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Roger B. J. Benson^a; Karl T. Bates^b; Mark R. Johnson^c; Philip J. Withers^c

^a Department of Earth Sciences, University of Cambridge, Cambridge, United Kingdom ^b Department of Musculoskeletal Biology, Institute of Aging and Chronic Disease, University of Liverpool, Liverpool, United Kingdom ^c Materials Science Centre, University of Manchester, Manchester, United Kingdom

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CRANIAL ANATOMY OF *THALASSIODRACON HAWKINSII* (REPTILIA, PLESIOSAURIA) FROM THE EARLY JURASSIC OF SOMERSET, UNITED KINGDOM

ROGER B. J. BENSON,^{*1} KARL T. BATES,² MARK R. JOHNSON,³ and PHILIP J. WITHERS³

¹Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, United Kingdom, rbb27@cam.ac.uk;

²Department of Musculoskeletal Biology, Institute of Aging and Chronic Disease, University of Liverpool, Sherrington Buildings, Ashton Street, Liverpool L69 3GE, United Kingdom, K.T.Bates@liverpool.ac.uk;

³Materials Science Centre, University of Manchester, Grosvenor Street, Manchester M1 7HS, United Kingdom, M.Johnson-6@postgrad.manchester.ac.uk; phillip.withers@manchester.ac.uk

ABSTRACT—The taxonomy and systematics of the earliest plesiosaurs is poorly resolved. This limits our understanding of the diversification of one of the most successful clades of secondarily aquatic tetrapods. Here we provide a robust diagnosis of *Thalassiodracon hawkinsii* from the Pre-*planorbis* Beds (Triassic–Jurassic boundary interval) of the United Kingdom, and suggest that at least two other, previously unrecognized plesiosaurs are present in the same deposits. Computed tomography of an exceptionally preserved skull, and examination of previously undescribed (or briefly described) specimens yields new anatomical data. *Thalassiodracon* has a dorsomedian ridge on the premaxilla, a squamosal bulb, four premaxillary teeth, and a heterodont maxillary dentition. Several features of *Thalassiodracon*, including the squamosal bulb, broad anterior termination of the pterygoids, heterodont dentition, and single foramen in the lateral surface of the exoccipital, are plesiomorphic or represent pliosauroid synapomorphies. Among pliosauroids, *Thalassiodracon* shares a parietal that extends far anteriorly, a broad, interdigitating posterior termination of the premaxilla, and a short posteroventral process of the postorbital with *Hauffiosaurus* and pliosaurids. Thus, we suggest pliosaurid affinities for *Thalassiodracon*, in contrast to most recent phylogenetic studies. The early stratigraphic position of *Thalassiodracon* coincides with the earliest occurrence of Rhomaleosauridae (the sister taxon of Pliosauridae). The relatively long neck and small skull of *Thalassiodracon* indicate that the robust skeleton and macropredaceous habits of rhomaleosaurids and pliosaurids were derived independently.

INTRODUCTION

Plesiosaurs were a successful diapsid radiation of marine predators spanning from the Late Triassic (Taylor and Cruickshank, 1993a; Storrs, 1994a) to the Cretaceous–Palaeogene extinction (e.g., Bardet, 1992, 1994; Bakker, 1993; Storrs, 1997; Benson et al., 2010). Their evolution is characterized by convergent trends, whereby forms with large skulls and short necks ('pliosauromorphs') and forms with small skulls and long necks ('plesiosauromorphs') evolved repeatedly from intermediate ancestors (Bakker, 1993; Carpenter, 1996; O'Keefe, 2002; O'Keefe and Carrano, 2005). The anatomy of derived, geologically younger taxa with extreme body plans is distinctive and well documented. These taxa include the pliosauromorph clades Pliosauridae and Polycotylidae, and the extreme plesiosauromorph clade Elasmosauridae (e.g., Williston, 1903; Andrews, 1913; Welles, 1943; O'Keefe, 2004a, 2008). Because of their many distinctive features, the existence of these clades is well supported by phylogenetic analyses (e.g., O'Keefe, 2001; Druckenmiller and Russell, 2008a; Ketchum and Benson, 2010). However, a full understanding of body plan evolution among plesiosaurs requires consensus on the interrelationships of derived clades, and of plesiomorphic basal taxa. This consensus has proved to be elusive. One reason is that the anatomy of early plesiosaurs conforming to 'intermediate' morphotypes is poorly understood, and there is little consensus on their phylogenetic relationships (e.g., O'Keefe, 2001; Druckenmiller and Russell, 2008a; Smith and Dyke, 2008; Ketchum and Benson, 2010; Benson et al., in press).

The early history of Plesiosauria is known primarily from the Jurassic deposits of Europe (e.g., O'Keefe, 2004b; Großmann, 2007), primarily in the U.K. (e.g., Owen, 1865–1881; Andrews, 1910, 1913). These specimens are historically significant because they include the first plesiosaur discoveries (e.g., Conybeare, 1822; Hawkins, 1834, 1840) and were a focus of early study. Among these discoveries are the geologically oldest taxonomically determinate plesiosaur remains are from the Pre-*planorbis* Beds of the Blue Lias Group, U.K. These carbonate-rich beds accumulated in low-energy, shallow marine conditions and are dated to the Triassic–Jurassic boundary interval (Wright, 1860; Warrington and Ivimey-Cook, 1990; Warrington et al., 1994; reviewed by Storrs and Taylor, 1996). During this interval, life may have been undergoing or recovering from a major mass extinction event (reviewed by Tanner et al., 2004). The Pre-*planorbis* Beds have yielded the large-bodied (ca. 5 m long) pliosauroids *Rhomaleosaurus megacephalus* and *Eurycleidus arcuatus* (e.g., Hawkins, 1834; Lydekker, 1889; Cruickshank, 1994a; Benton and Spencer, 1995; Storrs and Taylor, 1996). Additionally, 25 specimens from Street in Somerset, and the nearby village of Walton, represent smaller-bodied individuals (Table 1), most around 2 m in length or less. These include the type specimens of four nominal species (Owen, 1838; Huxley, 1858; Seeley, 1865a). Thus, they may represent a high taxic diversity, comparable to that among smaller plesiosaurs from other well-sampled units such as the Callovian Peterborough Member of the Oxford Clay Formation (Andrews, 1910; Brown, 1981). However, Storrs and Taylor (1996) synonymized all the small-bodied Pre-*planorbis* taxa with *Thalassiodracon hawkinsii* (as *T. hawkinsi*), suggesting a depauperate fauna, perhaps more consistent with the aftermath of a mass extinction event. Recently, Ketchum and Benson (2010)

*Corresponding author

TABLE 1. Revised taxonomy of specimens listed by Storrs and Taylor (1996:404) as *Thalassiodracon hawkinsii*, and other small-bodied plesiosaurian specimens of the same provenance.

