on the early evolution of Plesiosauria (Benton and Spencer 1995) and are central to understanding the

origins and early evolution of the group. Unfortunately, the taxonomy and anatomy of Lower Jurassic plesiosaurians are poorly understood, and detailed descriptive information is available only for a few taxa (Storrs and Taylor 1996; Storrs 1997; Smith and Vincent 2010).

Here, we describe a plesiosaurian from the Alum Shale Member of the Whitby Mudstone Formation (*Hildoceras bifrons* Zone, lower Toarcian: Howarth 1980). Abundant remains of marine reptiles have been collected from the cliffs and alum quarries near Whitby over the past 200 years (Benton and Taylor 1984), including ichthyosaurs, thalattosuchian crocodylomorphs and the plesiosaurians ‘*Macroplata*’ *longirostris* (Tate and Blake 1876;

White 1940), *Rhomaleosaurus cramptoni* (Carte and Baily 1863; Smith and Dyke 2008), *Rhomaleosaurus zetlandicus* (Phillips 1854; Taylor 1992; Vincent and Smith 2009), *Microcleidus homalospondylus* and *Microcleidus macropterus* (Owen 1881; Watson 1909, 1911) and *Sthenarosaurus dawkinsi* (Watson 1909). The Alum Shale (*Hildoceras bifrons* Zone) and underlying Jet Rock (*Harpoceras serpentinum* Zone) members of the Whitby Mudstone Formation are approximately coeval with the Posidonia Shale (*Harpoceras serpentinum* Zone, lower Toarcian) around Holzmaden, Germany, which has also yielded abundant marine reptile fossils (Howarth 1980; Röhl *et al.* 2001). As so many lower Toarcian fossils are known, this interval has been the focus of Lower Jurassic palaeobiogeographic hypotheses (Godefroit 1994; Maisch and Ansoerge 2004; O'Keefe 2004; Großmann 2007; Smith and Vincent 2010).

The specimen described here was discovered in 1960 by an undergraduate geologic field party from Manchester University (Broadhurst and Duffy 1970). The anterior part of the skull was noticed projecting above a wave-washed platform south of Robin Hood's Bay, Yorkshire, UK. The skull, neck, pectoral girdle and one forelimb were covered by a thin layer of shale and collected immediately, but the rest of the skeleton was more deeply buried and had to be collected on a second expedition. The skeleton was transported to the Manchester Museum, where its preparation was carried out using standard mechanical techniques (MANCH unpublished collections data). Subsequent acid preparation on the specimen was undertaken by Roger Vaughan (BRSMG), and the specimen is now on display at the Manchester Museum, UK.

The specimen was previously referred to '*Macroplata*' (or '*Rhomaleosaurus*') *longirostris* and has been discussed in the literature (Broadhurst and Duffy 1970; Benton and Taylor 1984; Cruickshank 1996) and included in phylogenetic analyses (O'Keefe 2001, 2004; Ketchum and Benson 2010). However, it is described in detail here for the first time. Several features indicate that it is distinct from '*M.*' *longirostris*, although this taxon and the new specimen form a closely related grouping with *Hauffiosaurus zanoni* from the Posidonia Shale of Germany, and all three are referred to the genus *Hauffiosaurus* herein.

In this article, use of specimen numbers denotes direct observation of fossil specimens by one of the authors unless otherwise noted.

GEOLOGIC SETTING

The Lower Jurassic Lias Group of Great Britain crops out in a band across the United Kingdom from Devon and Dorset in the south, to Yorkshire in the north-east, with

only small outcrops elsewhere (e.g. Howarth 1980). The rocks consist predominantly of marine mudstones deposited in a series of four interconnected basins separated by shelf areas. The new specimen was found in the Cleveland Basin of Yorkshire, which lies on the east coast of North Yorkshire, north of the Market Weighton high. Coastal exposures extend from Redcar in the north to Filey in the south, subtending Whitby, Ravenscar and Scarborough. Cleveland Basin deposits accumulated at the western margin of the North Sea Basinal system and comprise predominantly marine sediments (Rawson and Wright 1995).

The specimen was recovered from the '*H. bifrons* Zone of the Alum Shale Series of the Upper Lias' in the vicinity of Ravenscar (Broadhurst and Duffy 1970, p. 30). This equates to beds xvi–lvi of the Alum Shale Member of the Whitby Mudstone Formation south-east of Peak ('Old Peak' in some sources: Howarth 1962, 1980). The Whitby Mudstone Formation has been divided into five members (Rawson and Wright 1995), the middle of which is the Alum Shale Member (formerly the Alum Shale Series; Howarth 1962), consisting of medium to dark grey, flakey-weathering, nonlaminated, silty shale with numerous bands of scattered nodules of calcareous and sideritic concretions with a total thickness of 37.3 m near Ravenscar (Howarth 1980; Rawson and Wright 1995). Unfortunately, precise locality data for the new specimen are unknown. However, detailed geologic data and maps of the area can be found in Howarth (1962, pl. 27) and Rawson and Wright (2000, fig. 15).

Anatomic abbreviations. aiv, anterior interpterygoid vacuity; ang, angular; apr, anterior process of the articular; art, articular; atax, atlas-axis complex; atc, atlantal centrum; atic, atlantal inter-centrum; atna, atlantal neural arch; axi, axial intercentrum; axna, axial neural arch; axncs?, possible axial neurocentral suture; axr, axial rib; boc, basioccipital; bs, basisphenoid; ca1, first caudal vertebra; ca20, twentieth caudal vertebra; ca35, thirty-fifth caudal vertebra; ce3, third cervical vertebra; ce4, fourth cervical vertebra; ce34, thirty-fourth cervical vertebra; cl, clavicle; cor, coronoid; cora, coracoid; den, dentary; depr, depression; do1, first dorsal vertebra; do7, seventh dorsal vertebra; do14, fourteenth dorsal vertebra; do20, twentieth dorsal vertebra; do22/sa1?, posteriormost dorsal or first sacral vertebra; dob, dorsal blade of scapula; en, external naris; exoc, exoccipital; fem, femur; for, foramen; fr, frontal; frf, frontal facet on the parietal; gle, glenoid (of pectoral girdle); hum, humerus; in, internal naris; isc, ischium; lac, lacrimal; mx, maxilla; nc, neural canal; ncs, neurocentral suture; ns, neural spine; pal, palatine; par, parietal; pifor, pineal foramen; pmx, premaxilla; pofr, postfrontal; poz, postzygapophysis; prfr, prefrontal; pro, prootic; pra, prearticular; prj, projections of an unidentified ossification; prz, prezygapophysis; ps, parasphenoid; pt, pterygoid; pub, pubis; qu, quadrate; rap, retroarticular process; rug, rugosities; sa, surangular; sa1/2?, first or second sacral vertebra; scap, scapula; scf, subcentral foramen; soc, supraoccipital; spl, splenial; splf, splenial facet; sq, squamosal; tro, trough; vom, vomer.

Institutional Abbreviations. BEDFM, Bedford Museum, Bedford; NHMUK, Natural History Museum, London; BRSMG, Bristol City Museum and Art Gallery, Bristol; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge; FHSM, the Sternberg Museum of Natural History, Hays, Kansas; HAUF, Urwelt-Museum Hauff, Holzmaden; LEICS, New Walk Museum and Art Gallery, Leicester; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; MANCH, The Manchester Museum, Manchester; MOR, Museum of the Rockies, Bozeman, Montana; OXFUM, Oxford University Museum of Natural History, Oxford; QM, Queensland Museum, Brisbane; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart; USNM, National Museum of Natural History, Washington, DC; YORYM, The Yorkshire Museum, York.

SYSTEMATIC PALAEOONTOLOGY

SAUROPTERYGIA Owen, 1860

PLESIOSAURIA de Blainville, 1835

Genus HAUFFIOSAURUS O'Keefe, 2001

Type species. *Hauffiosaurus zanoni* O'Keefe, 2001, from the *Harpoceras serpentinum* Biozone (lower Toarcian) of Holzmaden, Germany.

Additional included species. *Hauffiosaurus longirostris* (Blake in Tate and Blake, 1876) [comb. nov.] from the *Harpoceras serpentinum* Biozone near Whitby, Yorkshire, UK; *Hauffiosaurus tomistomimus* sp. nov.

Diagnosis. Longirostrine, long-necked (c. 34 cervical vertebrae) plesiosaurians with 7–10 premaxillary teeth and the following unique synapomorphies: broad longitudinal troughs occupy the dorsolateral surface of the maxilla and the posterior half of the lateral surface of the dentary; basicranial fontanelle (midline opening in ventral surface of braincase on basioccipital–basisphenoid suture) bounded laterally by posterolaterally elongate projections of an undetermined ossification; neural arch extends ventrally over lateral surface of centrum and contacts dorsal portion of rib facet in all postaxial cervical vertebrae.

Remarks. Large foramina are present anteriorly and posteriorly between the rib heads and cervical centra in *H. tomistomimus* and postcranial material that may be part of the holotype of *H. longirostris*, and this may also be a synapomorphy of *Hauffiosaurus* (although the condition in *H. zanoni* was not determined during the present study). *H. zanoni* possesses an elongate ilium, approximately two-thirds of the femoral length, and transversely broad pubis with a subhexagonal outline resulting from distinct anteriorly, anterolaterally and laterally facing edges to the outline in ventral view. It is not possible to

determine whether these are autapomorphies of *H. zanoni* or synapomorphies of *Hauffiosaurus* as the condition of the pelvis cannot currently be determined in *H. longirostris* or *H. tomistomimus*.

Hauffiosaurus tomistomimus sp. nov.

Text-figures 1–15

1970 *Rhomaleosaurus longirostris* Blake in Tate and Blake; Halstead in Broadhurst and Duffy, p. 30, fig. 28.

1996 *Macroplata longirostris* (Blake in Tate and Blake); Cruickshank, p. 113.

2001 *Macroplata longirostris* (Blake in Tate and Blake); O'Keefe, fig. 9.

Derivation of the name. Species epithet composed from *Tomistoma*, the generic name of the false gharial, a long-snouted crocodylian, and *μίμος*, a Greek word meaning mimic.

Holotype. MANCH LL 8004 (Text-figs 1–15), an almost complete skeleton.

Type locality. The bay between Old Peak and Blea Wyke Point, south-east of Robin Hood's Bay (National Grid Reference NZ 99 02; Ordnance Survey 1963).

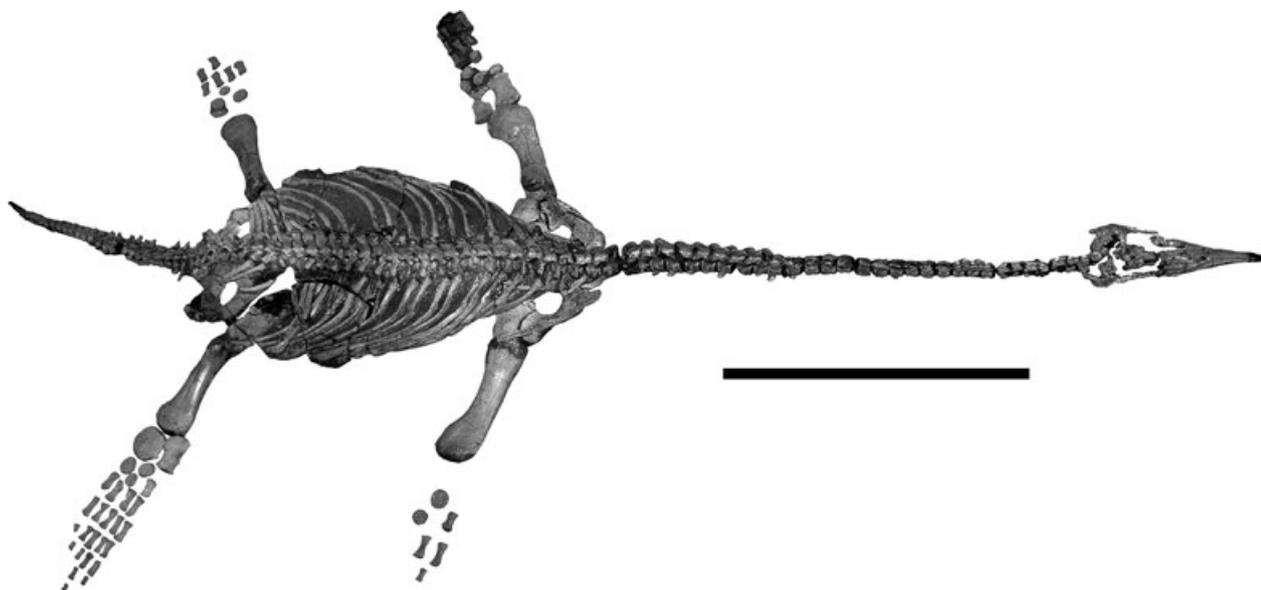
Type horizon. *Hildoceras bifrons* Zone, Alum Shale Member, Whitby Mudstone Formation, Lower Jurassic (lower Toarcian: Broadhurst and Duffy 1970; Howarth 1980; Gradstein *et al.* 2005).

Diagnosis. Representative of the genus *Hauffiosaurus* in which the preaxial margin of the tibia is strongly concave, the middle cervical centra have a ratio of width to anteroposterior length of approximately 1.2, the propodials are shorter than the pelvis, the pterygoids do not contact ventral to the basioccipital, and prominent longitudinal midline ridges are absent from the dorsal surface of the premaxillae or ventral surface of the mandibular symphysis.

Remarks. *Hauffiosaurus tomistomimus* possesses three additional features that may be autapomorphies, but their presence or absence in *H. longirostris* and *H. zanoni* cannot be determined: a long, distinct anterior process of the parietals; a transverse constriction in the outline of the pterygoid in ventral view at the base of the anterior process; and a depression on the dorsolateral surface of the third cervical neural arch.

DESCRIPTION

The skeleton of MANCH LL 8004 is almost complete and retains a high degree of articulation (Text-fig. 1). As preserved, missing



TEXT-FIG. 1. *Hauffiosaurus tomistomimus* sp. nov. Skeleton MANCH LL 8004 in right anterodorsolateral view. Scale bar represents 1 m. Image is compressed by parallax towards the left.

the snout tip, the specimen is 4230 mm long, with the skull just over one-tenth the length of the animal at 430 mm, the neck approximately the same length as the trunk (1350 mm), and the tail slightly shorter than the neck (1100 mm).