Taxon	Specimen	References and notes
<i>T. hawkinsii</i>	NHMUK 2018* (lectotype)	Hawkins (1834:42, pl. 24; 1840:pl. 24).
	NHMUK 2020* [14551]	Holotype of 'subregnum' <i>Plesiosaurus</i> 'genus' <i>pentatarsostinus</i> . Owen (1838:515; 1865–1881:pl. 16, fig. 2 [skull, reversed]), Hawkins (1840:22, pl. 27), Lydekker (1888:262, fig. 79 [right forelimb]).
	NHMUK 2021*	Partial postcranial skeleton from the Lower Lias of Walton, Somerset. Hawkins (1834:40, pl. 25; 1840:pl. 25), Lydekker (1889:263).
	NHMUK 2022* [14549]	Holotype of 'subregnum' <i>Plesiosaurus</i> 'genus' <i>hexatarsostinus</i> . Owen (1838:pl. 45; 1865–1881:pl. 16, fig. 1 [skull, reversed]), Hawkins (1840:p. 24, pl. 28), Lydekker (1888:263).
	CAMSM J.35181	Holotype of <i>P. eleutheraxon</i> comprising a partial postcranial skeleton. Barrett (1858:361, pl. 13, figs. 1–2 [atlas-axis complex]), Seeley (1865a:353, pl. 14; 1869:137).
	CAMSM J.46986	Skull, anterior cervical vertebrae, and fragments described by Storrs and Taylor (1996:figs. 2–13, 16).
	GSM 51235	Holotype of <i>Plesiosaurus etheridgii</i> . Huxley (1858a), Lydekker (1888:262).
' <i>P.</i> <i>cliduchus</i>	CAMSM J.35180 (holotype)	Partial postcranial skeleton missing most cervical vertebrae, the limbs, pelvic girdle, sacral, and caudal vertebrae. Seeley (1865a:356, pl. 15).
Distinct from <i>T. hawkinsii</i>	GSM 26035	Skull. Long posteroventral process of the postorbital, distinct basicranial morphology. Conybeare (1822:119, pl. 19).
	NHMUK 14550	Long posteroventral process of the postorbital, low cervical count (19 preserved), proportionally taller cervical neural spines. Sollas (1881:479), Lydekker (1888:263).
	OUNNH J.10337	Skull, and partial postcranial skeleton including anterior cervical and pectoral vertebrae, partial forelimb and ilium; O'Keefe (2001:fig. 4 [as <i>T. hawkinsii</i>]). Distinct from <i>T. hawkinsii</i> (Ketchum and Benson, 2010), e.g., five premaxillary alveoli, long posteroventral process of the postorbital, distinct basicranial morphology.
	TTNCM 8348	Partial postcranial skeleton with >38 cervical vertebrae (distinct from <i>T. hawkinsii</i> , but cannot be compared to <i>P. cliduchus</i>).
	TTNCM 9291	Cranium. Five premaxillary alveoli, long posteroventral process of the postorbital, basicranium distinct from <i>T. hawkinsii</i> .
Not determined	AGT 11	Skull. Not examined.
	AGT uncatalogued	Partial postcranial skeleton. Not examined.
	ANSP 15767	Not examined.
	MANCH MM L.9767	Fragmentary postcranium. Not determined.
	NHMUK R45	Not determined. Nichols (1795–1815:vol. 1:205), Lydekker (1889:264).
	NHMUK R1331	Limb. Not determined. Lydekker (1889:263; as <i>T. hawkinsii</i>).
	NHMUK 2039*	Mandible. Not determined. Storrs and Taylor (1996:figs. 14–15).
	OUNNH J.10327	Partial postcranial skeleton.
	RM 4110	Not examined.
	SWM uncatalogued	Not examined.
	TTNCM 8345	Not examined.
	UCD uncatalogued	Not examined.

All specimens are from the Triassic–Jurassic boundary interval of Street, Somerset, U.K., unless otherwise noted (NHMUK 2021*). All specimens constitute almost complete, partly, or fully articulated skeletons unless otherwise noted.

identified at least one specimen from Street as distinct from *Thalassiodracon* (OUNNH J.10337). This suggests that the taxonomy of plesiosaurians from Street must be revised, and clear morphological descriptions of the constituent taxa provided to elucidate the significance of this early fauna to our understanding of vertebrate evolution.

Understanding the anatomy of Pre-*planorbis* Beds plesiosaurians may be pivotal to understanding plesiosaur systematics. Many aspects of the cranial and postcranial anatomy of *Thalassiodracon* have been used to exemplify the plesiomorphic condition for the clade (e.g., Storrs and Taylor, 1996; Caldwell, 1997; O'Keefe, 2001, 2002, 2006). However, despite the abundance of specimens (Table 1), the postcranial anatomy of *Thalassiodracon* has not been clearly documented, and the skull has not been comprehensively described. Storrs and Taylor (1996) provided an excellent description of the external craniofacial and basicranial anatomy in CAMSM J.46986, a well-preserved skull of *Thalassiodracon*. Most details of this description were confirmed during our study. However, other parts of the skull were not described, or were only partly described (Storrs and Taylor, 1996). Thus, the description provided here focuses on the dentition, braincase, palate, and mandible of CAMSM J.46986, and incorporates information from X-ray microtomography, and from other specimens (listed in Table 1). Recently, Druckenmiller and Rus-

sell (2008a), Smith and Dyke (2008), and Ketchum and Benson (2010) recovered *Thalassiodracon* as a basal plesiosauroid. In contrast, O'Keefe (2001) recovered *Thalassiodracon* as a basal plesiosauroid, although he included data from OUMNH J.10337, which represents a distinct taxon. The objectives of the current study are to provide a clear taxonomic concept of *T. hawkinsii*, identify synapomorphies that may help to resolve its phylogenetic affinities, and comprehensively document the cranial anatomy for use in phylogenetic studies of Plesiosauria.

Institutional Abbreviations—AGT, Alfred Gillett Trust, C. & J. Clark International Ltd., Street, U.K.; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge, U.K.; GSM, Geological Survey Museum, Keyworth, U.K.; MANCH, The Manchester Museum, Manchester, U.K.; NHMUK, The Natural History Museum, London, U.K. (Note—asterisks following the numbers of specimens housed at this institution do not refer to footnotes. They are part of the specimen numbers); OUMNH, Oxford University Museum of Natural History, Oxford, U.K.; RM, Redpath Museum, Montreal, Canada; SWM, Swansea Museum, Swansea, U.K.; TTNCM, Somerset County Museum, Taunton, U.K.; UCD, Geology Department, University College, Dublin, Republic of Ireland.

METHODS

X-ray Microtomography

During the present study we performed X-ray microtomography (XMT) on a skull of *Thalassiodracon hawkinsii* (CAMS J.46986). XMT is a non-destructive evaluation technique that allows the internal structure of an object to be imaged by reconstructing the spatial distribution of the local linear X-ray absorption coefficients of the phases contained within (Elliott and Dover, 1982). This provides a virtual three-dimensional (3D) representation of the internal architecture of an object from which two-dimensional (2D) cross-sectional slices can be extracted along the three orthogonal planes of the object (Mumery et al., 1995; Babout et al., 2005).

Measurements were carried out using a 225/320-kV CT Custom X-ray microtomography (XMT) scanner from Nikon Metrology (formerly Metris X-Tek Systems Ltd.), capable of tube potentials up to 320 kV. The scanner used a fast CT collection method recording 1500 projections at 1 frame per second, resulting in a voxel length of 0.0977 μm . The radiographs were collected using a tube potential of 220 kV, current of 31 μA , and with a tungsten anode. All of the X-ray projections were saved as images in .tiff file format. The data were reconstructed using proprietary software utilizing the filtered back-projection reconstruction algorithm. Scan reconstructions presented here were constructed in Mimics (Materialise Interactive Medical Image Control System; Materialise BV, Leuven, Belgium). They are based directly on the XMT data with no additional processing or reconstruction of 'missing' anatomy.

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860

PLESIOSAURIA de Blainville, 1835

PLIOSAUROIDEA Welles, 1943

THALASSIODRACON Storrs and Taylor, 1996

THALASSIODRACON HAWKINSII (Owen, 1838)

(Figs. 1–4)

Plesiosaurus triatarsostinus Hawkins, 1834:41, pl. 24 (*nomen oblitum*).

Plesiosaurus hawkinsii Owen, 1838:515, pls. 43–45 (*nomen protectum*).

Plesiosaurus 'gen.' *pentatarsostinus* Hawkins, 1840:22, pl. 27.

Plesiosaurus 'gen.' *hexatarsostinus* Hawkins, 1840:24, pl. 28.

Plesiosaurus etheridgii Huxley, 1858:281.

Plesiosaurus eleutheraxon Seeley, 1865a:353.

Plesiosaurus hawkinsi Owen; Seeley, 1865b:50 (incorrect subsequent spelling).

Plesiosaurus hawkinsii Owen; Owen, 1865–1881:pl. 14, fig. 6; pl. 16.

Plesiosaurus hawkinsi Owen; Lydekker, 1889:260, fig. 79 (incorrect subsequent spelling).

Thalassiodracon hawkinsi (Owen); Storrs and Taylor, 1996:404, figs. 2–13, 16 (new genus, new combination; incorrect subsequent spelling of '*hawkinsii*').

Thalassiodracon hawkinsii (Owen); Maisch, 1998:240.

Lectotype—NHMUK 2018*, an almost complete, articulated skeleton embedded in matrix and visible in ventral view (Hawkins, 1834:pl. 24; 1840:pl. 24).

Paralectotypes—NHMUK 2020*[14551] and NHMUK 2022*[14549].

Materials—The lectotype, paralectotypes, CAMSM J.35181, CAMSM J.46986, GSM 51235, and NHMUK 2021*.

Diagnosis—Small plesiosaurian (ca. 2 m long) that differs from other taxa of similar provenance by its broad, interdigitating premaxilla-frontal contact, frontal makes narrow anterodorsal contribution to orbit margin, parietal extends to orbital mi-

length, short posteroventral process of the postorbital, co-ossified parabasisphenoid, cultriform process forms diamond-shaped ventral platform, 31 cervical, 22 dorsal (including three 'pectorals'), three sacral, and 33 caudal vertebrae. Possesses the following autapomorphies: four premaxillary alveoli (a local autapomorphy that is absent in all closely related taxa), closure or reduction of the endolymphatic foramen on the medial surface of the exoccipital, supraoccipital portions of semicircular canals fully enclosed in bone.

Occurrence—The uppermost Triassic (Rhaetian) or lowermost Jurassic (Hettangian), Pre-*planorbis* Beds, Blue Lias Formation, Lower Lias Group of Somerset, U.K. Most specimens were collected from Street, Somerset, and NHMUK 2021* was collected from Walton, just west of Street (the stratigraphy of referred specimens was reviewed by Storrs and Taylor, 1996).

Remarks—Hawkins (1834:41) described a specimen in his collection (now NHMUK 2018*) as the new species *Plesiosaurus triatarsostinus*. He misspelled the species epithet as "*tessarestarostinus*" in a plate caption (Hawkins, 1834:pl. 24), but issued an erratum notice within the volume, stating that it was intended as "*triatarsostinus*." This name was a reference to the three tarsal bones in NHMUK 2018*.

Owen (1838:515; 1840:57) proposed the name *Plesiosaurus hawkinsii* as a more appropriate name, noting "a second specimen of the same species in Mr. Hawkins' collection" with five tarsal bones (likely NHMUK 2020*[14551], which is the only specimen from Hawkins' collection that has five ossified tarsals). Owen (1838:515, pls. 43–45) did not explicitly specify a type specimen for *P. hawkinsii*. However, he mentioned NHMUK 2018*, 2020*[14551], and 2022*[14549] in his description, and these specimens may therefore be considered as syntypes under Article 73.2 of the ICZN (International Commission on Zoological Nomenclature, 1999). NHMUK 2018* was mentioned as the 'type' specimen of "*Plesiosaurus hawkinsi*, Owen" (sic) by Lydekker (1889:262), which constitutes a lectotype designation under Article 74.6 of the ICZN (International Commission on Zoological Nomenclature, 1999). Other specimens from the type series are therefore paralectotypes (NHMUK 2020*[14551], 2022*[14549]). Seeley (1865b:50), Lydekker (1889:260), and most subsequent authors have used "*P. hawkinsi*, Owen" instead of "*P. hawkinsii*." This does not constitute an emendation under Article 33.2 of the ICZN because it was not accompanied by an explicit statement of intention. Furthermore, '*hawkinsii*' cannot be justifiably emended under Article 32.5 (see Article 33.4; International Commission of Zoological Nomenclature, 1999; Maisch, 1998; contra Storrs and Taylor, 1996). Instead, *P. hawkinsi* is an incorrect subsequent spelling (Article 33.3; International Commission of Zoological Nomenclature, 1999). The spelling '*P. hawkinsii*' has been used at least once since 1899 (Maisch, 1998:240). Therefore, '*P. hawkinsi*' does not meet the criterion of prevailing usage described in Article 23.9.1.1 and cannot be maintained as a nominal "correct original spelling" under Article 33.3.1 (International Commission of Zoological Nomenclature, 1999). '*P. hawkinsii*' is therefore the correct original spelling of Owen's (1838) taxon.

As they have the same name-bearing type specimen (NHMUK 2018*), *P. hawkinsii* Owen, 1838, is an objective junior synonym of *P. triatarsostinus* Hawkins, 1834. However, to our knowledge, *P. triatarsostinus* has not been used as a valid name after 1899; it may have been used most recently by Seeley (1874:443; Storrs and Taylor, 1996). Also, *P. hawkinsii* is in prevailing usage (Appendix 1). Thus, *P. triatarsostinus* is here designated as a nomen oblitum, and *P. hawkinsii* as a nomen protectum in accordance with Articles 23.9.1.1, 23.9.1.2, and 23.9.2 of the ICZN (International Commission of Zoological Nomenclature, 1999). *P. hawkinsii* Owen, 1838, therefore now has precedence over *P. triatarsostinus* Hawkins, 1834.

Storrs and Taylor (1996) noted several major differences between *P. hawkinsii* and the type species of *Plesiosaurus*, *P.*

FIGURE 1. Skulls of *Thalassiodracon hawkinsii* in dorsal view. **A**, CAMSM J.46986, with magnification $\times 1.5$ (**B**) showing frontoparietal region; **C**, NHMUK 2022*[14549]; **D**, GSM 51235, with magnification $\times 2.0$ (**E**) showing premaxilla-frontal contact. **Abbreviations:** dmr, dorsomedian ridge; fr, frontal; fr-pmx, premaxilla-frontal contact; mx-pmx, maxilla-premaxilla contact; opr, orbital process of frontal; pa-fr, parietal-frontal contact; pa-pa, parietal midline contact; pmx-pmx, premaxillary midline contact; pmx1–4, first to fourth premaxillary teeth; poc, paraoccipital process; pofr, postfrontal; sqb, squamosal bulb. Scale bars equal 5 cm.

dolichodeirus. They therefore referred *P. hawkinsii* to the new genus *Thalassiodracon*, forming the new combination *T. hawkinsii* (as *T. hawkinsii*). Storrs and Taylor (1996) referred all small-bodied plesiosaurian specimens from the Lower Lias Group of Street to *T. hawkinsii*, including the holotypes of *Plesiosaurus etheridgii* Huxley, 1858 (GSM 51235), *Plesiosaurus cliduchus* Seeley, 1865a (CAMSM J.35180), and *Plesiosaurus eleutheraxon* Seeley, 1865a (CAMSM J.35181), which they considered subjective junior synonyms of *T. hawkinsii*. R.B.J.B. is currently reexamining all specimens from this locality. Preliminary data suggest that *P. etheridgii* (also in agreement with Lydekker, 1889:262) and *P. eleutheraxon* are subjective junior synonyms of *T. hawkinsii* (Table 1). However, *P. cliduchus* differs from *T. hawkinsii* in possessing anteroposteriorly elongate, mound-like tuberosities on the dorsolateral surfaces of the posterior cervical neural arches, anterodorsally inclined posterior dorsal neural arches, a prominent longitudinal keel on the ventral surface of the clavicle-interclavicle complex, and a ventral projection located distally on the scapular blade (CAMSM J.35180; Hulke, 1883:fig. 14). Thus, it may represent a distinct taxon. Ketchum and Benson (2010) also identified OUMNH J.10337 as an unnamed taxon, distinct from *T. hawkinsii*. Ongoing reassessment suggests that some other specimens can also be distinguished from *T. hawkinsii* (Table 1). The presence of multiple small plesiosaurians from the Lower Lias Group of Street casts uncertainty on the referral of fragmentary specimens to *T.*

hawkinsii (Table 1; e.g., the mandible NHMUK 2039*). Thus, in the present study we conservatively refer only relatively complete skeletons that conform to the diagnosis (above), including a diagnostic vertebral formula (Table 2). This formula is most clearly shown in GSM 51235, and is at least partly visible in the holotype (NHMUK 2018*; dorsal and sacral vertebrae obscured), CAMSM J. 35181, NHMUK 2020* [14551], 2021*, and 2022*[14549]. Vertebral counts are highly conserved among specimens referred to *T. hawkinsii* (Table 2; contra Huxley, 1858). In contrast, several specimens that are excluded from *T. hawkinsii* because they possess distinct apomorphies also show different vertebral formulae (Table 2). The specimens referred to *T. hawkinsii* here do not differ substantially, other than in features that are likely related to ontogeny (e.g., distal ossification of paraoccipital processes, closure of neurocentral sutures, ossification of propodial proximal articular surfaces, and ossification of distal tarsals; Owen, 1838; Hawkins, 1840; Caldwell, 1997).