Cranium

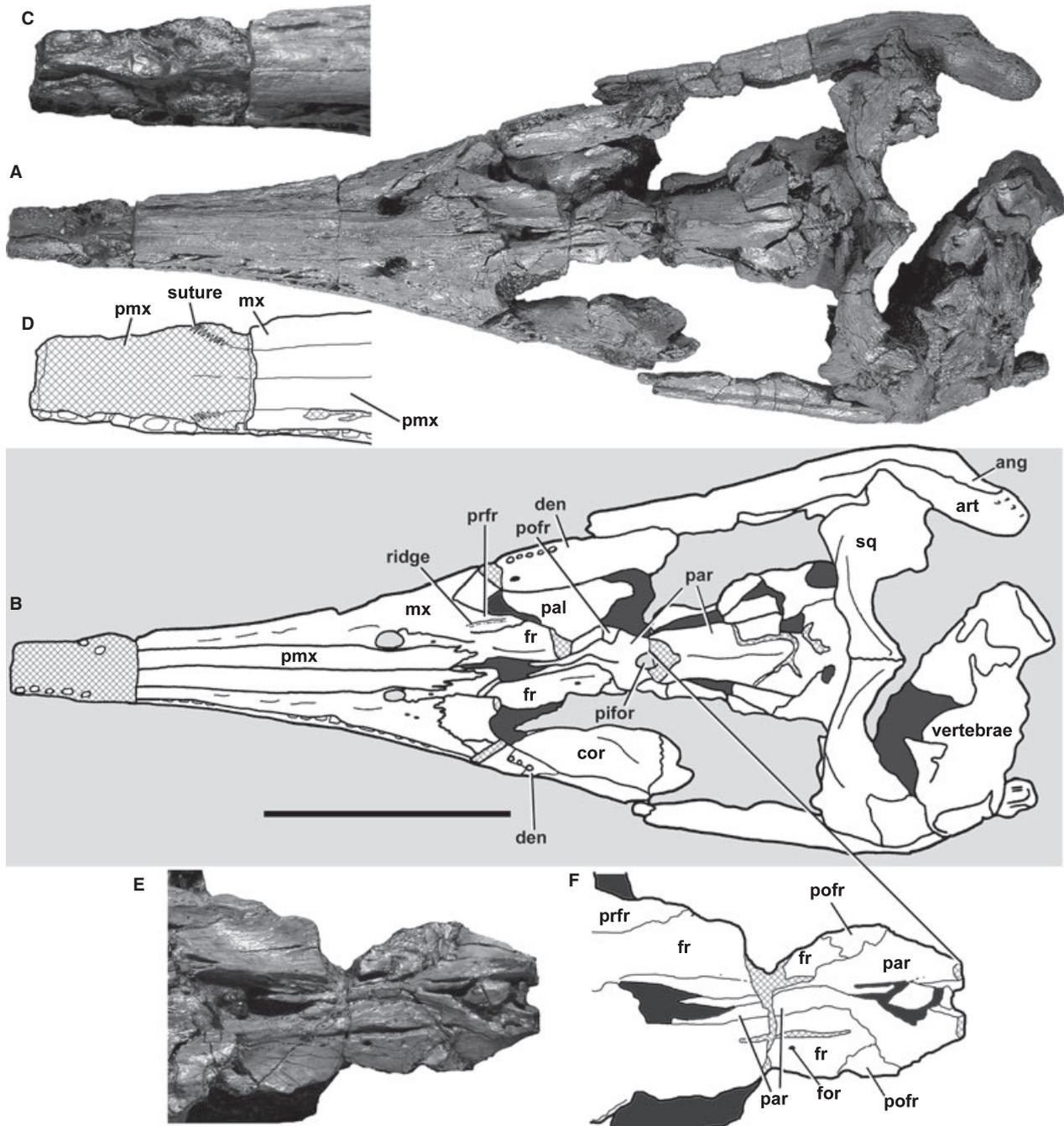
Despite moderate dorsoventral crushing, bone surface preservation is good, allowing many of the cranial and mandibular sutures to be confidently identified. The upper and lower jaws are preserved tightly closed.

The skull has the shape of an elongate isosceles triangle in dorsal view (Text-fig. 2). The distance between the quadrates is 265 mm, although this may have been exaggerated by dorsoventral crushing, which has affected the skull medial and posterior to the orbits. The external nares are small, anteroposteriorly oriented oval openings located posteriorly on the snout, close to the midline, anterior to the orbits. The postorbital bars are both missing. However, in plesiosaurians the postorbital bars are usually located at the level of the parietal foramen (e.g. Andrews 1913; Druckenmiller and Russell 2008a), which is preserved.

In lateral view, the skull is long and dorsoventrally low (Text-fig. 3); this has been accentuated by dorsoventral crushing posteriorly. Although it is incompletely preserved, the snout forms greater than half the total skull length. *H. tomistomimus* is therefore a longirostrine taxon. By contrast, most other plesiosaurians from the Toarcian of Europe have proportionally shorter rostra: the plesiosauromorphs *Microcleidus* (NHMUK 36186), *Hydrorion* and *Seeleyosaurus* (Maisch and Rücklin 2000; O'Keefe 2004; Großmann 2007) and *Occitanosaurus* (Bardet *et al.* 1999) have very short, rounded snouts; the pliosauromorphs *Rhomaleosaurus* (Watson 1910; Taylor 1992; Vincent and Smith 2009) and *Meyerasaurus* (Smith and Vincent 2010) have relatively longer snouts, but are brevirostrine compared to *H. tomistomimus* (the

snout is approximately 65 per cent of the length of the remaining portion of the skull in *R. zetlandicus*; Taylor 1992). Only *Hauffiosaurus zanoni* (HAUF 7; O'Keefe 2001) and *H. longirostris* (MCZ 1033; White 1940) have longirostrine snouts comparable to that of *H. tomistomimus*. In *H. longirostris*, the snout is slightly longer than the remaining portion of the skull (White 1940). In *Hauffiosaurus zanoni*, the dorsal surface of the skull is embedded in matrix (HAUF 7), but the approximate proportions are similar.

Premaxilla. The preserved portions of the premaxillae are primarily composed of their elongate posterior processes. These are firmly joined along a straight midline suture and extend posteriorly to the level of the anterior margin of the orbits, where they terminate in a deeply interdigitating contact with the frontals (Text-fig. 2). This is unlike the condition in many other relatively long-snouted plesiosaurians such as *Rhomaleosaurus zetlandicus* (YORYM G503; Taylor 1992; Vincent and Smith 2009), pliosaurids (e.g. Andrews 1913), polycotylids (O'Keefe 2008) and some elasmosaurids (Sato 2002, 2003), in which the premaxillae contact the parietals posteriorly (O'Keefe 2001; Druckenmiller and Russell 2008a; Ketchum and Benson 2010). The overall trend of the premaxilla–frontal contact is posteromedial (Text-fig. 4). The parallel lateral margins of the posterior processes contact the maxillae anterior to the external naris, forming approximately straight sutures along most of their length. However, these are slightly sinuous in places; anterior to the external naris the suture undulates to form a series of three peaks over approximately 15 mm (Text-fig. 3B). These small-scale undulations of the suture between the maxilla and posterior process of the premaxilla are also present in *Rhomaleosaurus megacephalus* (LEICS G221.1851), but absent in the pliosaurid *Peloneustes*, in which the suture is straight (Ketchum 2007). Posterior to the external nares, the posterior processes of the premaxillae are enclosed laterally by anterolat-

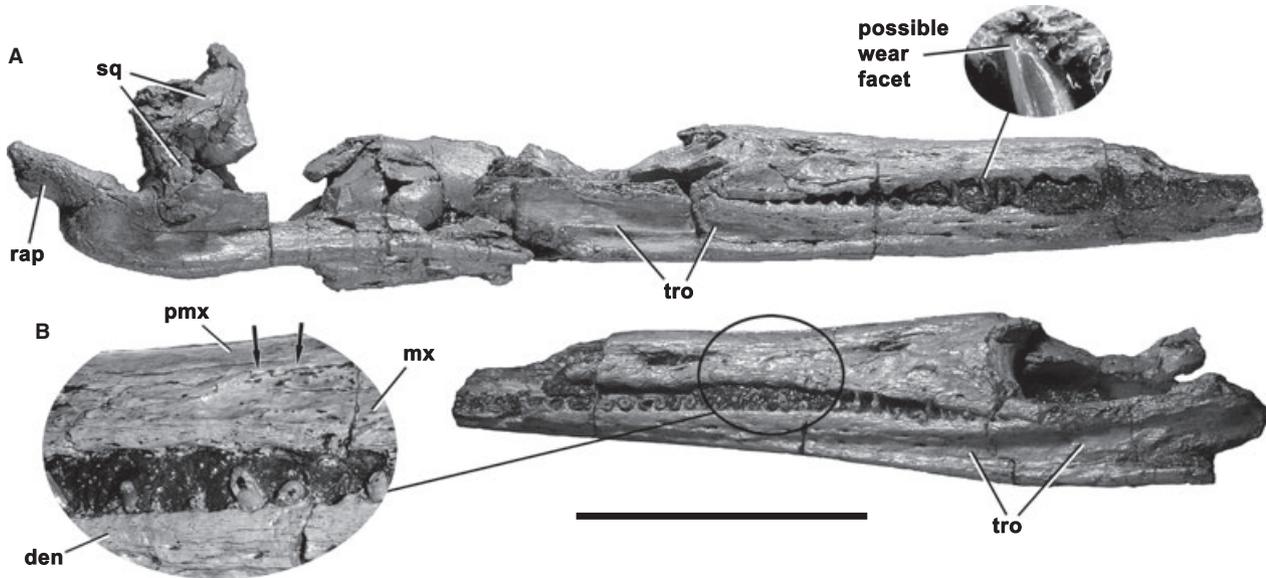


TEXT-FIG. 2. *Hauffiosaurus tomistomimus* sp. nov. Skull of MANCH LL 8004 in dorsal view. A–B, complete skull, C–D magnification ($\times 1.75$) of snout tip, E–F, magnification ($\times 2$) of skull roof anterior to pineal foramen. In line drawings (B, D, F), grey tone indicates matrix, crossed-hatching indicates broken bone. Scale bar represents 100 mm. Abbreviations are given in the text.

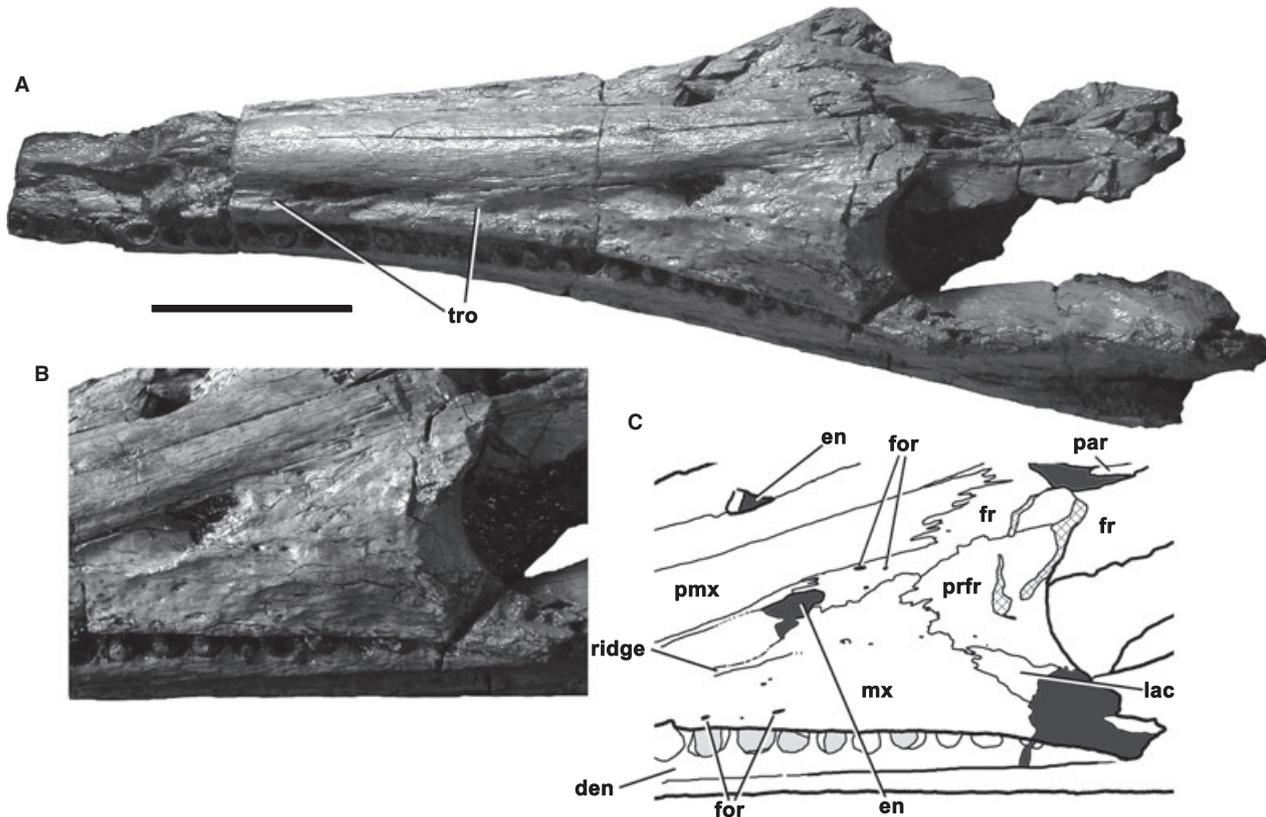
eral processes of the frontals that contact the maxillae lateral and medial to the external naris, excluding the premaxilla from the narial margin. Although White (1940, fig. 2A) figured a premaxilla–frontal contact that was restricted to the posterior end of the premaxilla in MCZ 1033 (referred to *Hauffiosaurus longirostris* herein), he also noted (p. 453) that preservation was too poor to allow detection of most craniofacial sutures. Our observations of MCZ 1033 confirm this. The dorsal sur-

faces of the premaxillae of *H. tomistomimus* are smoothly convex and dorsoventrally low, lacking the prominent dorsal midline crest that is present in *H. longirostris* (MCZ 1033: White 1940).

The tooth-bearing anterior portion of the premaxilla is poorly preserved and incomplete; the dorsal surface is broken. However, the anterior section of the premaxilla–maxilla contact is visible as a deeply interdigitating suture that curves anterolaterally,



TEXT-FIG. 3. *Hauffiosaurus tomistomimus* sp. nov. Skull of MANCH LL 8004. A, complete skull in right lateral view with magnification ($\times 10$) of dentary tooth showing possible apical wear facet, B–C, rostral portion of skull in left lateral view. B, magnification ($\times 2$) showing sinuous premaxilla–maxilla suture. Scale bar represents 100 mm.



TEXT-FIG. 4. *Hauffiosaurus tomistomimus* sp. nov. Skull of MANCH LL 8004 in left dorsolateral view. A, rostral portion of skull, B–C, magnification ($\times 1.5$) showing sutures in the region of the external naris and anterior to the orbit. In line drawing (C), grey tone indicates matrix and crossed-hatching indicates broken bone. Scale bar represents 50 mm.

delimiting the anterior end of the maxilla (Text-fig. 2D). It is likely that the superficial exposure of this suture was less strongly interdigitating than is the exposed, internal portion, as in other plesiosaurians (e.g. Andrews 1910, 1913; Brown 1981; O'Keefe 2001; Druckenmiller and Russell 2008a).

Maxilla. The maxillae enclose the anterior and lateral margins, and the anterior half of the medial margin, of the external naris (Text-figs 2, 4). Numerous small foramina are present on the external surfaces of the maxilla. A broad, longitudinal trough extends anteriorly from the naris along the dorsolateral surface of the maxilla (Text-fig. 4A), a distinct feature also noted by O'Keefe (2001). This trough is bounded laterally by a prominent ridge immediately anterior to the naris. A similar trough and ridge are present in *Hauffiosaurus longirostris* (MCZ 1033; White 1940), which is better preserved anteriorly, showing that the ridge terminates on the posterior part of the lateral surface of the premaxilla. It is unlikely that these well-defined structures result from dorsoventral crushing. In MANCH LL 8004, crushing is pronounced posteriorly, but does not seem to have affected the snout. O'Keefe (2001, character 37) described a trough on the maxilla in *Macroplata tenuiceps* (NHMUK R5488), *H. longirostris* ('*Macroplata*') and rhomaleosaurids. In *Macroplata* and rhomaleosaurids, this trough is shallow and does not extend far anteriorly (NHMUK R5488, Ketchum and Smith (2010); LEICS G221.1851, Cruickshank (1994a)), unlike the condition in *Hauffiosaurus* (MCZ 1033, MANCH LL 8004).

The maxilla contacts the frontal both medial and lateral to the external naris. The medial contact occurs approximately midway along the external naris and is deeply interdigitating with a posteromedial trend (Text-fig. 4B–C). Lateral contact between the maxilla and frontal occurs at the posterolateral margin of the external naris. It extends posteriorly as a weakly interdigitating suture that terminates at the anterior border of the prefrontal. The interdigitating maxilla–prefrontal suture curves posterolaterally and terminates at the anterodorsal margin of the lacrimal. The posterior portion of the maxilla is poorly preserved. It extends posteriorly, ventral to the lacrimal, which it contacts in a weakly interdigitating, posteroventrally oriented suture.

Lacrimal. An anterodorsally elongate ossification forms the anteroventral margin of the orbit, dorsal to the posterior process of the maxilla (Text-fig. 4). This forms interdigitating sutures with the prefrontal dorsally and maxilla ventrally. The interdigitating is weak, except for at the anterodorsal edge of the element. This bone is identified as a lacrimal (*sensu* Williston (1907) in *Brachauchenius*; Andrews (1913) in *Liopleurodon*; Linder (1913) in *Peloneustes*), only otherwise identified in pliosaurids among plesiosaurians (Druckenmiller and Russell 2008a). Other authors have interpreted this ossification as a long anterior extension of the jugal (e.g. Carpenter 1996; O'Keefe 2001), but our observations of well-preserved pliosaurid specimens indicate that the 'lacrimal' is separated from the jugal by an interdigitating suture ventral to the orbit (*Brachauchenius* USNM 4989, *Liopleurodon* NHMUK R2680, *Peloneustes* CAMSM X 50163, *Pliosaurus brachyspondylus* BRSMG Cc332). This region of the skull is poorly preserved in *H. longirostris* (MCZ 1033) and cannot be observed in *H. zanoni* (O'Keefe 2001).

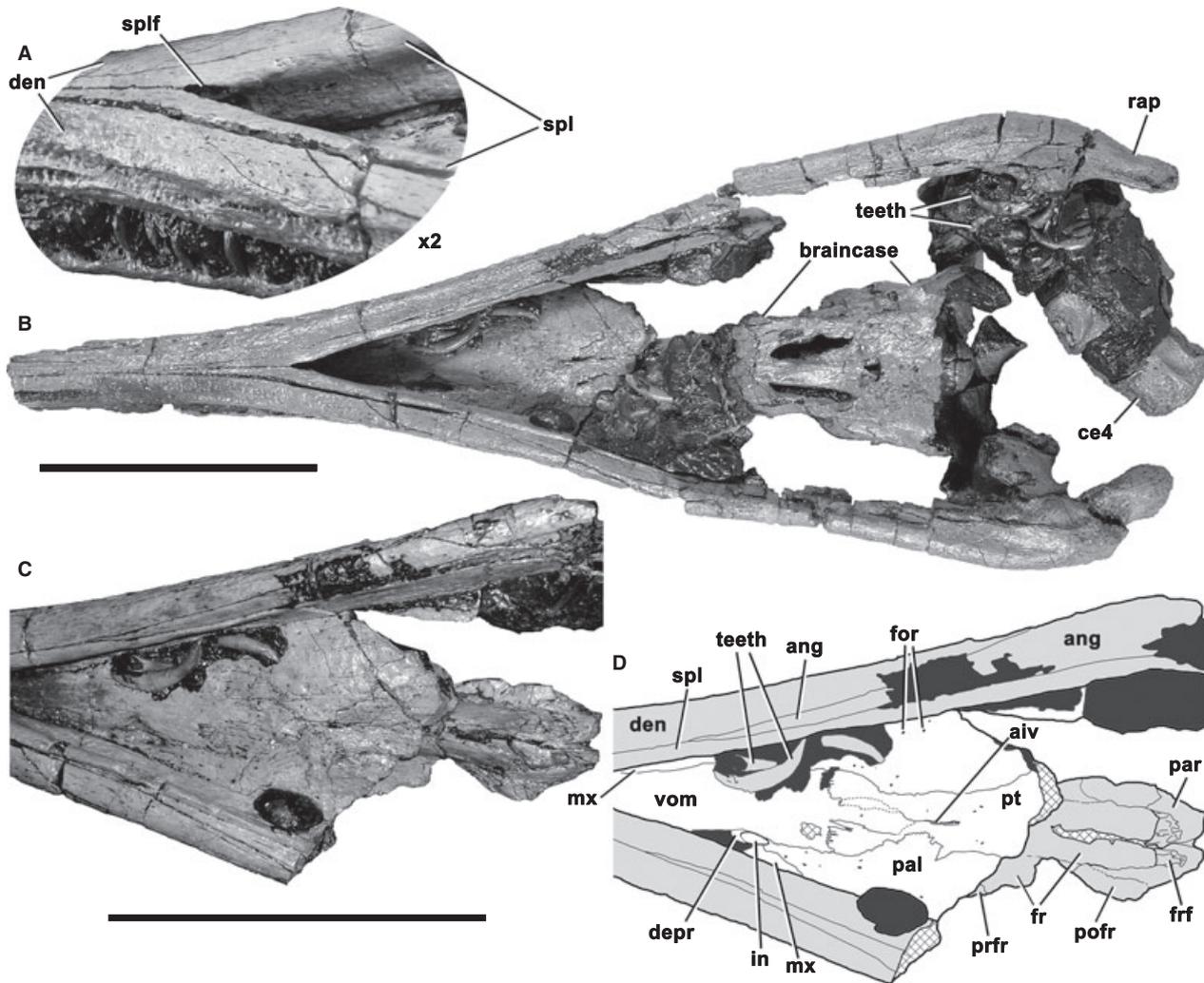
Prefrontal. The prefrontal forms the smooth, concave anterior and anterodorsal margins of the orbit (Text-figs 2, 4). Medially, the prefrontal overlaps the frontal. The posterodorsal process of the prefrontal tapers posteriorly to its termination at the intersection of the prefrontal–frontal contact and the orbital margin. Thus, the prefrontal extends approximately one-third of the way along the dorsal margin of the orbit. A narrow longitudinal ridge is present on the dorsal surface of the posterodorsal process (Text-fig. 2B). Anterior to the orbit, the prefrontal contacts the maxilla in a posterolaterally oriented, interdigitating suture that extends to the prefrontal–lacrimal contact.

Frontal. The frontals are large, complex elements that extend from the external nares to the posterior margins of the orbits, a short distance anterior to the parietal foramen. The dorsal surface of the frontal bears numerous small foramina (Text-figs 2, 4). The anterolateral processes of the frontals form the smooth posterior margins of the external nares and are separated along the midline by the posterior processes of the premaxillae. The lateral margins of the anterolateral processes of the frontals contact the maxillae anteriorly and the prefrontals posteriorly, forming interdigitating sutures with both elements. The premaxilla is excluded from the medial margin of the external naris by a small anterior extension of the frontal, which contacts the maxilla (Text-fig. 4B–C). There is no evidence for the presence of a separately ossified nasal in this region, which is well preserved. A nasal has been identified in a range of plesiosaurians (reviewed by Druckenmiller and Russell 2008a, p. 28) and more basal pistosaurians (e.g. Meyer 1847–1855; Sues 1987; Cheng *et al.* 2006; but see Rieppel *et al.* (2002) who suggested that *Augustasaurus* and *Pistosaurus* lack nasals). However, these observations remain tentative as little direct, photographic evidence has been published, and different authors regard the 'nasals' of different taxa as having highly variable proportions and morphology (e.g. Noè 2001; O'Keefe 2001; Cheng *et al.* 2006; Druckenmiller and Russell 2008a; Sato and Wu 2008; Gasparini 2009). Our observations suggest that the 'nasals' of at least some taxa may simply be a narrow posteromedial extension of the maxilla similar to that in *H. tomistomimus* (Text-fig. 4B–C), a broad anterior extension of the prefrontal that contacts the posterior margin of the naris (e.g. '*Kronosaurus*', QM F51291), or are delimited by cracks in the specimen that have been misidentified as sutures (e.g. *Peloneustes*, NHMUK R8574; O'Keefe 2001). The variety of means by which nasals may have been mistakenly identified explains the highly variable apparent morphology, and we doubt that they are widely present among adult plesiosaurians. Although a separate ossification may be present in this region in *Liopleurodon* (Noè 2001) and *Nichollsaura* (Druckenmiller and Russell 2008b), we consider that it is absent in most other taxa.

The frontals contact each other posterior to the premaxillae, forming a straight, midline butt joint. The central and posterior portion of the left frontal is broken and displaced to the left, and the right frontal has been displaced slightly to the right. This reveals the longitudinally grooved medial contact surfaces of the frontals (Text-fig. 2E–F). There is no evidence that a medial aperture was present between the frontals prior to deformation. However, more posteriorly, narrow anterior processes of the parietals divide the frontals across the midline. The medial

margins of the frontals slightly overlap the anterior processes of the parietals. The posterolateral borders of both frontals are broken. However, the preserved morphology suggests that the frontal contributes to the dorsal margin of the orbit posterior to the prefrontal and anterior to the postfrontal. The frontal enters the dorsal margin of the orbit in most plesiosaurians, but are excluded by contact between the prefrontal and the postfrontal in some Lower Jurassic taxa [*Macroplata tenuiceps*, NHMUK R5488, Ketchum and Smith (2010); unnamed taxon, NHMUK 49202], plesiosaurids (e.g. Storrs 1997), Cretaceous pliosaurids such as *Kronosaurus queenslandicus* (QM F51291) and an unnamed taxon (FHSM VP 321, referred to *Brachauchenius lucasi* by Carpenter (1996), but see Ketchum and Benson (2010)), and many Cretaceous plesiosauroids including leptocleidians and elasmosaurids (see Ketchum and Benson (2010), character 19 for the distribution of this feature).

The exposure of the frontals on the ventral surface of the skull roof differs from that on the dorsal surface. Paired, bar-like processes extend posteriorly along the ventral surfaces of the parietals adjacent to the midline, terminating immediately anterior to the parietal foramen (Text-fig. 5C–D). Both processes are broken posteriorly, revealing that they formed an interdigitating sutural attachment to the parietal. The ventromedial surfaces of these posterior processes bear deep troughs. Together, these troughs form a midline channel in the ventral surface of the frontals posteriorly. Anteriorly, this channel is closed ventrally by contact between ventromedial flanges of the frontals, forming a canal. This morphology was also described in the pliosaurid *Peloneustes* by Andrews (1913, text-fig. 13), who suggested that it accommodated the olfactory nerves. A well-preserved ventral skull roof is also known in the plesiosauroid *Seeleyosaurus* (SMNS 16812). In *Seeleyosaurus*, the posterior



TEXT-FIG. 5. *Hauffiosaurus tomistomimus* sp. nov. Skull of MANCH LL 8004. A, magnification (×2 from B) of posterior portion of the symphysis in right ventrolateral view, B, complete skull in ventral view, C–D, posterior portion of rostral section of skull in ventral view. In line drawing (D), dark-grey shading indicates matrix, crossed-hatching indicates broken bone, and light-grey tone indicates bone other than the palate (i.e. mandible, skull roof, teeth). Scale bars represent 100 mm.

processes of the frontals are narrow and elongate and bear a ventral channel that is not enclosed (Großmann 2007).

Postfrontal. A small part of each postfrontal is preserved antero-lateral to the parietal foramen (Text-fig. 2). The exposure of the postfrontal on the dorsal surface of the skull roof is small and triangular and contacts the parietal posteromedially and the frontal anteromedially. However, because the postfrontal slightly underlaps the parietal and significantly underlaps the frontal, exposure on the ventral surface of the skull roof is more extensive (Text-fig. 5C–D).

Parietal. The parietals are large, unfused elements that contact each other dorsally in a straight midline suture (Text-figs 2, 6A). The parietal encloses the anteroposteriorly oriented, ovate parietal foramen. Anterior to this foramen, the parietals form narrow, prong-like anterior processes that separate the posterior portions of the frontals along the midline. Short anterior processes of the parietals are exposed on the dorsal surface of the skull in most plesiosaurians other than cryptoclidids (Andrews 1910; Brown 1981; Maisch 1998), including *Thalassiodracon* (CAMSM J.46986: Storrs and Taylor 1996). In pliosaurids, the parietals extend far anteriorly to contact the posterior processes of the premaxillae, but these anterior extensions are not distinct from the body of the parietal as they are not transversely narrow (e.g. Andrews 1913), unlike those of *H. tomistomimus*. In *H. tomistomimus*, the anterior processes of the parietals are both distinct and elongate (Text-fig. 2), even considering lateral displacement of the frontals, which may have dorsally exposed an otherwise concealed anterior portion of the processes. Long anterior processes of the parietals may be an autapomorphy of *H. tomistomimus*, although as the condition cannot be determined in *H. longirostris* or *H. zanoni* this may represent a synapomorphy of *Hauffiosaurus*. These processes are underlain by the posterior processes of the frontals (Text-fig. 5C–D).

Posterior to the pineal foramen a low, sharp parietal crest marks the apex of a robust vault over the braincase. This crest divides the temporal fenestrae medially and has been displaced slightly to the left and crushed ventrally over the supraoccipital. Many other longirostrine plesiosaurians, such as the pliosaurids *Peloneustes* (NHMUK R8574: Ketchum 2007) and an unnamed taxon (FHSM VP321), some polycotyliids such as *Dolichorhynchops* (O’Keefe 2004; Sato 2005) and *Trinacromerum* (O’Keefe 2008), and even some shorter-snouted taxa, including most elasmosaurids (e.g. Carpenter 1999; Sato 2002, 2003), have tall, narrow parietal crests. The low crest of *H. tomistomimus* is comparable to those of more basal plesiosaurians such as *Rhomaleosaurus megacephalus* (LEICS G221.1851: Cruickshank 1994a), *Plesiosaurus* (Storrs 1997), *Thalassiodracon* (CAMSM J.46986: Storrs and Taylor 1996) and cryptoclidids (Andrews 1910; Brown 1981).

Squamosal. The anterior processes of the squamosals, comprising the lateral margins of the temporal fenestrae, are broken on both sides (Text-figs 2–3). The dorsal rami of the squamosals enclose the posterior margins of the temporal fenestrae (Text-fig. 2). They contact across the midline posterior to the parietal crest, forming an arch-like suspensorium over the braincase.

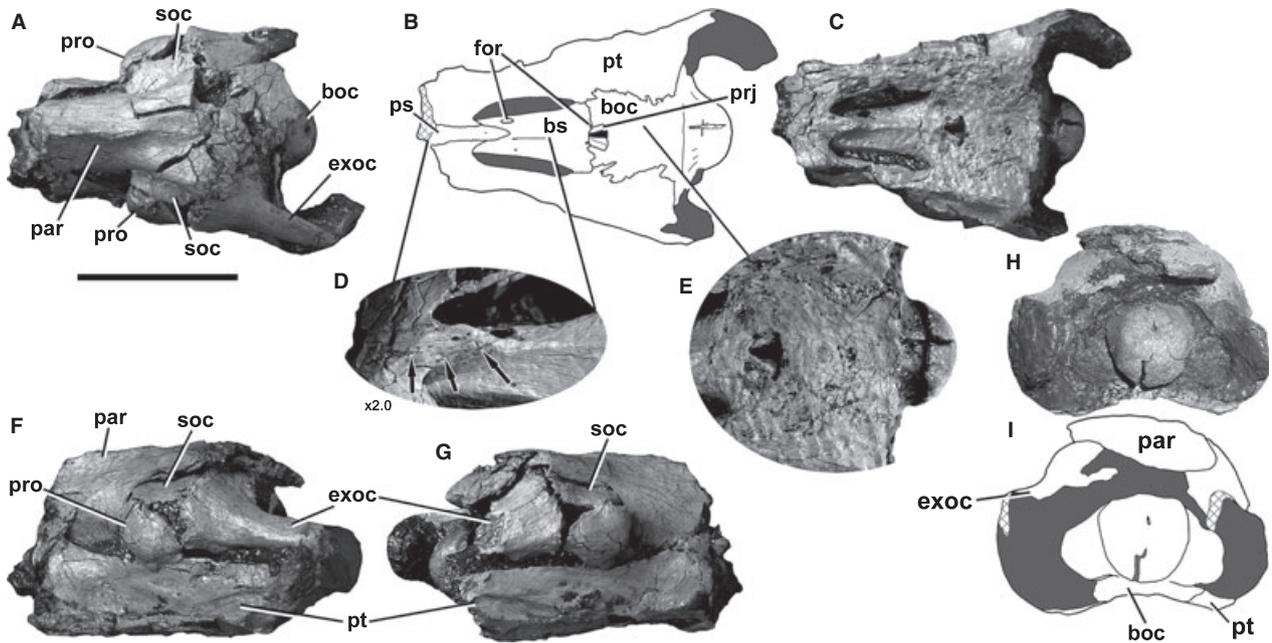
This has been crushed anteroventrally so that the concave ventromedial margins of the dorsal rami of the squamosals are visible in dorsal view (Text-fig. 2A–B). The dorsomedial intersquamosal contact interdigitates and is expanded posteriorly to form a peaked squamosal bulb. The posterior surface of the left squamosal is well preserved. It bears a series of rugose excrescences, forming a mediolaterally oriented ridge (Text-fig. 7D–E). A rugose ridge is also present in this location in many other plesiosaurians, including *Thalassiodracon* (CAMSM J.46986), *Borealonectes* (Sato and Wu 2008) and the pliosaurid *Peloneustes* (Ketchum 2007). However, it is generally a low, rugose, angular ridge rather than a series of prominent rugosities.