DESCRIPTION

Craniofacial Skeleton

Storrs and Taylor (1996) described the craniofacial skeleton of CAMSM J.46986 clearly, so limited detail is provided here, focusing on reinterpreted regions and features of systematic importance. The posterior rami of the premaxillae are poorly

FIGURE 2. Skull of *Thalassiodracon hawkinsii* (CAMS J.46986; **A–B**) in ventral view and reconstructions of the posterior mandible (**C–E**), anterior portions of the maxilla and palate (**F–H**), and dentary (**I–K**) in medial (**C, I**), dorsal (**D, J**), lateral (**E**), and ventral (**F–H, K**) views. In the interpretive drawing (**A**) dark grey tone indicates broken surface and light grey tone indicates matrix. **Abbreviations:** ang, angular; art, articular; bo-bs, basioccipital-basisphenoid contact; boc, basioccipital; cor, coronoid; den, dentary; ect, ectopterygoid; epi, epipterygoid; for, foramen; in, internal naris; mc, Meckel’s canal; mx1–5, first to fifth maxillary alveoli; pa-pa, parietal midline contact; pa-so, parietal contact for supraoccipital; pal, palatine, palc, palatine contact of the vomer; pdp, paradental plate; pifor, pineal foramen; pmx3, third premaxillary tooth; po, postorbital; pov, posteroventral process of the postorbital; pra, prearticular; pt, pterygoid; ptc, pterygoid contact of the vomer; qu, quadrate; rfor, foramina for replacement teeth; sa, surangular; spl, splenial; sq, squamosal; vom, vomer. Scale bars equal 5 cm (**A–B**) or 1 cm (**C–K**).

TABLE 2. Vertebral counts in specimens of small-bodied Plesiosauroidea from Street, Somerset, U.K.

Specimen	Cervical (of which pectoral)	Dorsal (of which pectoral)	Sacral	Caudal
<i>T. hawkinsii</i>				
NHMUK 2018* (lectotype)	31	?	?	33
CAMS J.35181	> 18	22 (3)	3	>8
CAMS J.46986	> 6	?	?	?
GSM 51235	31	22 (3)	3	33
NHMUK 2020*[14551]	31	>11	?	33
NHMUK 2022*[14549]	31	> 15 (?)	?	>18
Specimens distinct from <i>T. hawkinsii</i> (Table 1)				
NHMUK 14550	>23 (4)	18 (3)	4	>11
TTNCM 8348	>38	?	?	33 estimated
CAMS J.35180 (holotype of ‘ <i>Plesiosaurus</i> ’ <i>cliduchus</i>)	>6 (2)	> 12 (?)	?	?

Because these specimens represent articulated partial skeletons, cervical vertebrae can be confidently identified by position anterior to the scapula and the presence of a gracile, cervical rib. Most cervical ribs have prominent anterior and posterior processes, but the posterior-most cervical rib resembles a miniaturized dorsal rib. ‘Pectoral’ vertebrae are identified by the position of the rib facet partly on the centrum and partly on the neural arch. They can be part of the neck (cervical) or trunk (dorsal). The total number of ‘pectoral’ vertebrae in the cervical and dorsal series are given in brackets. Pectoral vertebrae represent anterior dorsal vertebrae in *T. hawkinsii*, and both posterior cervical and anterior dorsal vertebrae in NHMUK 14550 and ‘*Plesiosaurus*’ *cliduchus*. Sacral vertebrae have short, distally expanded ribs that converge distally.

FIGURE 3. Skull of *Thalassiodracon hawkinsii* (CAMSJ.46986) in right lateral (A–B, E), left lateral (C–G, D), and left ventrolateral (F, H) views. Interpretive line drawings (E, G, H) show the positions of disarticulated braincase elements, which are shaded separately. Scale bars equal 5 cm.

preserved in CAMSJ.46986 (Fig. 1A–B). Despite this, Storrs and Taylor (1996) suggested that they formed a narrow splint. However, in GSM 51235 this region is well preserved and shows that in *Thalassiodracon* the premaxilla terminates at orbital midlength in a transversely broad, deeply interdigitating contact with the frontal (Fig. 1E), as in *Hauffiosaurus* (Benson et al., in press) and pliosauids (contact with the parietal: e.g., Andrews, 1913; Taylor and Cruickshank, 1993b; Ketchum and Benson, in press a). The dorsal surface of the conjoined premaxillae is obscured by damage, pathology, and slight displacement in CAMSJ.46986. Thus, it is difficult to interpret. However, GSM 51235 and NHMUK 2022* [14549] show a robust dorsomedian ridge (Fig. 1C–E), as is present in the pliosauids *Hauffiosaurus longirostris* (White, 1940), *Macroplata* (Ketchum and Smith, 2010), and *Rhomaleosaurus* (Taylor, 1992; Cruickshank, 1996; Smith and Dyke, 2008). A more prominent dorsomedian ‘crest’ is present in leptocleidids (Cruickshank, 1997; Kear et al., 2006; Druckenmiller and Russell, 2008a, 2008b) and some elasmosaurids (Sato, 2003; Druckenmiller and Russell, 2008a).

Storrs and Taylor (1996:fig. 7) suggested that the prefrontal and postfrontal were restricted to the anterodorsal and posterodorsal margins of the orbit, resulting in an extensive frontal contact with the dorsal margin of the orbit. Indeed, in CAMSJ.46986 the interorbital skull roof is transversely narrow and composed of midline elements, the premaxilla, frontal, and parietal. However, this is due to disarticulation of the pre- and postfrontals. These are articulated in GSM 51235 and NHMUK 2022* [14549], demonstrating that the skull roof was transversely broad (Fig. 1C–E). Tapering anterolateral (orbital) processes of the frontals entered the anterodorsal margin of the orbit, but the postfrontal extends far anteriorly, excluding the frontal from the dorsal margin for most of its length. The prefrontal must have been a small element restricted to the anterodorsal margin of the orbit anterior to the frontal, as suggested by Storrs and Taylor (1996). Poor preservation of this region in all specimens renders the anatomy of this area problematic.

The frontal-parietal suture is clearly visible in CAMSJ.46986 and is located just posterior to orbital midlength (Fig. 1B; Storrs and Taylor, 1996) so that it is <10 mm short of contacting the premaxilla. The sagittal crest is low and broadly convex. The straight parietal midline suture is open for its entire length in all specimens of *Thalassiodracon*, including NHMUK 2022* [14549], a skeletally mature individual. The ventral surface of the parietal bears a transversely oriented contact for the supraoccipital (Fig. 2A–B). The dorsal rami of the squamosals are abraded in CAMSJ.46986, but well preserved in NHMUK 2022* [14549]. They are restricted to the posterior surface of the skull roof. They form an interdigitating midline contact that expands posteriorly as a bulbous eminence, the ‘squamosal bulb’ (Fig. 1C). This was recovered as a pliosauid synapomorphy by O’Keefe (2001:character 55), but may be plesiomorphic (Druckenmiller and Russell, 2008a; Ketchum and Benson, 2010) because it is present in pistosauids (Rieppel et al., 2002).

Palate

Storrs and Taylor (1996) did not attempt an interpretation of the palate of CAMSJ.46986. However, much of the anatomy can be confidently described. The palate is exposed in NHMUK 2018* and 2020* [14551] but is damaged or incompletely prepared, and thus provides little information. The vomer is a single, midline element (Fig. 2G–H). If it originally comprised paired vomers, their midline suture is closed. The right posterolateral portion of the vomer is broken, but the left side is well preserved. A posterolateral projection divides the palatine contact from the transversely broad, posteriorly facing pterygoid contact. This indicates that the anterior termination of the pterygoids was transversely broad, as in pliosauids (e.g., Williston, 1903; Cruickshank, 1994a; O’Keefe, 2001; Smith and Dyke, 2008; Benson et al., in press; Ketchum and Benson, in press a). The internal naris is enclosed by the vomer medially, the palatine posteriorly, and the maxilla laterally (Fig. 2G–H). The distinct groove

FIGURE 4. Reconstructions of basicranium (A–B), left (C–G) and right (H–I) exoccipital-opisthotic, and supraoccipital (J–N) of *Thalassiodracon hawkinsii* (CAMS J.46986) in right lateral (A), ventral (B, N), medial (C, H), anteromedial (D), anterior (E, J), posterior (F, I, K), left lateral (G, L), and dorsal (M) views. Matrix is colored black. **Abbreviations:** amut, chamber for ampulla and utricle; avc, anterior vertical canal; bat, basal tuber; bo, basioccipital; bo-bs, basioccipital-basisphenoid contact; bpt, basiptyergoid process; bs, basisphenoid; crus, foramen ventral to crus communis; cp, cultriform process; efor, endolymphatic foramen; exo-op, exoccipital-opisthotic contact; exof, exoccipital facet; for, foramen; icf, internal carotid foramen; jug, jugular foramen; mpr, median process; parf, parietal facet; pila, pila antotica; pilm, pila metoptica; poc, paraoccipital process; prof, prootic facet; pvc, posterior vertical canal; rug, rugose surface; ?XI, possible accessory foramen; XII, hypoglossal foramen. Scale bars equal 1 cm.

that extends anteriorly from the internal naris of rhomaleosaurids (Cruikshank et al., 1991; Cruikshank, 1994a, 1996) is absent and there are no openings between the maxilla and vomer anterior to the internal naris, unlike in some pliosaurids (Taylor and Cruikshank, 1993b; Ketchum and Benson, in press a).