The squamosal forms sheet-like ventral processes that overlap the medial and lateral surfaces of the quadrate. Thus, the quadrate shaft is visible only in posterior view, as a subrectangular surface (Text-fig. 7D–E), bounded medially and laterally by vertically oriented sutures with the squamosal. The lateral squamosal–quadrate suture is located at the apex of an angular, dorsoventrally oriented crest on the posterolateral surface of the suspensorium. A subcircular depression is present on the posterior surface of the squamosal immediately dorsal to the quadrate (Text-fig. 7D–E). This is widely present among plesiosaurians, although in OXFUM J.28585 (Cruickshank (1994b), referred therein to *Euryycleidus* but probably representing a distinct, unnamed taxon), *Rhomaleosaurus cramptoni* (Smith and Dyke 2008) and *Rhomaleosaurus zetlandicus* (Taylor 1992), a large foramen is present in this location (Smith and Dyke (2008), character 31). It is possible therefore that this depression is a vestige of fusion between the quadrate and squamosal, and its presence may be ontogenetic. The medial surface of the squamosal around midheight of the quadrate bears two small pits (Text-fig. 7F–G). A single pit in this location was described in *Thalassiodracon* as the ‘stapedial pit’ by Storrs and Taylor (1996), but its function remains uncertain, as does the function of the second pit in *H. tomistomimus*.

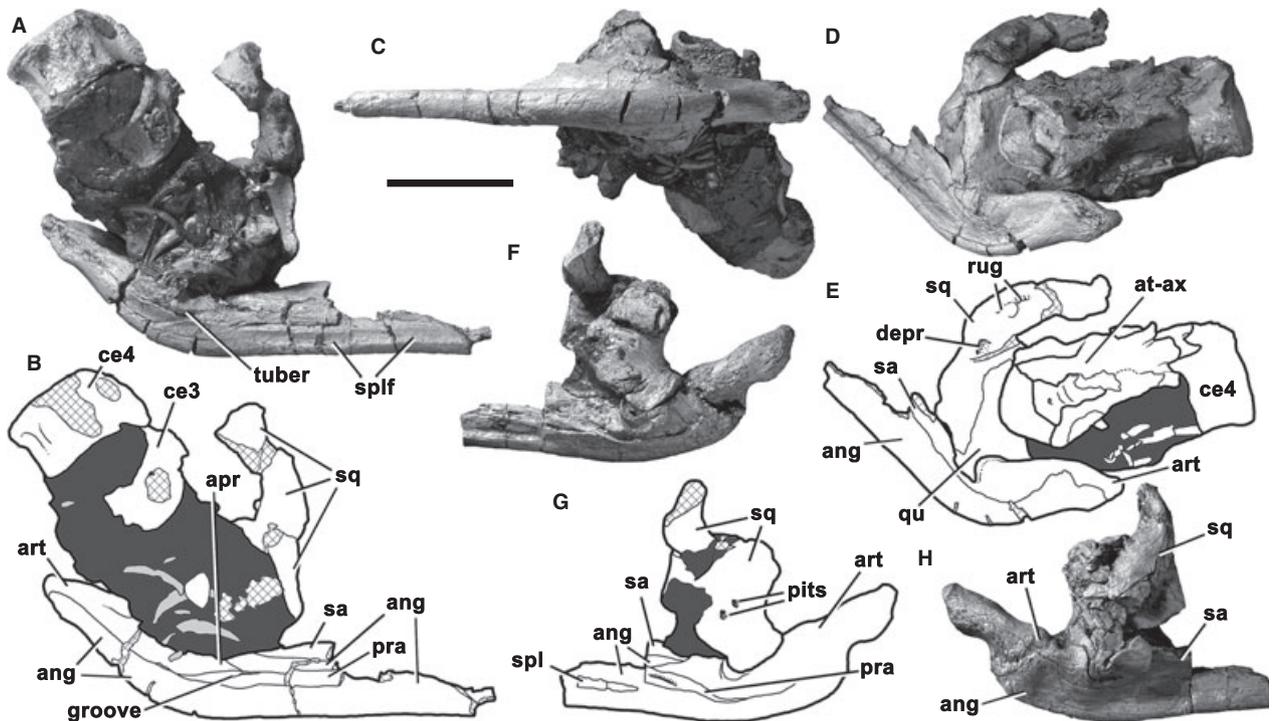
Palate

The palate of *H. tomistomimus* is almost planar. It is well preserved with little evidence of distortion or crushing. However, it is broken posteriorly, and a large portion remains covered by matrix or obscured by the articulated mandible (Text-fig. 5).

Vomer. The vomers form the anterior portion of the palate, including the medial and anterior margins of the internal nares (Text-fig. 5). The vomer is depressed immediately anterior to the internal naris, although the deep groove extending anteriorly from the naris described by Cruickshank *et al.* (1991) and Cruickshank (1994a) in *Rhomaleosaurus megacephalus*, and observed in *Rhomaleosaurus cramptoni* and *Rhomaleosaurus thorntoni* by Smith and Dyke (2008), is absent in *H. tomistomimus*. The midline suture between the vomers is fused and cannot be distinguished. The vomer is bounded laterally by contact with a narrow palatal shelf of the maxilla. At the posterior margin of the internal naris, the lateral edge of the vomer contacts the anterior process of the palatine in a gently sinuous suture that extends posteriorly for a short distance and terminates at the



TEXT-FIG. 6. *Hauffiosaurus tomistomimus* sp. nov. Braincase of MANCH LL 8004 in A, dorsal, B–C, E, ventral, D, right ventrolateral, F, left lateral, G, right lateral, and H–I, posterior views. D, magnification (×2) showing parasphenoid-basisphenoid suture (indicated by arrows), E, magnification (×1.5) showing ventral surface of posterior basicranium. In line drawings (B, I), dark-grey tone indicates matrix and crossed-hatching indicates broken bone. Scale bar represents 50 mm.



TEXT-FIG. 7. *Hauffiosaurus tomistomimus* sp. nov. MANCH LL 8004, A–E, posterior portion of left mandible and anterior four cervical vertebrae shown with mandible in A–B, medial, C, ventral and, D–E, posterolateral views, F–H, posterior portion of right mandible in F–G, medial, and H, lateral views. In line drawings (B, G, E), dark-grey tone indicates matrix, light-grey tone indicates teeth, and crossed-hatching indicates broken bone. Scale bar represents 50 mm.

transversely oriented, interdigitating vomer–pterygoid contact. A short posterior projection of the vomers separates the anterior processes of the pterygoids across the midline. Owing to poor preservation in this region, the posterior extent of the vomers cannot be precisely determined.

Palatine. The palatines form most of the palate posterior to the vomers and lateral to the pterygoids. They bear numerous small nutrient foramina on their ventral surfaces. The palate is incompletely preserved, and the posterior portions of the palatines are broken away. Transversely narrow, tapering anterior processes of the palatines contact the posterior margins of the internal nares (Text-fig. 5). Entry of the palatine into the internal narial margin is highly variable among plesiosaurians. For instance, the palatine participates in the narial margin in some rhomaleosaurids (e.g. *Rhomaleosaurus megalcephalus*, LEICS G221.1851, Cruickshank (1994a)), but is excluded in others (e.g. *Maresaurus coccai*, Gasparini (1997); *Meyerasaurus victor*, SMNS 12478; Smith and Vincent 2010); it participates in the margin in the pliosaurid *Peloneustes* (Ketchum 2007), but is excluded in *Liopleurodon* and *Simolestes* (Noè 2001). The right palatine is displaced medially in MANCH LL 8004 so that it overlaps the pterygoid. The left palatine is well preserved and apparently not displaced. The medial contact with the pterygoid is interdigitating and forms a laterally concave curve.

Pterygoid. The anterior processes of the pterygoids extend anteriorly, lateral to the posterior process of the vomers and between the anterior processes of the palatines. O’Keefe (2001, fig. 9) figured only a small anterior process in this position, and only on the right side. However, the processes are transversely broad, subrectangular, and present on both sides (Text-fig. 5C–D). They are separated from more posterior portions of the pterygoids by a transverse constriction. This constriction has not previously been observed in any other plesiosaurian palate (e.g. Andrews 1910, 1913; O’Keefe 2001; Druckenmiller and Russell 2008a) and may be an autapomorphy of *H. tomistomimus*. As the palate is not well preserved in *H. longirostris* or *H. zanoni*, this may alternatively represent a synapomorphy of *Hauffiosaurus*. A narrow, slit-like anterior interpterygoid vacuity is present between the pterygoids just posterior to the anterior processes (Text-fig. 5). This slit-like morphology seems to arise from lack of fusion along the midline interpterygoid suture; it is present in smaller, likely ontogenetically immature, specimens of *Liopleurodon* (LEICS G418.1956/58a4; Noè 2001) and *Peloneustes* (NHMUK R3803; Andrews 1913), but absent in larger individuals [*Liopleurodon*, NHMUK R3536, Noè (2001); *Peloneustes*, NHMUK R5874]. However, it is distinct from the transversely wide anterior interpterygoid vacuity of many leptoclidians, some rhomaleosaurids and plesiosaurids (see Druckenmiller and Russell (2008a), character 49; Ketchum and Benson (2010), character 59 for the distribution of this feature).

A large central portion of the pterygoids is not preserved or is covered by matrix (Text-fig. 5B). The posterior parts of the pterygoids form sheets that underlie the braincase, forming the ventral and ventrolateral surfaces of the cranium (Text-fig. 6B–G) and are separated along the midline by the parasphenoid, posterior interpterygoid vacuity and ventral exposure of the

basioccipital. The medial margins of the pterygoids form interdigitating sutures with the parasphenoid, basisphenoid and the ventral plate of the basioccipital (Text-fig. 6B–C). They also form the smooth edges of the large, oval posterior interpterygoid vacuity. The ventral surfaces of the pterygoids are smooth and lack the posterolaterally oriented ridges that are present adjacent to the posterior interpterygoid vacuity in pliosaurids (e.g. Andrews (1913); Druckenmiller and Russell (2008a), character 51; Ketchum and Benson (2010), character 64) and *Microcleidus* (NHMUK 36184).

Posterodorsally, the pterygoids contact the basal tubera of the basioccipital. Posterior to the ventral exposure of the basioccipital, the posterior rami of the pterygoids diverge posterolaterally, forming transversely narrow, dorsoventrally high quadrate flanges. They are incompletely preserved, and the morphology of the pterygoid–quadrate contact cannot be determined.

Braincase

Supraoccipital. The dorsolateral portions of the supraoccipital (located anterolaterally owing to dorsoventral crushing of the posterior part of the skull) are exposed in dorsal and lateral views (Text-fig. 6A, F–G). The central portions of the bone are concealed by the parietal. The supraoccipital was dorsoventrally low, estimated as between two and three times as wide transversely as it was high dorsoventrally. Its anteroposterior depth cannot be determined. Typically in plesiosaurians, the supraoccipital contacts the parietals dorsally and the exoccipital–opisthotics ventrolaterally, forming the dorsal margin of the foramen magnum.

Exoccipital–opisthotic. The exoccipital–opisthotics have also been displaced so that the paraoccipital processes are directed more horizontally than they were in life. Hence, their original orientation cannot be precisely determined. The paired exoccipital–opisthotics form the lateral margins of the foramen magnum. The body (primarily comprising the opisthotic) forms a robust pillar, and the paraoccipital process (comprising the lateral portion of the exoccipital) is slender; the sutures between the two elements are not clearly preserved. The distal ends of the paraoccipital processes are broken, and their morphology and contacts cannot be determined.

Prootic. The prootics have convex lateral surfaces and approximately subcircular outlines in lateral view. The posterior and dorsal surfaces are flattened and form contact surfaces for the opisthotic and supraoccipital respectively.

Parasphenoid. Our interpretation of the identities and extent of ventral braincase elements (Text-fig. 6B–E) differs from those of O’Keefe (2001, fig. 9) and White (1940) for *H. longirostris* (MCZ 1033). These differences are summarized in Table 1. The parasphenoid forms interdigitating sutures with the pterygoids anteriorly (Text-fig. 6D), although breakage and attached matrix obscure the anterior extent of the parasphenoid. Its preserved posterior portion extends a short distance posteriorly along the ventral surface of the basisphenoid as a triangular process

TABLE 1. Identification of ventral braincase elements herein compared to that of O'Keefe (2001).

	Anterior			Posterior
Herein	Parasphenoid anteriorly; basisphenoid keel posteriorly	Basisphenoid	Basioccipital, ventral plate	Basioccipital, main body and occipital condyle
O'Keefe (2001)	Parasphenoid, ventral keel	Parasphenoid, main body	Basisphenoid	Basioccipital

between the interpterygoid vacuities (Text-fig. 6D). O'Keefe (2001, fig. 9) interpreted the short, triangular element (which is here interpreted as the entire parasphenoid) as a ventral keel ornamenting a larger, robust parasphenoid body (interpreted as the basisphenoid herein). However, interdigitating sutures demarcate the boundary between this small triangular element and the larger more robust element dorsal to it (Text-fig. 6D), indicating that the 'ventral keel' of O'Keefe (2001) is a separate ossification constituting the entire parasphenoid.

Basisphenoid. The basisphenoid is a robust element that bisects the posterior interpterygoid vacuity (Text-fig. 6B–C). A ventral longitudinal ridge on the basisphenoid extends a short distance posterior to the parasphenoid. A single large foramen on the left side and several, scattered, smaller foramina pierce the basisphenoid lateral to the midline ridge. A large ventrolateral foramen on the left side of the basisphenoid is also present in a specimen of *Thalassiodracon* (CAMSM J.46986), although other specimens are too poorly preserved to determine whether the presence of this foramen is polymorphic. The function of this opening is uncertain, but it may simply be an enlarged nutrient foramen. Posteriorly, the basisphenoid contacts the basioccipital in a transversely oriented, interdigitating suture. A large midline opening is present at this junction, similar to that of some cryptoclidids, such as *Cryptoclidus* (NHMUK R2860: Andrews 1910, pl. 9, fig. 5) and *Muraenosaurus* (NHMUK R2422: Maisch 1998; Ketchum and Benson 2010). This opening was noted by O'Keefe (2001) as a possible autapomorphy of *Hauffiosaurus longirostris* ('*Macroplata*'), to which he referred MANCH LL 8004 (*H. tomistomimus* herein). However, it is also present in *H. zanoni* (HAUF 7) and was found as a synapomorphy of a clade comprising *H. longirostris*, *H. tomistomimus* (MANCH LL 8004) and *H. zanoni* by Ketchum and Benson (2010, character 70). The foramen may represent the basicranial fontanelle, an unossified area at the basisphenoid–basioccipital contact of some tetrapods, representing the embryonic fenestra basicranialis. Its location is consistent with our interpretation of the anterior extent of the basioccipital. The basicranial fontanelle is present in some extant squamates and may close during ontogeny in some taxa (Conrad (2004) and references therein), although this is unlikely in at least some plesiosaurians as *H. longirostris* represents a large, and possibly mature individual that retains the fontanelle (MCZ 1033). Posterolaterally elongate ventral projections from within the braincase form the lateral margins of the basicranial fontanelle and are clearly demarcated from the enclosing portions of the basisphenoid and basioccipital. These are also present in *H. longirostris* and were identified by White (1940) and O'Keefe (2001) as the only visible portion of the basisphenoid ('clivus'), consistent with White's (1940, fig. 4A) illustrations of the basicranial complex of *H. longirostris*. Although our interpretation of

the braincase of *Hauffiosaurus* is different (Table 1), it is still possible that these projections are part of a vertical notch in the posterior surface of a dorsally located basisphenoid body. This notch is primitively present in plesiosaurians (Druckenmiller and Russell 2008a). The presence of these projections cannot be determined owing to poor preservation in *H. zanoni* (HAUF 7).

Basioccipital. The basioccipital forms a robust palatal process that projects ventral to the occipital condyle as a rectangular plate (Text-fig. 6B–C, E). The posterior margin of this structure was interpreted as a transversely oriented sutural connection between the basisphenoid and the basioccipital by O'Keefe (2001, fig. 9). However, close examination reveals no clear evidence for a suture in this region.

Posteriorly the basioccipital forms the subcircular occipital condyle (Text-fig. 6E, H, I). A small notochordal pit is located dorsally on the posterior surface of the condyle. It is not possible to determine whether the exoccipital-opisthotic facets were separated from the occipital condyle by a groove or neck as they are in some plesiosaurians (Druckenmiller and Russell 2008a), including *H. longirostris* (White 1940, fig. 4A). However, a distinct groove encircles the ventral and lateral surfaces of the neck of the condyle.

Mandible

The mandible is almost complete, measuring 420 mm long as preserved. Only a small anterior portion of the symphysis is missing, and both mandibular rami are broken in the region between the coronoid eminence and jaw articulation (Text-fig. 3). The preorbital mandible is firmly attached to the cranium (Text-figs 3, 5). Posterior to the orbit, however, the mandible is visible from most angles (Text-fig. 7). The mandibular symphysis is 110 mm long. As it is incompletely preserved, it must have originally comprised more than 0.26 times the length of the mandible.

Dentary. The dentaries are the largest elements of the mandible. They taper anteriorly until the lateral surfaces are approximately parallel in the anterior half of the symphyseal rostrum (Text-fig. 5). Therefore, *Hauffiosaurus tomistomimus* has a narrow, unexpanded snout tip, similar to that of *H. longirostris* (MCZ 1033: White 1940), *H. zanoni* (HAUF 7) and some polycotylids (e.g. Carpenter 1996; O'Keefe 2008), but unlike those of longirostrine plesiosaurids, in which the rostrum is transversely expanded anteriorly to form a spatulate tip, separated from the remaining portion of the snout by a rostral constriction (e.g. *Peloneustes*: Andrews 1913; O'Keefe 2001; Ketchum 2007). The ventral and lateral surfaces of the dentary bear numerous anteroposteriorly elongate foramina; those of the lateral surface are relatively large (Text-fig. 3). A shallow longitudinal trough occupies the lateral surface of the dentary

posterior to its midlength. This is also present in *H. longirostris* (MCZ 1033; White 1940) and *H. zanoni* (HAUF 7).

Much of the medial surface of the dentary is covered by the splenial, with which it forms a straight, longitudinal suture along the ventral surface of the mandible (Text-fig. 5). This contact is divided by the anterior process of the angular from approximately 40 mm posterior to the symphysis. The dentaries are separated ventrally on the midline by the splenials for much of the length of the symphysis. Only in the anterior one-third of the symphysis, as preserved, do the dentaries contact one another along the midline in a straight butt joint that is visible in ventral view (Text-fig. 5A–B). As the rostrum is incomplete, this proportion would originally have been greater. The ventral surface of the symphysis is smooth and gently convex. This is unlike the condition in *Hauffiosaurus longirostris*, in which a prominent, broad ventral keel is present (MCZ 1033); the ventral surface of the symphysis of *H. zanoni* is unknown.

Splenial. In ventral view, the narrow anterior ends of the splenials enter the mandibular symphysis medial to the dentaries and are joined along a straight midline suture (Text-fig. 5). The splenials have been separated by slight deformation and displacement at the posterior end of the symphysis, revealing that their medial contact surfaces are concave, perhaps because of incomplete ossification (Text-fig. 5A–B). A large, oval opening dorsal to this contact represents the anterior opening of Meckel's canal. The splenial forms the smooth, ventromedial surface of the mandible posterior to the mandibular symphysis; it is restricted to the medial surface of the mandible from about midlength of the postsymphysial mandibular rami by broadening of the ventral exposure of the angular.

Coronoid. The coronoid covers the medial surface of the dentary dorsal to the splenial anteriorly, but is not well exposed. It is primarily visible in dorsal view, forming the dorsomedial surface of the mandible ventral to the orbit (Text-fig. 2). It extends posteriorly to an almost vertical, crenulated suture with the surangular adjacent to the level of the parietal foramen. However, the coronoid is incompletely preserved and may have overlapped the surangular further posteriorly.

Angular. The angular forms a long anterior process that separates the dentary and splenial on the ventral surface of the mandible anteriorly and forms the ventral portion of the postsymphysial mandible (Text-fig. 5), expanding posteriorly. It terminates in an interdigitating suture with the articular that transversely crosses the posterior surface of the retroarticular process (Text-fig. 7).

A shallow longitudinal trough located ventrally on the medial surface of the angular anterior to the glenoid is identified here as the splenial facet (Text-fig. 7). A small sheet-like fragment of bone covering this trough in the right angular is likely a posterior fragment of the splenial. However, the posterior part of the splenial has otherwise not been preserved.

Surangular. The surangular is visible immediately anterior to the mandibular glenoid. More anteriorly it is broken, so it is not clear whether it formed a transversely narrow plate of bone as in most

plesiosaurians, including the long-snouted polycotyliids, or was transversely broad, bearing a longitudinally elongate elliptical depression as in pliosaurids (Druckenmiller and Russell 2008a; Ketchum and Benson 2010). Druckenmiller and Russell (2008a, p. 47) also noted the broad condition in *Rhomaleosaurus zetlandicus*. The surangular forms a straight, longitudinal contact with the angular. This contact is visible on both the medial and lateral surfaces. The contact plane slants dorsolaterally so that the lateral sutural exposure is higher dorsally than the medial exposure (Text-fig. 7). The surangular contacts an anterior projection of the articular posteroventrally on the medial surface of the mandible. However, other details of the surangular–articular contact cannot be determined, and it is possible that the two were fused.

Prearticular. The prearticular is a dorsoventrally narrow, splint-like element on the medial surface of the mandible (Text-fig. 7). It lies within a shallow facet on the angular and is approximately horizontal. The dorsomedial surface of the prearticular bears a longitudinal groove around midlength. The ventral margin of this groove is marked by a medially projecting longitudinal ridge. Anterior to this, the mandible is poorly preserved, and the morphology of the prearticular cannot be determined. The posterior portion of the prearticular tapers dorsoventrally. It forms a dorsally convex projection, housed in a groove between the angular and articular (Text-fig. 7). This terminates ventral to approximately glenoid midlength, whereas in pliosaurids such as *Peloneustes* the prearticular terminates ventral to the anterior margin of the glenoid (Ketchum 2007). In an unnamed Lower Jurassic taxon (OXFUM J.28585; Cruickshank (1994b), referred to *Euryleidus*, but see Ketchum and Benson (2010)), the prearticular terminates posterior to the glenoid and does not extend far anteriorly. Unfortunately, this region of the mandible is often poorly preserved, so the phylogenetic distribution of prearticular morphology is unclear.

Articular. The articular forms the glenoid and dorsal portion of the retroarticular process (Text-fig. 7). The glenoid is obscured by the quadrate. It has a slightly thickened, sharp medial lip, but its lateral surface is smooth and only slightly expanded. A rugose, triangular process of the articular extends along the medial surface of the mandible anterior to the glenoid. This is widespread among plesiosaurians. Ventrally, at the base of this process, a raised tuber projects medially (Text-fig. 7A).

The retroarticular process is transversely narrow and posterodorsally inclined. Its dorsal surface is weakly transversely concave, and the ventral surface is highly convex, bearing a robust longitudinal ridge of the angular. The retroarticular process of the right mandible is heavily pitted, rugose and swollen in places such that the angular–articular suture cannot be identified (Text-fig. 7F–H). This is probably pathologic as the left retroarticular process is smooth, well formed and clearly shows the sutural line between the two constituent elements.

Dentition

The left dentary contains 33 alveoli (Text-fig. 4A). This is a minimum estimate, as the anterior end of the bone is not preserved,

and the maxilla obscures it posteriorly. We estimate that three further alveoli may have been present in this region, and one or two more were likely present anteriorly (based on comparison with *H. zanoni*, HAUF 7). *H. tomistomimus* therefore had 37–38 dentary alveoli, the most posterior of which was located just anterior to orbital midlength. By contrast, only 16 alveoli are preserved in the right maxilla (Text-fig. 3A: 14 are preserved in the left maxilla, which is less complete). The most posterior preserved alveolus is ventral to the anterior margin of the orbit. In *Hauffiosaurus zanoni*, the maxillary tooth row continues posteriorly just anterior to the postorbital bar, and in this region the alveoli are small and closely packed. Comparison suggests that *H. tomistomimus* may have had approximately the same number of maxillary alveoli as *H. zanoni* (there are at least 24 alveoli in HAUF 7). Therefore, the maxilla contained approximately two-thirds as many alveoli as the dentary in *H. tomistomimus*. This discrepancy is partly attributable to the large size of the maxillary alveoli, the largest of which are widely spaced and anteriorly located. These enlarged anterior maxillary alveoli are also present in *H. zanoni* (HAUF 7). They are preceded by a small anterior-most maxillary tooth, which is likely present but not well preserved in MANCH LL 8004. This indicates the presence of a ‘heterodont’ dentition, which is also present in *H. longirostris*, pliosaurids (Andrews 1913; O’Keefe 2001; Druckenmiller and Russell 2008a), some polycotylids such as *Edgarosaurus* (MOR 751: Druckenmiller 2002), and a range of other plesiosaurians (e.g. Druckenmiller and Russell 2008a). As the premaxilla is very poorly preserved, the number of premaxillary alveoli cannot be determined directly. However, comparison with the broken section of the dentary anterior to the maxilla suggests that at least five premaxillary teeth were present. Seven premaxillary teeth are present in *H. zanoni* (HAUF 7; O’Keefe 2001), and nine and a half are present in *H. longirostris* (MCZ 1033; White 1940; the posteriormost premaxillary alveolus is bisected by the premaxilla-maxilla suture).

Some broken teeth are preserved in their alveoli, and numerous disarticulated teeth adhere to the palate and the posterior end of the right mandible (Text-figs 5, 7). The teeth are tapering, slender and recurved, with a circular cross-section. The degree of curvature is more pronounced in more posterior teeth, as in *Pliosaurus* (Taylor and Cruickshank 1993). Each tooth has an enamelled crown and an unenamelled base (‘root’), approximately twice the length of the crown. The crown bears a series of coarse enamel ridges, most of which extend the full apicobasal length. A possible wear facet is located laterally on the apex of one of the teeth of the left dentary (Text-fig. 3A). Apical wear facets were also identified in *Liopleurodon* by Noè (2001, p. 145, figs 22–23).

Axial skeleton

The holotype of *H. tomistomimus* (MANCH LL 8004) possesses an articulated series of 34 cervical vertebrae (including the atlas and axis) anterior to the pectoral girdle. This results in a long neck compared to most other longirostrine plesiosaurians (O’Keefe 2002; O’Keefe and Carrano 2005). Thirty-three cervical vertebrae could be removed from the exhibit and studied in detail (Text-

figs 8–11). Other vertebrae could not be studied in detail, although the complete axial column is preserved (Text-fig. 12).

The centrum is firmly joined to the neural arch in all vertebrae, although the neurocentral suture is still visible. The sequence of closure of neurocentral sutures has yet to be studied in detail for any plesiosaurian, and it is not clear what relation this has to the termination of growth or the onset of sexual maturity. However, this and other indicators suggest that MANCH LL 8004 represents a subadult individual (see Discussion, below).

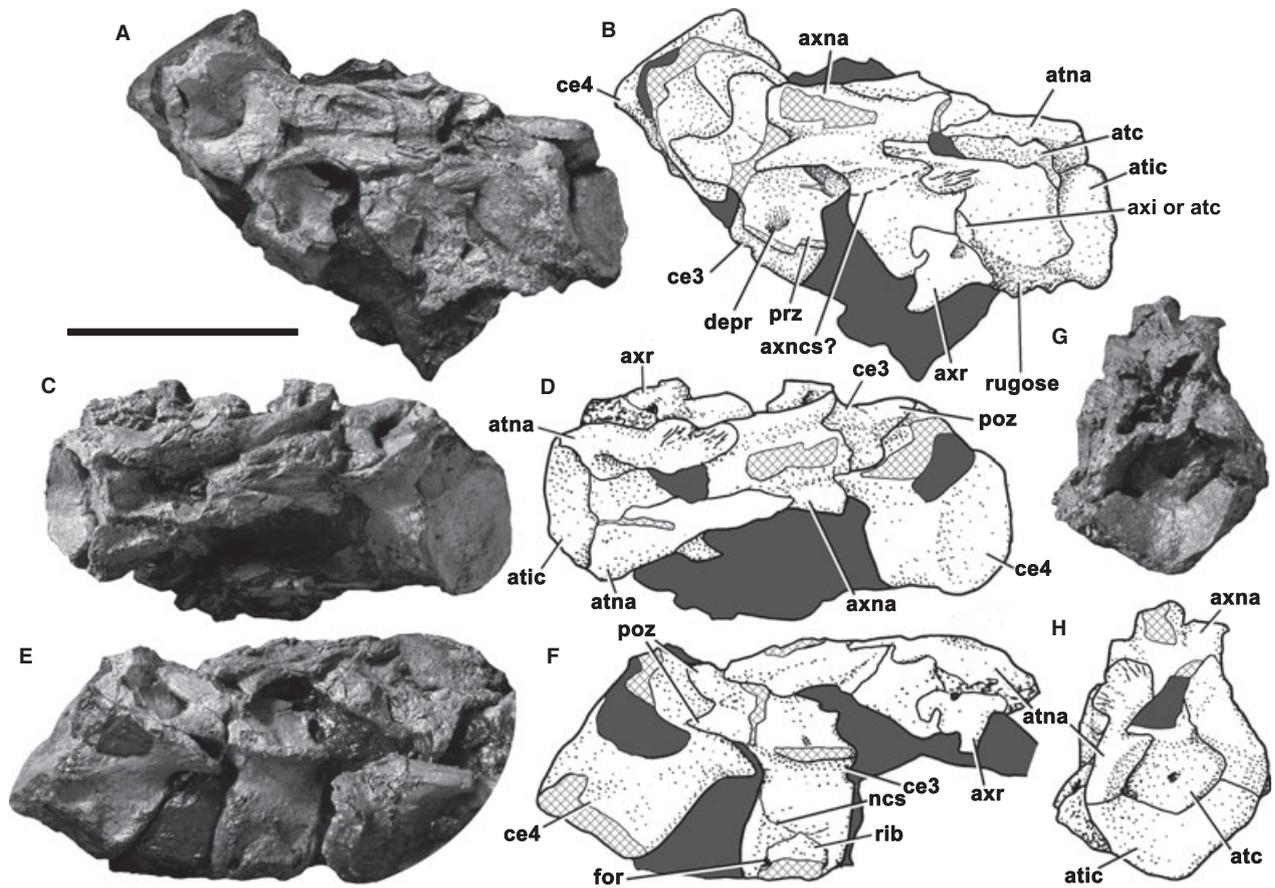
Atlas-axis complex. The elements of the atlas-axis complex are preserved in articulation, partly embedded in matrix and associated with the posterior part of the skull and the third and fourth cervical vertebrae (Text-fig. 8). The sutures between the atlantal elements are widely open, forming deep grooves on the anterior surface of the atlantal cup (Text-fig. 8G–H). However, the sutures between the atlantal and axial neural arches are not visible, and it is therefore difficult to interpret the dorsal surface of the complex. The atlantal cup is concave and has a slightly rugose surface texture. The anterior surface of the atlas centrum forms the dorsal half of the cup medial to the atlantal neural arches. It bears a small notochordal pit centrally on its anterior surface (Text-fig. 8G–H). The dorsal surface of the centrum is transversely concave, forming the ventral floor of the neural canal.