The remaining palatal bones are dorsoventrally thin and sheet-like anterior to the posterior interpterygoid vacuity. The palatine extends posteriorly from the internal naris, forming the lateral portion of the palate. It bears three small foramina adjacent to its anterior margin. Due to breakage, it is impossible to determine the position of the posterior margin of the palatine (Fig. 2A–B). Thus, the anterior extent of the ectopterygoid, which forms the lateral part of the palate posteriorly, cannot be precisely located. It is also difficult to determine whether a suborbital vacuity was present.

The anterior rami of the pterygoids are broken so it is impossible to determine whether an anterior interpterygoid vacuity is present. However, a very large anterior interpterygoid vacuity, as is present in NHMUK 49202 (Andrews, 1896), *Meyerasaurus victor* (Smith and Vincent, 2010), *Tricleidus*, and polycotyliids (Williston, 1903; Andrews, 1910; O’Keefe, 2004a), is certainly absent in *Thalassiodracon*. A V-shaped notch in the pterygoids anterior to the posterior interpterygoid vacuity accommodates the cultriform process. Because the right pterygoid has been displaced onto the ventromedial surface of the left pterygoid, this platform is occluded in ventral view. The pterygoids extend posterolaterally around the posterior interpterygoid vacuity, forming dorsoventrally tall, transversely narrow quadrate flanges that were described by Storrs and Taylor (1996). The ventral surface of the quadrate flange projects laterally into the adductor fossa as a dorsoventrally thin shelf (Fig. 2A–B). A pterygoid-ectopterygoid boss (sensu Storrs, 1997) is absent.

Both epipterygoids are preserved. The right epipterygoid is clearly visible. It forms a transversely thin triangular plate that

has been displaced dorsally from the base of the quadrate ramus of the pterygoid. The left epipterygoid is in its original position, lateral to the internal carotid foramen.

Braincase

The ventral surface of the basicranium is visible, but poorly preserved in the lectotype (NHMUK 2018*) and NHMUK 2020*[14551]. The parabasisphenoid, basioccipital, both exoccipital-opisthotics, and the supraoccipital are preserved in CAMS J.46986 (Fig. 3). These bones are disarticulated within the skull and digital reconstructions based on our XMT data are presented here (Fig. 4).

The parasphenoid and basisphenoid form the anterior part of the basicranium. They are fused so the suture between them cannot be located, and they are therefore jointly referred to as the parabasisphenoid. The cultriform process forms an anteroposteriorly long, diamond-shaped platform that projects ventrally from the parabasisphenoid (Fig. 4). This topology is also present in another specimen of *T. hawkinsii* (NHMUK 2020*[14551]; the lectotype is poorly preserved), in *Hauffiosaurus* (Benson et al., in press), and was reconstructed in *Plesiosaurus* by Storrs (1997; although the cultriform process extends much further anteriorly in *Plesiosaurus*). In *Hauffiosaurus* the parasphenoid-basisphenoid suture is visible, indicating that the cultriform process represents the entire parasphenoid (Benson et al., in press). Topographic similarity suggests that this may also be the case in *Thalassiodracon*. A large foramen on the left side of the basicranium posterolateral to the cultriform process is also identical to that in *Hauffiosaurus* (Fig. 4B; Benson et al., in press), and is present in the basal pistosaur *Yunguisaurus* (Cheng et al., 2006). This foramen was identified as an internal carotid foramen by Storrs and Taylor (1996).

Posterior to the cultriform process, the ventral surface of the parabasisphenoid is transversely convex. Sheet-like posterolateral extensions of the parabasisphenoid wrap around the anterior portion of the basal tuber ventrally and laterally, forming the anterior portion of the rugose pterygoid contact. Medial to these ventrolateral extensions, a dorsoventrally thin anterior sheet of the basioccipital underlaps the ventral surface of the parabasisphenoid (Figs. 2A–B, 4A–B). These structures reinforce the basioccipital-basisphenoid contact, which is represented on the dorsal surface of the basicranium by a deep, mediolaterally oriented fissure, similar to that described in OUMNH J.10337 by O’Keefe (2006:fig.12.3). The body of the basioccipital (‘clivus’; O’Keefe, 2006) bears a V-shaped notch that is primitive for plesiosaurs, and perhaps pistosauroids (O’Keefe, 2006).

The lateral surface of the parabasisphenoid is penetrated by a large foramen for the internal carotid at the level of the posterior end of the cultriform process (Fig. 4A–B). A prominent pila antotica extends anterodorsally from this region, and a pila metoptica is present more anteriorly (Fig. 4A–B). A low, anteroposteriorly elongate basiptyergoid process extends from the lateral surface of the parabasisphenoid ventral to the pila metoptica. This process is well preserved on the left side, and articulates with a facet on the dorsal surface of the pterygoid in the anterior half of the posterior interptyergoid vacuity.

The posteroventral surface of the basioccipital is separated from its ventral surface by a distinct step (Fig. 4B). O’Keefe (2001:fig. 22; 2006) identified this as a suture, suggesting that the anterior sheet of the basioccipital (as identified here, and by Storrs and Taylor [1996:fig. 11] and Ketchum and Benson [2010:fig. A6B]) instead represents the ventral surface of the basisphenoid. However, close inspection reveals that the suture is definitely absent. The occipital condyle is convex and bears a notchordal pit. It is ringed by a groove, forming a distinct neck ventrally and laterally, but contacts the exoccipital facets dorsally.

Both exoccipital-opisthotics are well preserved. Because they are disarticulated within the skull and difficult to observe, Storrs and Taylor (1996:fig. 9B) figured only part of the medial surface. We present reconstructions based on our XMT data (Fig. 4C–I). However, due to low contrast between bone and matrix in our XMT images, some portions were difficult to reconstruct (black in Fig. 4C–I). The exoccipital-opisthotic contact is partly fused, but still evident. It originates anteriorly on the ventral surface and extends posterodorsally as a transversely oriented plane that intersects the jugal foramen (Fig. 4C). The exoccipital lies posterior to this contact and contains the cranial nerve and endolymphatic foramina. The opisthotic lies anterodorsal to this contact and comprises the bony labyrinth and paraoccipital process.

Two foramina penetrate the medial surface of the exoccipital adjacent to its ventral surface (Fig. 4C, H). The more posterior foramen is larger and housed the hypoglossal nerve (XII; Storrs and Taylor, 1996). XMT data indicate that the smaller, anterior foramen forms a laterally trending canal that joins the hypoglossal canal within the exoccipital, and is also confluent with the complex system of internal chambers of the cancellous exoccipital body. A larger foramen in this position in cryptoclidids (Brown, 1981; Maisch, 1998; Evans, 1999) and basal sauropterygians (Rieppel, 1994) has been identified as a second hypoglossal foramen or an accessory nerve (XI) foramen (Storrs and Taylor, 1996 [in *Thalassiodracon*]; Maisch, 1998; Evans, 1999). A third foramen dorsal to the hypoglossal foramen is present in the right exoccipital, but absent in the left. This small opening is present, but larger, in OUMNH J.28585 (referred to *Euryclidus* by Cruickshank, 1994b; but see O’Keefe, 2004b; Ketchum and Benson, 2010), *Peloneustes* (Andrews, 1913; Ketchum and Benson, in press a), *Liopleurodon* (Noë et al., 2003), and *Tricleidus* (Andrews, 1910:fig. 72), in which taxa it was identified as the opening of an endolymphatic duct. Closure of the left foramen in CAMSM J.46986 may be related to pathologies on the right

side of the snout (Fig. 1A; Storrs and Taylor, 1996). The jugal, ?accessory, and hypoglossal canals extend medially through the exoccipital, join within the bone, and exit laterally through a single foramen (Fig. 4G).