The ventral and left lateral surfaces of the atlantal intercentrum are enclosed in matrix, and the right lateral surface is highly and irregularly rugose, likely a pathologic condition (Text-fig. 8). Because of these factors, it is not clear whether the atlantal centrum is exposed on the ventral surface of the atlas-axis complex, or whether it is excluded from the ventral surface by contact between the atlantal and axial intercentra.

The atlantal neural arch forms the dorsal half of the atlantal cup lateral to the centrum, unlike in cryptoclidids, in which the centrum extends to the lateral surface (Andrews 1913; O’Keefe 2001). The neural arches have smooth, weakly convex lateral surfaces. Two prong-like processes emerge posterodorsally from the neural arch (Text-fig. 8). These have rugose, longitudinally striated surfaces. The more ventral of these processes emerges horizontally and overlaps a small anterior projection of the axial neural arch. The more dorsal of the two processes of the atlantal neural arch overlaps the dorsal surface of the axial neural arch. Both of these processes could plausibly be identified as atlantal postzygapophyses, and their homologies are unclear.

The axial rib is short and triangular with a proximal articulation divided into two, anteroventrally elongate heads (Text-fig. 8). The anterior head attaches to the axial intercentrum or atlantal centrum ventrolaterally. The posterior head attaches to the lateral surface of the axial centrum anteriorly, just ventral to centrum midheight.

The body of the axis, which may represent the axial centrum, is only visible in right lateral view. It has a weakly convex, approximately rectangular lateral surface. The axial neurocentral suture is difficult to identify, but may be represented by a thin horizontal groove a short distance ventral to the axial postzygapophysis (Text-fig. 8A–B). If this interpretation is correct, then the axis is the only cervical vertebra in



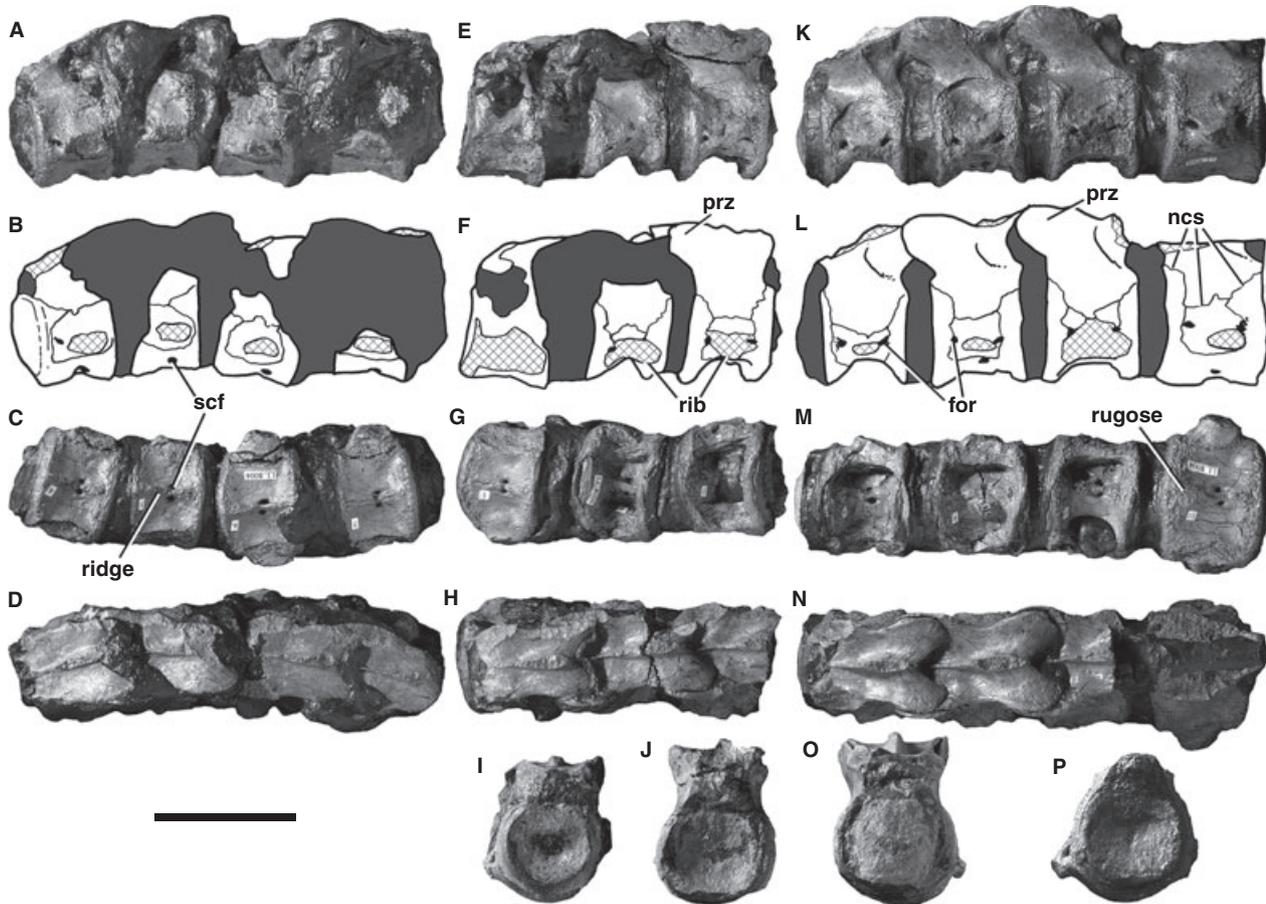
TEXT-FIG. 8. *Hauffiosaurus tomistomimus* sp. nov. First four cervical vertebrae of MANCH LL 8004, including atlas and axis with atlas-axis complex shown in A–B, right lateral, C–D, dorsal, and G–H anterior views and third–fourth cervical vertebrae shown in E–F, right lateral view. In line drawings (B, D, F, H), dark-grey tone indicates matrix, and crossed-hatching indicates broken bone. Scale bar represents 50 mm.

which the neural arch does not contact the rib facet (see below). Furthermore, a small, prezygapophysis-like anterolateral projection from the axis underlies the more ventral posterior process of the atlantal neural arch. If the axial neurocentral suture has been identified correctly herein, then this prezygapophysis-like structure is located on the axial centrum and not on the neural arch (as might be expected of a true prezygapophysis). As there is no other clear candidate for the axial neurocentral suture, the only other possibility is that most or all of the lateral surface of the axis seen in right lateral view represents the axial neural arch and the neurocentral suture, located far ventrally, is mainly or entirely obscured by matrix and the articulated axial rib.

The axial postzygapophyses project posterodorsolaterally. They are comparable in morphology and relative size to those of more posterior vertebrae: they are dorsoventrally low and have approximately ventrally facing facets (Text-fig. 8). The axial neural spine is rugose, and a large central portion is broken. The neural spine is transversely broad and dorsoventrally low, similar to the condition in pliosaurids, but unlike those of other pliosaurians, in which the spine is taller dorsally (Andrews 1910, 1913).

Postaxial cervical vertebrae. The postaxial cervical centra have gently concave articular surfaces, although in some cases these are obscured by attached matrix including parts of the posterior surface of the preceding centrum, thus giving the false impression of an opisthocoelous condition. All centra are slightly shorter anteroposteriorly than they are high dorsoventrally and slightly broader mediolaterally than dorsoventrally (Table 2). The height and width steadily increase among more posterior cervical vertebrae, whereas vertebral length reaches a maximum among posterior cervical vertebrae and then decreases anterior to the pectoral girdle (Table 2). A suboval depression is present on the dorsolateral surface of the neural arch of the third cervical vertebra. This has not been described in any other pliosaurian and may be an autapomorphy of *H. tomistomimus*.

The ventral surfaces of all cervical centra are rugose adjacent to the anterior and posterior articular surfaces (Text-figs 9–11). A rugose ventral longitudinal ridge is present on the ventral surface of the anterior cervical centra (Text-fig. 9). This is less prominent in the twelfth–sixteenth vertebrae and does not continue across the central portion of the centrum, instead forming separate anterior and posterior ridges, separated by a smooth area adjacent to the subcentral foramina (Text-fig. 10B). The



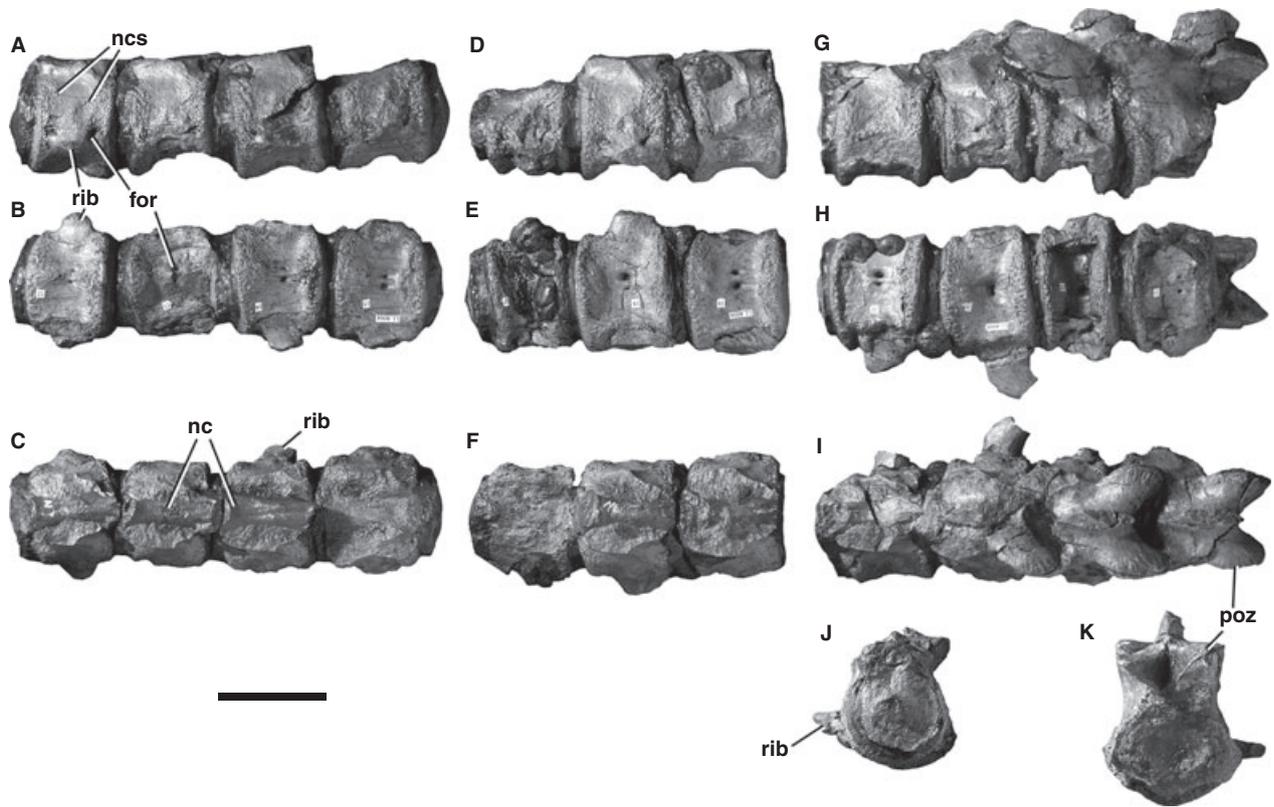
TEXT-FIG. 9. *Hauffiosaurus tomistomimus* sp. nov. Fifth to 15th cervical vertebrae of MANCH LL 8004. A–D, fifth–eighth, E–H, 9th–11th, I, ninth, J, 11th, K–N, 12th–15th, O, 12th, and P, 15th cervical vertebrae. A–B, E–F, K–L, left lateral, C, G, M, ventral, D, H, N, dorsal, I, O, anterior, and J, P, posterior views. In line drawings (B, F, L), grey tone indicates matrix, and crossed-hatching indicates broken bone. Scale bar represents 50 mm.

seventeenth–thirtieth cervical vertebrae lack a ventral ridge, and in more posterior cervical vertebrae a broad, rounded ridge is present (Text-fig. 11C). Small, paired nutrient foramina (subcentral foramina) are located on the ventral surfaces of the centra adjacent to the midline. The spacing between these foramina is short, and in the twenty-fifth centrum the foramina are confluent, forming a single, bilobed opening (Text-fig. 10H).

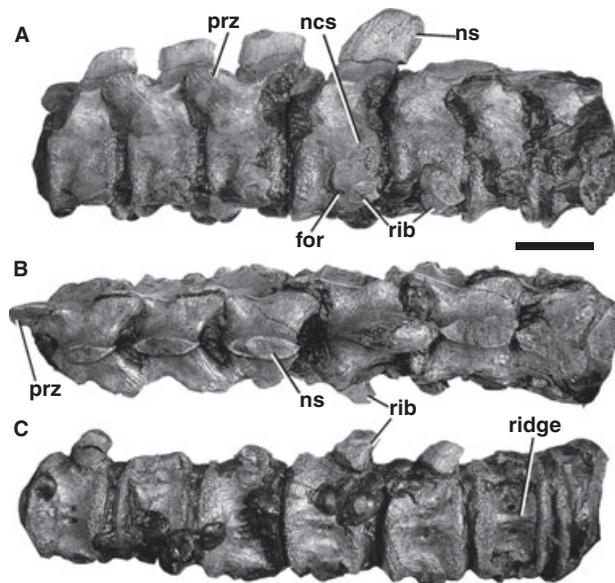
The lateral surfaces of the cervical centra are rugose. This contrasts with the smooth neural arch pedicles. The neurocentral suture extends ventrally around midlength so that it contacts the diapophyses along the entire length of the neck, often forming a small lappet that slightly overlaps the dorsal surface of the rib (Text-figs 9–11). This contrasts with the situation in most plesiosaurs, in which the neural arch does not contact the ventrolaterally located rib facet in the cervical vertebrae and only contacts the rib facet in anterior dorsal vertebrae ('pectoral' vertebrae: Seeley 1874). However, both *H. zanoni* (HAUF 7) and postcranial material that may represent the holotype individual of *H. longirostris* (White 1940) shows the same condition as *H. tomistomimus* (Text-figs 8–11), so this feature may be a synapomorphy of *Hauffiosaurus* (Ketchum and Benson 2010).

Most cervical zygapophyses are broken. However, they are large and emerge anterolaterally or posterolaterally from the neural arch, rising dorsally. Most zygapophyseal facets face dorsomedially or dorsolaterally at approximately 45 degrees, but they are approximately horizontal in anterior cervical vertebrae (Cruikshank 1996). The neural spines of the third and fourth cervical vertebrae are very low and transversely broad, comparable to that of the axis (Text-fig. 8). The neural arches of other anterior–middle cervical vertebrae are poorly preserved. However, in the twenty-sixth and more posterior cervical vertebrae, the neural spine is tall, sheet-like and angled posterodorsally (Text-fig. 11). The cross-section of the spine is anteroposteriorly long, approximately four-fifths of centrum length, and tapers to a sharp edge anteriorly and posteriorly.

Cervical ribs. The cervical rib facets are located just ventral to midheight on the lateral surfaces of the centra (Text-figs 8–11). All are either broken, or preserved with articulated ribs, suggesting that the ribs were firmly joined to the centrum, although the sutures between the ribs and the centra are still visible. The anterior–middle cervical rib facets are relatively



TEXT-FIG. 10. *Hauffiosaurus tomistomimus* sp. nov. MANCH LL 8004, A–C, 16th–19th, D–F, 21st–23rd (20th not pictured), G–I 24th–27th, J, 24th, and K, 27th cervical vertebrae. A, D, G, left lateral, B, E, H, ventral, C, F, I, dorsal, J, anterior, and K, posterior views. Scale bar represents 50 mm.

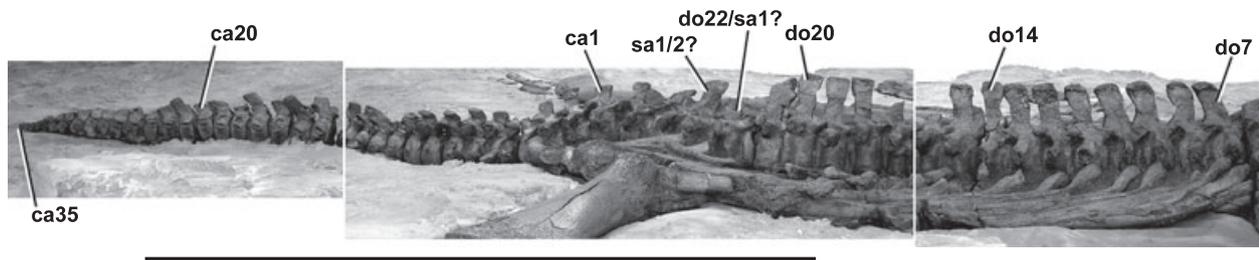


TEXT-FIG. 11. *Hauffiosaurus tomistomimus* sp. nov. 28th–34th cervical vertebrae in A, right lateral, B, dorsal, and C, ventral views (all images reversed). Scale bar represents 50 mm.

narrow dorsoventrally, but anteroposteriorly elongate, occupying most of the centrum length between the articular rims. More posterior rib facets (from approximately the twenty-ninth

vertebra) are shorter, approximately half the length of the centrum, but are higher dorsoventrally. The rib facets are paired, constituting a dorsal diapophysis and a ventral parapophysis, and support double-headed ribs, which are primitive for Plesiosauria (e.g. O’Keefe 2001). The rib heads are divided proximally by a channel. This is broad relative to that in other plesiosaurians, thus forming large foramina anteriorly and posteriorly, enclosed by the rib heads and lateral surface of the centrum (Text-figs 8–11). This may also be present in *H. longirostris* as White (1940, fig. 5) figured large foramina in the cervical rib heads of postcranial material that may belong to the holotype specimen. This morphology may be an autapomorphy of *Hauffiosaurus*. However, the condition in *H. zanoni* was not determined in the present study. Unfortunately, the cervical ribs are all broken distally.

Postcervical axial column. As the postcervical series could not be studied thoroughly, only a summary description is provided here (Text-fig. 12). The dorsal vertebrae (including ‘pectoral’ vertebrae) are preserved in articulation with the pectoral and pelvic girdles, so they are visible in dorsal and lateral views (Text-fig. 13). There are at least 21 dorsal vertebrae (if four sacral vertebrae are present), and there may have been 22 if only three sacral vertebrae are present. In the anterior three dorsal vertebrae, the position of the rib facet is intermediate between that in the cervical vertebrae (just ventral to centrum midheight) and in



TEXT-FIG. 12. *Hauffiosaurus tomistomimus* sp. nov. Composite image showing middle dorsal–distal caudal axial column of MANCH LL 8004 in right lateral view. Scale bar represents 100 mm.

TABLE 2. Selected measurements in millimetres of the cervical vertebrae of MMUM LL 8004.

	Length	Posterior width	Posterior height
Atlas	–	–	–
Axis	–	–	–
3	24	–	–
4	25	–	–
5	27	35 (anterior)	31 (anterior)
6	25	–	–
7	28	–	–
8	27	38	–
9	31	37	34
10	29	–	–
11	30	40	35
12	33	–	–
13	33	–	–
14	34	–	–
15	36	45	40
16	38	46	42
17	41	–	–
18	39	–	–
19	40	50	42
20	–	–	–
21	35*	54	–
22	43	–	–
23	45	54	47
24	48	57	52
25	45	–	–
26	38*	–	–
27	45	–	–
28	47	64	54
29	44	–	–
30	45	–	–
31	45	–	–
32	45	–	–
33	45	–	–
34	–	–	–

*Measurement of crushed specimen.

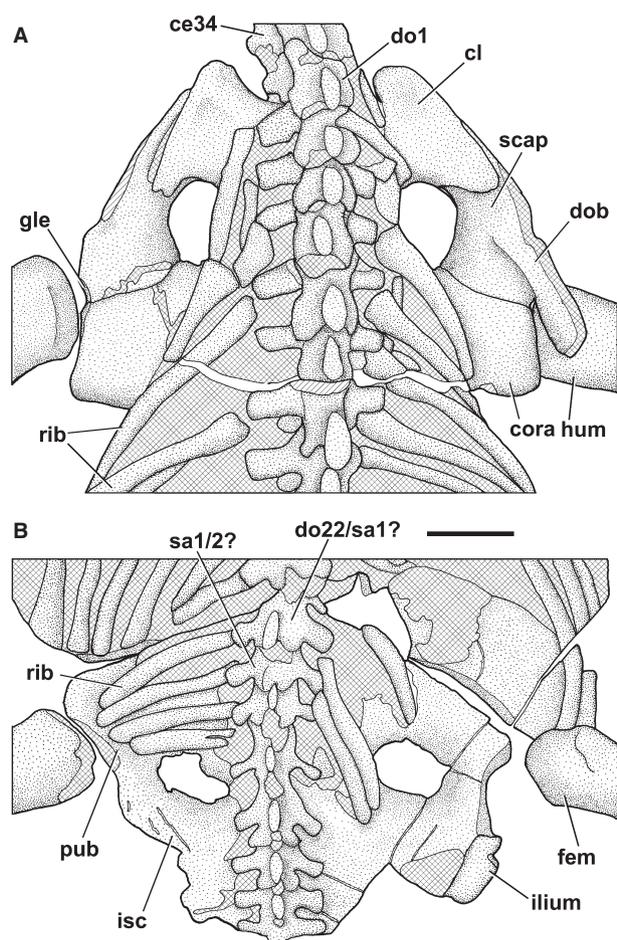
the more posterior dorsal vertebrae (on the transverse process of the neural arch). Hence, the rib facet is successively more dorsally placed in each of these anterior three dorsal vertebrae, and significant portions are located on both the centrum and neural arch. They can thus be classified as ‘pectoral’ vertebrae (*sensu*

Seeley 1874). The neural arches of the anterior 15 dorsal vertebrae form short, low and ventrally angled transverse processes, with approximately circular diapophyses, located adjacent to centrum midheight. In more posterior vertebrae, the transverse processes extend laterally so the diapophysis is dorsal of the centrum (Text-fig. 12). The zygapophyseal facets of the dorsal vertebrae emerge horizontally and are small compared to the neural arch, relative to the proportions of cervical zygapophyses. The zygapophyseal facets face dorsomedially or posterolaterally at a low angle.

The anterior dorsal vertebrae have sheet-like, posterodorsally inclined neural spines, comparable to those of the posterior cervical vertebrae. In the middle of the series (fourteenth–nineteenth dorsal vertebrae), the neural spines are vertically oriented and almost symmetrical in lateral view; weakly expanded anteriorly and posteriorly. In more posterior dorsal and sacral vertebrae, the neural spines are inclined anterodorsally (Text-fig. 12). This is unlike the situation in many Jurassic plesiosaurs, such as *Archaeonectrus* (NHMUK 38525: Owen 1881), *Macroplata* (NHMUK R5488: Ketchum and Smith 2010), *Microcleidus* (NHMUK 36184) and *Thalassiodracon* (NHMUK 14550), in which all dorsal neural spines are inclined posterodorsally. All of the dorsal neural spines of *H. tomistomimus* are just less than 1.5 times the centrum and are between two and three times as high as they are broad anteroposteriorly. This is similar to the proportions in many plesiosaurs, but unlike the condition in the Toarcian plesiosaurs *Microcleidus* (NHMUK 36184: Watson 1909), *Occitanosaurus* (Bardet *et al.* 1999) and *Seeleyosaurus* (SMNS 16812), in which the neural spines are exceptionally tall, more than twice the height of the centrum. Three definite sacral vertebrae are present, identified by the presence of a short rib with a transversely expanded distal portion that terminates adjacent to the partly disarticulated pelvic girdle (Text-fig. 13B). The vertebra immediately anterior to these three definite sacrals may also be a sacral vertebra or may be the most posterior dorsal vertebra: the rib is short, but longer than the other sacral ribs, and has only a slightly expanded distal portion, although this converges posterolaterally towards the positions of the distal ends of the other sacral ribs. Thus, it is intermediate in morphology, and more detailed information is required to determine its identity. The sacral neural spines of *H. tomistomimus* are lower than the dorsal neural spines (Text-fig. 12).

Thirty-five caudal vertebrae are present (Text-fig. 12). The caudal centra are anteroposteriorly short. The anterior 23 of these are relatively large; a pronounced size decrease, indicated

by a steady decline in estimated linear dimensions, occurs over the following seven vertebrae, and the posteriormost five vertebrae are reduced to small, cylindrical nubbins of bone that lack neural arches. Large rib facets are present on the lateral surfaces of anterior caudal centra. These diminish in size posteriorly and are absent in the twentieth and more posterior caudal vertebrae. The rib facets of the first nine caudal vertebrae are dorsoventrally oval, but in more posterior elements they are approximately circular. The caudal neural arches contact the dorsal portion of the rib facet. Many proximal fragments of caudal ribs are preserved attached to the centra by matrix. The well-developed zygapophyses of the anterior caudal vertebrae are approximately horizontal with slightly dorsomedially or ventrolaterally inclined facets. In some more posterior caudal vertebrae, the facets are steeply angled. However, this may be the result of transverse crushing. The caudal zygapophyses decrease in relative size posteriorly and are absent in the fourteenth and more posterior caudal vertebrae. The caudal neural spines are low, rectangular and angled posterodorsally. Chevrons are not easily visible in the specimen as displayed.



TEXT-FIG. 13. *Hauffiosaurus tomistomimus* sp. nov. Interpretive drawings of A, pectoral, and B, Pelvic regions of MANCH LL 8004 in dorsal view. Crossed-hatching indicates broken bone or matrix. Scale bar represents 100 mm.

Appendicular skeleton

As with the postcervical axial column, the appendicular skeleton was not thoroughly examined during the present study. Therefore, for much of the material, we can only provide a summary description in dorsal view (Text-fig. 13). Much of the pectoral girdle is obscured by the articulated vertebral column. It is therefore impossible to determine whether an interclavicle is present. However, the lateral portions of the paired clavicles are visible. They are triangular, with well-defined, rounded anterior borders. The scapulae lie superficial to the clavicles, such that the anterior part of the scapula underlaps the clavicle ventrally. The glenoid lies on the scapulocoracoid contact and faces laterally. The right scapula preserves a partial dorsal process that extends posterolaterally dorsal to the glenoid fossa. Only small portions of the coracoids adjacent to the glenoid are preserved.

The left humerus is well preserved and is 400 mm long (Text-fig. 14). It is thus slightly shorter than the pelvis (Table 3), unlike in *H. zanoni*, in which the propodials are autapomorphically longer than the pelvis (Table 3; O'Keefe 2001). The proximal articular surface is large, as the combined dorsoventral depth of the well-developed trochanter and capitulum is approximately one-third of the length of the humerus. The preaxial (anterior) margin of the humerus is almost straight. However, the postaxial (posterior) border is concave, primarily because of the development of a posterodistal expansion. The postaxial surface of the right humerus is pierced by three large foramina; on the left humerus, there is a single oval foramen at just over one-third of the shaft length. The distal end of the humerus is convex and coarsely pitted, indicating a cartilaginous covering in life (Robinson 1977). The radial and ulnar articular facets are not distinct as only a slight angle separates the two. The radial facet is larger.

A partial ulna is preserved associated with the left forelimb (Text-fig. 15A). It is subequal to the radius in length, but the proximal end of the ulna is narrower. The preaxial margin is broken. The radius is longer than wide and has concave preaxial and postaxial borders (Text-fig. 15A). The proximal end of the radius is straight with a rounded anteroproximal 'corner'. The distal end bears articular facets for the radiale (preaxial) and



TEXT-FIG. 14. *Hauffiosaurus tomistomimus* sp. nov. Left humerus of MANCH LL 8004 in A, anterior, B, ventral, C, posterior, and D, dorsal views. Scale bar represents 100 mm.

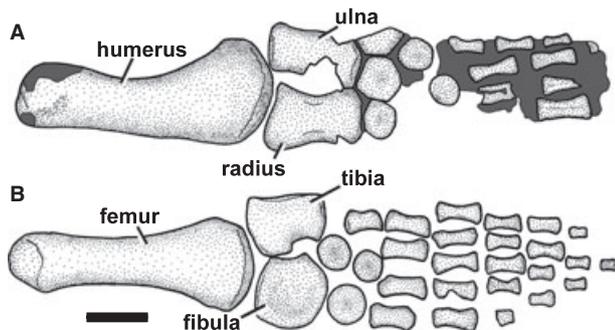
TABLE 3. Postcranial measurements (in metres) of MMUM LL 8004 *Hauffiosaurus tomistomimus* species, gen. et sp. nov. compared to those of *H. longirostris* and *H. zanoni*.

	<i>H. longirostris</i> MCZ 1033	<i>H. tomistomimus</i> MMUM LL 8004	<i>H. zanoni</i> HAUF 7
Skull length	0.68	>0.42	0.41
Skull width	0.27	0.19	0.17
Skeleton length	–	4.3	3.4
Neck length	–	1.35	1.00
Trunk length	–	1.35	1.16
Tail length	–	1.1	0.86
Humerus length	–	0.40	0.32
Ulna length	–	0.14	0.09
Radius length	–	0.14	0.10
Femur length	–	0.37	0.34
Tibia length	–	0.11	0.09
Fibula length	–	0.11	0.08
Pelvis length	–	0.43	0.30

Measurements were taken to the nearest 10 mm and were estimated from photographs for *H. zanoni*.

intermedium (postaxial). The radiale is small and rounded. The intermedium is subhexagonal and bears a larger ulnar contact surface than radial contact surface. The ulnare is the largest of the proximal carpals but is broken along its postaxial margin. Distal carpal III is rounded and articulates with the intermedium and ulnare. A second round distal carpal is present, but has become disarticulated and is attached to a large block of matrix containing nine partial phalanges. The metacarpals and phalanges are proximodistally elongate and hourglass-shaped, as in other plesiosaurs (Text-fig. 15A).

Much of the pelvis is obscured by the articulated vertebrae and ribs (Text-fig. 13B). The right pubis has an approximately straight, anteromedially slanting anterior margin, which is obscured by matrix medially. Posteriorly, the pubis contacts the ischium to form the acetabulum. It is difficult to determine the precise location of the puboischial suture on either side



TEXT-FIG. 15. *Hauffiosaurus tomistomimus* sp. nov. Interpretive drawings of articulated limbs of MANCH LL 8004 in dorsal view. A, left forelimb, B, right hindlimb. Grey tone indicates matrix, and crossed-hatching indicates broken bone. Scale bar represents 100 mm.

because of poor preservation. A fragment of the right ilium is preserved adjacent to the right ischium. Both ischia are broken posteriorly.