The anteromedial surface of the opisthotic bears a deep recess for the ampulla and utricle (Fig. 4C–D). The morphology of the prootic portion of this structure is not known. Foramina in the posterodorsal and anterodorsal regions of this recess enter the posterior vertical and horizontal semicircular canals. The dorsal exit of the posterior vertical semicircular canal is located on the supraoccipital facet. The exit of the horizontal semicircular canal is obscured by matrix on the prootic facet in both opisthotics. The straight paraoccipital process extends posteroventrolaterally from the opisthotic. The distal end is expanded, and its anterior surface is slightly rugose for articulation with the paraoccipital facet on the squamosal (Storrs and Taylor, 1996). The distal surface of the paraoccipital process is poorly ossified and thus concave in CAMSM J.46986 (Fig. 4D–G, I). Thus, the distal portion of the outline in posterior view is straight, giving the distal expansion a truncated appearance. This is unlike the condition in other plesiosaurs and basal plesiosaurs, in which the distal paraoccipital process forms a suboval, spatulate terminus (e.g., Andrews, 1913; Smith and Dyke, 2008; Ketchum and Benson, in press a). However, in NHMUK 2022 [14549], a larger individual, the terminus is more completely ossified and is spatulate (Fig. 1C), suggesting that complete ossification of the paraoccipital process is retarded in *Thalassiodracon*.

The stapes (identified by Storrs and Taylor, 1996) contacts the anterior surface of the opisthotic (Fig. 4D–F, I). This contact is identically positioned on the left and right opisthotics of CAMSM J.46986. This is surprising, considering the disarticulated condition of the otic complex, combined with the fragile nature of the stapes, and its typically loose articulation with the braincase in tetrapods. These observations suggest that the stapes was fused, or otherwise firmly attached to the opisthotic during biostratigraphy, and has not been displaced. XMT data reveal the absence of any opening that may represent a fenestra ovalis under the stapedial footplate. Thus, although the fenestra ovalis may have been present in CAMSM J.46986, it did not articulate with the stapedial footplate. The stapedial footplate is suboval, and expanded in the plane of the stapedial shaft. It thus has an ‘oar-like’ appearance. The anterior surface of the footplate is rugose. A prominent longitudinal flange extends along the entire anterior surface of the preserved stapes.

The supraoccipital of CAMSM J.46986 is arch-shaped, enclosing the dorsal and dorsolateral margins of the foramen magnum (Fig. 4J–M). The dorsal surface of the supraoccipital bears a depressed region for articulation with the ventral surface of the parietal. It is transversely convex, unlike in *Peloneustes* (Andrews, 1913; Ketchum and Benson, in press a) and some plesiosaurs (Storrs, 1997; Maisch, 1998; O’Keefe, 2004a), in which the dorsal surface of the supraoccipital is horizontal. A prominent median process, widely present among plesiosaurs (O’Keefe, 2001:character 56) extends ventrally into the foramen magnum.

The ventrolateral portions of the supraoccipital are expanded anteroposteriorly to accommodate the semicircular canals (Fig. 4K). These canals are fully enclosed in bone. This may be an autapomorphy of *Thalassiodracon*, because in many other plesiosaurs the anteroventral walls of the canals are not ossified (Andrews, 1913; Maisch, 1998; O’Keefe, 2004a; Ketchum and Benson, in press a). Semicircular canals occupy approximately half the dorsoventral height of the supraoccipital, unlike in *Muraenosaurus* (Maisch, 1998), *Peloneustes* (Andrews, 1913; Ketchum and Benson, in press a), and polycotylids (O’Keefe, 2004a), in which they occupy almost the entire height of the bone. Thus, *Thalassiodracon* may have a proportionally small membranous labyrinth. The exoccipital facet faces ventrally and is penetrated by a foramen for the posterior vertical semicircular

canal (Fig. 4J–K). A foramen for the anterior vertical semi-circular canal exits just medial to the anteriorly facing prootic facet (Fig. 4K–L). The anterior and posterior vertical semicircular canals join within the supraoccipital at the crus communis and extend ventrally towards the ampulla, exiting through a foramen in the anteroventromedial surface of the supraoccipital (Fig. 4M).

Mandible

Storrs and Taylor (1996:figs. 14–15) briefly described a mandible from Street (NHMUK 2039⁷) that they referred to *Thalassiodracon* based on its expanded symphysis. However, specimens not referable to *Thalassiodracon* also have an expanded symphysis (GSM 26035; OUMNH J.10337), which is widespread among Lower Jurassic plesiosaurs (e.g., Cruickshank, 1994a; Smith and Dyke, 2008; Ketchum and Smith, 2010). Thus, NHMUK 2039⁷ cannot be confidently referred to *Thalassiodracon*, and a description of the mandible of CAMSM J.46986 is provided here.

The dentary forms most of the mandibular symphysis and lateral surface of the mandible. The left dentary is almost complete, including the entire row of 27 alveoli. The lateral portion of the dentary is broken posteriorly, revealing the lateral surfaces of the angular and surangular. The symphysis is expanded dorsoventrally and slightly transversely to accommodate four enlarged alveoli. The symphysis is shorter than that of many longirostrine taxa such as *Hauffiosaurus* (White, 1940; Benson et al., in press), polycotyliids (Williston 1903; Sato 2003; O’Keefe 2004a, 2008), and some Middle Jurassic pliosaurs (Andrews, 1913; Ketchum and Benson, in press a), but longer than in basal plesiosauroids (e.g., Storrs, 1997). This approximate ‘intermediate’ symphyseal length is common among rhomaleosaurids and basal pistosaurians (e.g., Andrews, 1986; Cruickshank, 1994a; Rieppel et al., 2002; Cheng et al., 2006; Smith and Dyke, 2008), and is likely plesiomorphic. Posterior to the symphysis of CAMSM J.46986, the alveoli diminish in size. The coronoid is a transversely thin, sheet-like bone that covers the dorsal portion of the medial surface of the mandible anterior to the coronoid eminence (Fig. 2A–B). Due to breakage, it is impossible to determine whether it terminates posterior to the symphysis. The splenial is a sheet-like bone that covers the ventral portion of the mandible medially. It is damaged anteriorly (so its participation in the symphysis, or lack thereof, cannot be determined) and displaced dorsally posteriorly. It terminates just posterior to the level of the coronoid eminence. The posterior portion of the mandible comprises the angular ventrally and surangular dorsally (Fig. 2C–E). The angular-surangular contact plane slants dorsomedially so exposure of the angular is higher dorsoventrally on the medial surface. The medial surface of the angular accommodates a longitudinal trough, likely representing the posterior portion of Meckel’s canal. The medial wall of this trough is a transversely narrow crest on the angular that underlies the prearticular ventrally (Fig. 2A–D). This crest is emarginated by an anteroposteriorly long, suboval notch posterior to the level of the coronoid eminence. This notch forms the ventral margin of a foramen. The dorsal margin is enclosed by the prearticular, which has been displaced slightly medially (Fig. 2A–C). The prearticular is a transversely thin splint of bone that extends from the glenoid posteriorly to the posterior end of the splenial anteriorly. The surangular is transversely narrow, unlike the transversely broad, dorsally excavated condition in Middle Jurassic pliosaurs and *Rhomaleosaurus zetlandicus* (Druckenmiller and Russell, 2008a). A large, anteroposteriorly elongate foramen penetrates the surangular posteroventral to the coronoid eminence (Fig. 2A–C, E). This extends anteriorly as a narrow fissure and is identical to a foramen in the surangular of OUMNH J.28585 (Cruickshank, 1994b:fig. 10). More posteriorly, two additional, smaller foramina are present just dorsal to the angular-surangular contact (Fig. 2C). A small, abraded portion of the angular is preserved posteriorly.

Dentition

The teeth of *Thalassiodracon* resemble those of *Plesiosaurus* (Storrs, 1997); they are slender, weakly curved, have a circular or weakly suboval cross-section, and bear fine, apicobasally oriented ridges. Unlike in *Plesiosaurus*, many of these ridges terminate around midheight and only one or two extend to the apex, so broad apical portions of the teeth are smooth. The lingual surfaces of the crowns are not visible in any specimen. The maxillary and dentary alveoli are bounded medially by subpentagonal paradental plates (Fig. 2H–I).