The right femur is 370 mm long, only slightly shorter than the humerus (Text-fig. 15B). Both preaxial and postaxial edges are gently concave, resulting in an approximately symmetrical outline. However, the postaxial edge is slightly more expanded proximally and distally. The distal end of the femur is uniformly convex and lacks distinct tibial and fibular facets. The epipodials of the hind limb differ substantially from those of the forelimb (Text-fig. 15B). The fibula has a rounded outline in dorsal view and is as wide transversely as it is long proximodistally, with a concave preaxial margin. The tibia is robust and approximately the same length as the fibula. The preaxial margin of the tibia is broken. Three ovate tarsals are preserved; definitive identification is impossible because of partial disarticulation. A number of elongate, hourglass-shaped metatarsals and phalanges are also present (Text-fig. 15B). These are arranged as they were preserved, with portions of matrix remaining.

DISCUSSION

Ontogenetic stage

MANCH LL 8004 shares some ontogenetic features noted by Brown (1981) in adult cryptoclidids. The ribs and neural arches are firmly joined to the cervical centra, as in 'adults', although the sutures between them are not closed (i.e. are still visible), unlike in 'old adults'. The cervical centra are rugose, comparable to older individuals. However, other observations indicate incomplete ossification, suggesting subadult status: the midline parietal suture is open; atlantal sutures are widely open; the propodials lack well-defined facets for the epipodials; and the phalanges and metapodials have rounded edges. The nutrient foramina in the vertebral centra (Ketchum and Smith 2010) and humeri are absent in older individuals, but are present in MANCH LL 8004, so it is unlikely that MANCH LL 8004 had reached maturity.

The affinities and validity of *H. tomistomimus*

MANCH LL 8004 was originally referred to the plesiauroid *Rhomaleosaurus* (as '*Rhomaleosaurus*' *longirostris*, considered herein as *Hauffiosaurus longirostris*) by Halstead (in Broadhurst and Duffy 1970). However, recent phylogenetic analyses have recovered MANCH LL 8004 as a basal member of Plesosauridae (O'Keefe 2001, 2004) or Plesiosauroidea (Ketchum and Benson 2010). In both analyses, MANCH LL 8004 was phylogenetically proximate to *Hauffiosaurus zanoni*.

MANCH LL 8004 ('Yorkshire taxon') and *Hauffiosaurus zanoni* formed successive sister taxa to a clade

comprising Middle Jurassic–Cretaceous pliosaurids in O’Keefe’s (2001) analysis, and formed a clade with *H. longirostris* (= ‘*Macroplata*’ *longirostris*) in the analysis of Ketchum and Benson (2010). These three taxa were united on the basis of two unambiguous synapomorphies (Ketchum and Benson 2010). One was unique: contact between the neural arch and the diapophysis occurs along the entire neck region via a ventral extension of the neural arch that causes the neurocentral suture to project ventrally around midlength (126.1; missing data in *H. longirostris*). The presence of a basicranial fontanelle (70.1) was also an unambiguous synapomorphy of the clade and is also present in some cryptoclidids. However, in cryptoclidids this foramen closes during ontogeny (e.g. *Muraenosaurus*: foramen absent in NHMUK R2421, present in NHMUK R2422) and lacks the separately ossified lateral walls that are visible in *H. tomistomimus* and *H. longirostris* (White 1940; the condition cannot be determined in *H. zanoni*). The presence of extensive longitudinal troughs on the dorsolateral surface of the maxilla and in the posterior half of the lateral surface of the dentary may also unite this clade (although the condition of the maxilla cannot be determined in *H. zanoni*), as they are absent on the dentaries of all other plesiosaurians, and only extend a short distance anteriorly in the maxillae of rhomaleosaurids (Cruickshank 1994a; O’Keefe 2001; Druckenmiller and Russell 2008a). Overall, *H. longirostris*, *H. tomistomimus* and *H. zanoni* show striking, detailed similarity. Furthermore, they have broadly comparable skull and vertebral proportions, and tooth and vertebral counts (Table 3). Comparisons between the three are complicated as *H. longirostris* is only certainly represented by a skull, and *H. zanoni* is only visible in ventral view (HAUF 7 is embedded in matrix, exposed only in ventral view and is currently exhibited in a case that cannot be opened), and the potentially highly informative palate is broken and abraded in places, making interpretation difficult. However, several distinctive differences indicate that each represents a distinct species: *H. zanoni* possesses seven premaxillary teeth whereas *H. longirostris* possesses nine, and a tenth alveolus is intersected by the premaxilla–maxilla suture (MCZ 1033; White 1940). In *H. longirostris*, the pterygoids contact across the midline ventral to the basioccipital (White 1940), whereas the pterygoids are not in contact in *H. tomistomimus* (Text-fig. 6); *H. longirostris* possesses prominent midline ridges occupying the dorsal surface of the premaxilla along most of its length, and the ventral surface of the mandibular symphysis that are absent in *H. tomistomimus* (Text-figs 2–5). The propodials are longer than the pelvis in *H. zanoni* (O’Keefe 2001), but shorter in *H. tomistomimus* (Table 3). The preaxial margin of the tibia of *H. zanoni* is only weakly concave, whereas in *H. tomistomimus* it is strongly concave (Text-fig. 15B). The middle cervical centra of *H. tomistomimus* have a ratio of

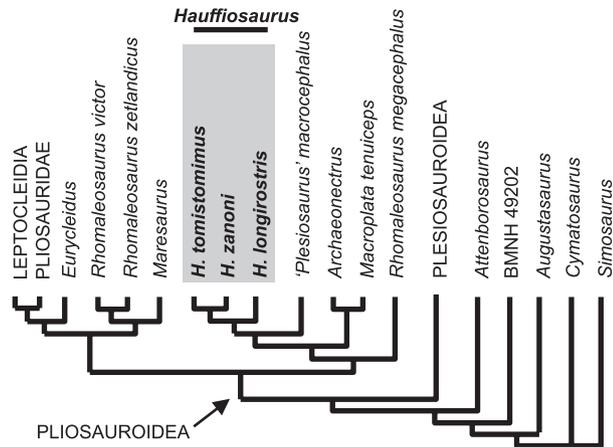
width to anteroposterior length of approximately 1.2 (Table 2; Text-fig. 10), whereas in *H. zanoni* the ratio is 1.6, and the neck length is longer as a proportion of the total body length (Table 3). Differences between *H. zanoni* (body length of 3.4 m; HAUF 7) and *H. tomistomimus* (body length of 4.2 m; MANCH LL 8004) are primarily proportional and may be allometric, reflecting the slightly larger size of MANCH LL 8004. However, the size difference is small, and the two taxa are from successive ammonite zones, suggesting that chronospecies-level distinction is a more plausible explanation for these differences.

To test the monophyly of *Hauffiosaurus* using new data accumulated during the present study, we analysed a modified version of the data matrix of Ketchum and Benson (2010). Scores for *H. longirostris*, *H. tomistomimus* (MANCH LL 8004) and *H. zanoni* were revised. Character 30, describing the presence or absence of a lacrimal, was rescored to include data from a higher proportion of taxa. The scores for character 70, which describes the basicranial fontanelle, were also revised. Two new characters were added:

179. Maxilla, prominent longitudinal trough on dorsolateral surface: absent (0); present (1; *H. longirostris*, *H. tomistomimus*).
180. Dentary, prominent longitudinal trough occupies posterior half of lateral surface: absent (0); present (1; *H. longirostris*, *H. tomistomimus*, *H. zanoni*).

Revised and new scorings can be found in Electronic Appendix S1, and a nexus file of the full data matrix is in Electronic Appendix S2.

The matrix was analysed following the search strategy of Ketchum and Benson (2010), in which the Parsimony Ratchet (Nixon 1999) implemented by PAUPRat (Sikes and Lewis 2001) was used to find islands of short trees that were explored using Tree Bisection and Reconnection. This resulted in 135 shortest trees, with lengths of 15947 steps. The tree length is long owing to the use of gap weighting to code continuously varying characters (Thiele 1993). Despite only minor alterations to the data matrix, the strict consensus of shortest length cladograms recovered in the present study (summarized in Text-fig. 16; full version in Electronic Appendix S1) is different to that recovered by Ketchum and Benson (2010). Major differences include recovery of Leptocleidia within Pliosauroidae, rather than Plesiosauroidae, as the sister taxon of Pliosauridae; and recovery of Plesiosauridae *sensu* Ketchum and Benson (2010) as a paraphyletic grade within Plesiosauroidae leading to a derived clade comprising Cryptoclididae and Elasmosauridae. All three species of *Hauffiosaurus* were recovered within Pliosauroidae in a monophyletic group that forms part of a basal clade that also includes ‘*Plesiosaurus*’ *macrocephalus*, *Archeonectrus rostratus* and *Macroplata tenuiceps* [recovered as non-neoplesiosaurian plesiosaurians by Ketchum and Benson



TEXT-FIG. 16. Simplified cladogram representing the strict consensus of 135 shortest length cladograms arising from analysis of a modified version of the data matrix of Ketchum and Benson (2010) showing the monophyly of *Hauffiosaurus*.

(2010)] and *Rhomaleosaurus megacephalus* (recovered as a rhomaleosaurid by Ketchum and Benson (2010)).

This result indicates that relationships among Lower Jurassic plesiosaurians are far from certain. In our view, this is symptomatic of the sparse anatomical data currently available for these taxa. Plasticity in the phylogenetic position of Leptocleidia has been documented previously (O’Keefe 2001; Druckenmiller and Russell 2008a), and the details of Jurassic plesiosaurian anatomy will be central in forming a consensus on leptocleidian affinities among pliosauroids or plesiosauroids.

Tree support metrics were generally low in the analysis of Ketchum and Benson (2010), and as they are computationally expensive to calculate we do not present them again here. We anticipate that future analyses will recover a monophyletic *Hauffiosaurus* as representatives of the genus are distinctly and strikingly similar to one another. However, the precise phylogenetic position of *Hauffiosaurus* is considered uncertain, pending more detailed description of other Lower Jurassic plesiosaurians. Features shared uniquely with pliosaurids such as the presence of a lacrimal and the transversely broad, deeply interdigitating morphology of the posterior termination of the premaxilla suggest the possibility that *Hauffiosaurus* may be a basal pliosaurid, as recovered by O’Keefe (2001). Relationships among basal plesiosaurians are uncertain (see the differing arrangements of O’Keefe (2001), Druckenmiller and Russell (2008a) and Ketchum and Benson (2010)), and further work is required to establish synapomorphies of Plesiosauroidae, Pliosauroidae and Plesiosauria as a whole. For instance, during this study, it was difficult to make detailed comparisons with rhomaleosaurids, for which published description is almost limited to the craniofacial sutural anatomy (e.g.

Taylor 1992; Smith and Dyke 2008; Vincent and Smith 2009).

Toarcian plesiosaurian biogeography

Several authors have suggested that the distribution of Toarcian marine reptiles, including thalattosuchians and ichthyosaurs (Godefroit 1994; Maisch and Ansorge 2004) or plesiosaurs considered in isolation (O’Keefe 2004; Großmann 2007; Smith and Vincent 2010), indicates the existence of discrete biogeographic provinces in Europe. Maisch and Ansorge (2004) suggested that the London-Brabant Massif acted as a barrier to dispersal between hypothesized British and Germanic provinces, allowing faunal differentiation. Plesiosaurs are a central component of this hypothesis as they show the highest degree of apparent endemism (Maisch and Ansorge 2004, p. 169), based on the observation that British and German Toarcian taxa form nonoverlapping sets.

O’Keefe (2004), additionally posited that the German Toarcian fauna was more primitive, based on a phylogenetic result in which the German Toarcian taxa *Hydrorion*, *Seeleyosaurus* [both considered as ‘*Plesiosaurus*’ by O’Keefe (2004)] and ‘*Plesiopterys*’ [considered as a subjective junior synonym of *Seeleyosaurus* by Großmann (2007)] were more basal than *Microcleidus* among plesiosauroids and *Meyerasaurus victor* (‘*Rhomaleosaurus victor*’) was considered more plesiomorphic than *Rhomaleosaurus zetlandicus*. However, the more recent phylogenetic hypothesis of Ketchum and Benson (2010) recovered *Hydrorion*, *Seeleyosaurus* and *Microcleidus* within a monophyletic Plesiosauridae, the youngest representatives of which are Toarcian, and *Rhomaleosaurus zetlandicus* and *Meyerasaurus victor* in a monophyletic Rhomaleosauridae. Strong support herein for a monophyletic *Hauffiosaurus* further undermines support for a ‘plesiomorphic’ German Toarcian fauna.

Furthermore, we question the evidence for biogeographic provincialism among Toarcian plesiosaurians in Europe. Plesiosauroids are abundant in both Germany and the United Kingdom and represent separate, nominally valid taxa. However, detailed descriptions of the British taxa *Microcleidus homalospondylus*, *Microcleidus macropterus* and *Sthenarosaurus dawkinsi* have not yet been published, and only future detailed comparative work can establish whether the German taxa are genuinely distinct from the British taxa. Furthermore, minor anatomic differences between the apparent regional variants may reflect temporal, rather than geographic, separation: the German taxa are from the *Harpoceras serpentinum* ammonite Zone, whereas most of the UK specimens are from the succeeding *Hildoceras bifrons* Zone (Table 4). The plesiosauroid *Occitanosaurus tournemirensis* from southern France is also of Toarcian age,

TABLE 4. Summary of plesiosaur taxa from the Alum Shale Member and Jet Rock Member of the Whitby Mudstone Formation of Yorkshire, UK and the Posidonia Shale of Germany.

Ammonite zone	Alum Shale Member	Jet Rock Member	Posidonia Shale
<i>Hildoceras bifrons</i> 181.2–180.7 Ma	<i>Hauffiosaurus tomistomimus</i> (1) <i>Microcleidus homalospondylus</i> (7) <i>Microcleidus macropterus</i> (1) <i>Rhomaleosaurus cramptoni</i> (1) <i>Rhomaleosaurus thornstoni</i> (1) <i>Rhomaleosaurus zetlandicus</i> (2) <i>Sthenarosaurus dawkinsi</i> (1)		
<i>Harpoceras serpentinum</i> (formerly <i>H. falciferum</i>) 182.7–181.2 Ma		<i>Hauffiosaurus longirostris</i> (1)	<i>Hauffiosaurus zanoni</i> (1) <i>Hydrorion brachypterygius</i> (5) <i>Seeleyosaurus guilelmiimperatoris</i> (3) <i>Meyerasaurus victor</i> (1)

Taxon lists, counts of referred specimens (in brackets) and stratigraphical data follow Benton and Taylor (1984: all Yorkshire taxa), Vincent and Smith (2009: *Rhomaleosaurus zetlandicus*), O’Keefe (2001: *Hauffiosaurus zanoni*), Großmann (2007: *Hydrorion brachypterygius*, *Seeleyosaurus guilelmiimperatoris*) and Smith and Vincent (2010: *Meyerasaurus victor*). Chronostratigraphical ages of ammonite zones follow Gradstein *et al.* (2005).

leading Großmann (2007) to support a distinct biogeographic province in southern France. However, *Occitanosaurus* is from the *Pleydellia aalensis* Zone of the uppermost Toarcian (Bardet *et al.* 1999), the base of which is currently dated at 176.6 Ma, 4.1 myr above the top of the *Hildoceras bifrons* Zone (Gradstein *et al.* 2005). Given this large time interval, *Occitanosaurus* does not provide evidence for geographic provincialism over short time spans of <4 myr.

Other taxa are rarer faunal elements, and most, such as *Meyerasaurus victor* from Germany and *Sthenarosaurus dawkinsi* from the UK, are represented by single specimens. Failure to detect such rare taxa in both ‘geographic provinces’ is as easily explained by incomplete faunal sampling as by provincialism. It is also important to consider that other pelagic, free-swimming animals, such as the ammonites on which biostratigraphic zones and subzones are based, do not show geographic provincialism across the region.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Phylogenetic data and figure showing complete cladogram.

Appendix S2. Nexus file of data matrix.

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