Our XMT data allow an accurate count of the alveoli in CAMSM J.46986. Most alveoli in other specimens are obscured by matrix or the articulated mandible. Storrs and Taylor (1996:fig. 11) described four teeth in both premaxillae of CAMSM J.46986 and suggested that a small mesialmost alveolus was additionally present, but difficult to confirm due to damage. Our observations, confirmed by XMT data, indicate that the right premaxilla bears three large, fully erupted teeth, and that there is no space for an additional alveolus, either mesially or distally. The left premaxilla bears four alveoli. The mesial two alveoli contain broken, erupted teeth. The distal two alveoli contain small, replacing teeth. Four alveoli are also present in the right premaxilla of NHMUK 2022⁷ [14549] (Fig. 1C). The low tooth count in the right premaxilla of CAMSM J.46986 is likely pathological; the right external naris is pathologically small and close to the midline (Storrs and Taylor, 1996). Thus, *Thalassiodracon* has four premaxillary alveoli, as in NHMUK 49202 (referred to ‘*Plesiosaurus macrocephalus*’ by Lydekker, 1889; Andrews, 1896), *Eromangasaurus australis* (Kear, 2005, 2007), and *Kronosaurus queenslandicus* (Ketchum and Benson, 2010). In contrast, most plesiosaurs have five premaxillary alveoli (e.g., Brown, 1981; O’Keefe, 2001; Druckenmiller and Russell, 2008a) and the presence of four in *Thalassiodracon* may be a local autapomorphy.

The left maxilla contains 21 alveoli, confirming the estimate of Storrs and Taylor (1996). The incomplete right maxilla bears 11 alveoli. The mesial two maxillary alveoli are smaller than either the preceding premaxillary or succeeding maxillary alveoli. The third to fifth maxillary alveoli are large and widely spaced (Fig. 2B, F–H). Thus, *Thalassiodracon* has a heterodont dentition, similar to those in pistosauroids (Rieppel et al., 2002), pliosauroids (e.g., Andrews, 1913; Taylor and Cruickshank, 1993b; Benson et al., in press), and some Cretaceous plesiosauroids (Druckenmiller and Russell, 2008a; Ketchum and Benson, 2010). The sixth and more distal maxillary alveoli are small and closely packed. They gradually diminish in size posteriorly.

DISCUSSION

Systematic Comparisons

There is little consensus on the relationships of *Thalassiodracon*. Although large-scale phylogenetic studies consistently recover the taxon near the base of the plesiosaurian tree, its precise affinities are unclear. It has been recovered as a basal representative of both Pliosauroidea (O’Keefe, 2001) and Plesiosauroidea (Druckenmiller and Russell, 2008a; Ketchum and Benson, 2010). Many previously unrecognized features of the skull of *Thalassiodracon* were observed during the present study. These include the dorsomedian ridge on the premaxilla, broad, interdigitating premaxilla-frontal contact, the far anterior extension of the parietal, the presence of a squamosal bulb, aspects of palatal and braincase anatomy, the presence of four premaxillary teeth, and a heterodont maxillary dentition. These novel observations complement previously noted features (Storrs and Taylor, 1996; O’Keefe, 2001; Ketchum and Benson, 2010:fig. A6B) and are used here as the basis for a preliminary discussion of the likely affinities of *Thalassiodracon*, and its significance for understanding the early evolution of Plesiosauria.

Thalassiodracon possesses a transversely expanded mandibular symphysis and squamosal bulb. These may be plesiomorphic (Druckenmiller and Russell, 2008a; Ketchum and Benson, 2010) or represent pliosauroid synapomorphies (O'Keefe, 2001). *Thalassiodracon* also has a short posteroventral process of the postorbital. A long posteroventral process is plesiomorphic (Storrs, 1991:character 17; O'Keefe, 2004b:character 168), and the short morphology is derived independently in pliosaurids and plesiosauroids (Ketchum and Benson, 2010:character 33).

Several other features suggest pliosauroid (sensu Ketchum and Benson, 2010) affinities, or are plesiomorphic. These are discussed below and represent new phylogenetic character states that are included in a reassessment of pliosauroid relationships by Ketchum and Benson (in press b).

(1) Posterior Termination of Premaxilla Broad and Interdigitating—In *Thalassiodracon* (Fig. 1D–E), *Hauffiosaurus* (White, 1940; Benson et al., in press), pliosaurids (Andrews, 1913; Taylor and Cruickshank, 1993b; Ketchum and Benson, in press a), and cryptoclidids (Brown and Cruickshank, 1994; Evans, 1999), the posterior termination of the premaxilla is transversely broad and interdigitating. The broad morphology was used by Druckenmiller and Russell (2008a:character 5) and Ketchum and Benson (2010:character 14) to describe the parietal-premaxilla contacts of some elasmosaurids and pliosaurids. However, the presence of a broad, interdigitating posterior termination of the premaxilla in *Thalassiodracon*, cryptoclidids, and *Hauffiosaurus* suggests that this morphology is independent of the presence of a parietal-premaxilla contact. In most plesiosaurs the premaxilla tapers posteriorly, and regardless of contact with the frontal or parietal, the posterior termination of the premaxilla is narrow and non-interdigitating. This is seen in rhomaleosaurids (Taylor, 1992; Cruickshank, 1994a; Smith and Dyke, 2008), leptocleidids (Cruickshank, 1997; Druckenmiller and Russell, 2008a), plesiosaurids (Storrs, 1997; Bardet et al., 1999; Maisch and Rücklin, 2000), and polycotyliids (Williston, 1903; Carpenter, 1997; O'Keefe, 2004a, 2008).

The presence of a tapering posterior termination of the premaxilla in pistosauroids (*Augustasaurus* and *Pistosaurus*; Rieppel et al., 2002; H. F. Ketchum, pers. comm., 2010; although Sues, 1987:fig. 11, provided an alternative interpretation) suggests that this morphology is plesiomorphic. Thus, a transversely broad, interdigitating posterior termination of the premaxilla may be a synapomorphy linking *Thalassiodracon*, *Hauffiosaurus*, and pliosaurids.

(2) Parietal Extends Anterior to Orbital Midlength—In *Thalassiodracon* (Fig. 1A–B) and *Hauffiosaurus* (Benson et al., in press), the parietal terminates anteriorly at the level of orbital midlength. This contrasts with the situation in other taxa that lack a premaxilla-parietal contact, in which the parietal terminates posterior, or adjacent to, the posterodorsal margin of the orbit. This occurs in pistosauroids (Sues, 1987; Rieppel et al., 2002; Cheng et al., 2006), basal plesiosaurs (Andrews, 1896; Ketchum and Smith, 2010), some rhomaleosaurids (Cruickshank, 1994a), plesiosaurids (Storrs, 1997; Bardet et al., 1999; Maisch and Rücklin, 2000), and some cryptoclidids (Andrews, 1910; Brown and Cruickshank, 1994). In pliosaurids (Andrews, 1913; Taylor and Cruickshank, 1993b; Ketchum and Benson, in press a), some rhomaleosaurids (Taylor, 1992; Smith and Dyke, 2008), elasmosaurids (Welles, 1943; Sato, 2003), and polycotyliids (Williston, 1903; Carpenter, 1997; O'Keefe, 2004a, 2008), the premaxilla contacts the parietal. In all these taxa, the parietal extends anteriorly to approximately orbital midlength, and in pliosaurids it extends further anteriorly (Ketchum and Benson, 2010:character 14).

Phylogenetic studies have assumed that the anterior extent of the parietals is not independent of the presence of a parietal-premaxilla contact (O'Keefe, 2001; Ketchum and Benson, 2010). However, the presence of an anteriorly extensive parietal that does not contact the premaxilla in *Thalassiodracon* and *Hauf-*

fiosaurus demonstrates that these features vary independently. Thus, the presence of an anteriorly extensive parietal in *Thalassiodracon* may indicate affinities with Jurassic pliosaurids or rhomaleosaurids. It is possible, but less likely, that this condition in *Thalassiodracon* is homologous with that in Cretaceous elasmosaurids or polycotyliids, because a relationship with these taxa has never been recovered.

(3) Anterior Termination of Pterygoids Transversely Broad—In *Thalassiodracon* (Fig. 2H) and many pliosauroids the anterior termination of the pterygoids is transversely broad (Cruickshank, 1994a; O'Keefe, 2001:fig. 3; Smith and Dyke, 2008; Smith and Vincent, 2010; Benson et al., in press; Ketchum and Benson, in press a). In contrast, the pterygoids taper anteriorly to a point in basal sauropterygians (e.g., Sues, 1987; Rieppel, 2000; Rieppel et al., 2002) and plesiosauroids (e.g., Williston, 1903; Storrs, 1997; Carpenter, 1996; O'Keefe, 2004a), representing the plesiomorphic condition. Thus, the presence of a transversely broad anterior termination of the pterygoids in *Thalassiodracon* suggests pliosauroid affinities.

(4) Cultriform Process Projects Ventrally as an Anteroposteriorly Short, Diamond-Shaped Platform—In *Thalassiodracon* (as interpreted here; Figs. 2A–B, 4A–B), *Hauffiosaurus* (Benson et al., in press; MANCH LL 8004), and OUMNH J.28585 (Cruickshank, 1994b; although O'Keefe, 2001:fig. 1, provided an alternative interpretation), the parasphenoid does not extend posteriorly past the anterior part of the posterior interpterygoid vacuity. The parasphenoids of *Thalassiodracon* and *Hauffiosaurus* (*tomistomimus* ("Yorkshire taxon")) were scored as "keeled anteriorly" by O'Keefe (2001:character 72), the same as in pliosaurids. However, in pliosaurids the parasphenoid forms the entire ventral surface of the basicranium (Ketchum and Benson, in press a) and bears a narrow longitudinal keel that extends most of its length within the posterior interpterygoid vacuity (Andrews, 1913; Ketchum and Benson, in press a). This situation is topographically distinct from that in *Thalassiodracon* and *Hauffiosaurus*, in which the cultriform process (comprising the entire parasphenoid) projects ventrally as an anteroposteriorly elongate, diamond-shaped platform. This is true regardless of the osteological composition of the basicranium, which is controversial (e.g., Storrs and Taylor, 1996; O'Keefe, 2001, 2006; Benson et al., in press). The same topology may also be present in *Plesiosaurus* (Storrs, 1997). However, all specimens of *Plesiosaurus* are poorly preserved and O'Keefe (2001) and Druckenmiller and Russell (2008a) scored the ventral surface of the basicranium of *Plesiosaurus* as missing data. The condition in *Thalassiodracon*, *Hauffiosaurus*, and OUMNH J.28585 is also distinct from that in most other plesiosaurs, in which the ventral surface of the basicranium is flat (e.g., cryptoclidids: Andrews, 1910; polycotyliids: Williston, 1903; O'Keefe, 2004a), weakly concave (basal plesiosaurs/pliosauroids: Owen, 1865–1881:pl. 13; Ketchum and Smith, 2010), or bears a narrow keel along its entire length (elasmosaurids: Carpenter, 1997; leptocleidids: Andrews, 1922; Kear et al., 2006; Druckenmiller and Russell, 2008a, 2008b).

(5) Single Foramen Exits Lateral Surface of Exoccipital—In *Thalassiodracon* (Fig. 4G), pliosauroids (Andrews, 1913:text-fig. 12; Noè et al., 2003; Ketchum and Benson, in press a), and *Leptocleidus superstes* (NHMUK 4828), only a single foramen exits through the lateral surface of the exoccipital. This is formed from multiple canals entering through the medial surface, which join up internally. In contrast, two foramina exit the medial surface of the exoccipital in most cryptoclidids (Andrews, 1910:text-fig. 72; Maisch, 1998; Evans, 1999), polycotyliids (Carpenter, 1997:fig. 7; Sato, 2005), and other plesiosauroids such as *Brancaesaurus* (Wegner, 1914) and *Microcleidus* (NHMUK 36184). Three lateral foramina are present in *Kimmerosaurus* (Brown, 1981:fig. 36). The presence of a single foramen may be plesiomorphic because it is present in basal sauropterygians (Rieppel, 1994; Rieppel and Werneberg, 1998).

Possible Pliosaurid Affinities of *Thalassiodracon*—The status of many proposed synapomorphies of Pliosauroida discussed above is uncertain. Many are present in pistosauroids, and may therefore represent plesiomorphies. Ambiguity in the status of many possible pliosauroid synapomorphies means it is difficult to determine whether Pliosauroida is an inclusive, monophyletic clade uniting the Jurassic pliosauromorph taxa (Pliosauridae and Rhomaleosauridae; e.g., O'Keefe, 2001; Smith and Dyke, 2008), or whether some taxa suggested as pliosauroids, including *Thalassiodracon*, are basal plesiosauroids or outside of the clade comprising Pliosauroida + Plesiosauroida (Druckenmiller and Russell, 2008a; Ketchum and Benson, 2010). Among pistosaurians, only the transversely broad anterior termination of the pterygoids, and transversely expanded mandibular symphysis, are restricted to Lower Jurassic pliosauromorphs and could support an inclusive Pliosauroida (sensu O'Keefe, 2001, and Smith and Dyke, 2008). If *Thalassiodracon* is a pliosauroid, we note that it possesses several, previously unrecognized, derived features: an anteriorly extensive parietal, a broad, interdigitating posterior termination of the premaxilla, and a short posteroventral process of the postorbital. These are shared with pliosaurids and *Hauffiosaurus*, suggesting a possible monophyletic clade comprising *Thalassiodracon*, *Hauffiosaurus*, and Pliosauridae.

Pliosaurids are a distinctive, well-characterized clade of robust, pliosauromorph predators (e.g., Andrews, 1913; Tarlo, 1960). They are abundant in the Callovian deposits of the U.K. (161.2–164.7 Ma; Gradstein et al., 2005) (e.g., Andrews, 1913), which represent their first definite occurrence. The pliosaurid ghost lineage extends back approximately 40 million years to the Triassic–Jurassic boundary interval (ca. 199.6 Ma; Gradstein et al., 2005), marked by the earliest occurrence of Rhomaleosauridae (the sister taxon of Pliosauridae) (Cruickshank, 1994a; Storrs and Taylor, 1996). However, identifying basal pliosaurids from this lineage has proved difficult. O'Keefe (2004b) identified *Hauffiosaurus*, from the Toarcian (175.6–183.0 Ma; Gradstein et al., 2005), as a basal pliosaurid (a taxon more closely related to *Pliosaurus brachydeirus* than to *Leptocleidus superstes*, *Polycotylus latipinnis*, or *Rhomaleosaurus*; Ketchum and Benson, in press b). Our data support this viewpoint, and the possible inclusion of *Thalassiodracon* within Pliosauridae. Identification of *Thalassiodracon* as a basal pliosaurid would dramatically reduce the pliosaurid ghost lineage. The relatively long neck and small skull of *Thalassiodracon* (Hawkins, 1834, 1840; O'Keefe, 2002; O'Keefe and Carrano, 2005) indicate that the robust skeleton and macropredaceous habits of Early Jurassic rhomaleosaurids (Taylor, 1992) and Middle Jurassic–Cretaceous representatives of Pliosauridae (Massare, 1987) were derived independently.

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LITERATURE CITED

- Andrews, C. W. 1896. On the structure of the plesiosaurian skull. *Quarterly Journal of the Geological Society*, London 52:246–253.
- Andrews, C. W. 1910. A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay. Part I. British Museum (Natural History), London, 205 pp.
- Andrews, C. W. 1913. A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay. Part II. British Museum (Natural History), London, 206 pp.
- Andrews, C. W. 1922. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). *Quarterly Journal of the Geological Society*, London 78:285–298.
- About, L., P. M. Mummery, T. J. Marrow, A. Tzelepi, and P. J. Withers. 2005. The effect of thermal oxidation on polycrystalline graphite studied by x-ray tomography. *Carbon* 43:765–774.
- Bakker, R. 1993. Plesiosaur extinction cycles—events that mark the beginning, middle, and end of the Cretaceous. *Geological Survey of Canada, Special Paper* 39:641–664.
- Bardet, N. 1992. Evolution et extinction des reptiles marins au cours du Mésozoïque. *Paleovertebrata* 24:177–283.
- Bardet, N. 1994. Extinction events among Mesozoic marine reptiles. *Historical Biology* 7:313–324.
- Bardet, N., P. Godefroit, and J. Sciau. 1999. A new elasmosaurid plesiosaur from the Lower Jurassic of southern France. *Palaeontology* 42:927–952.
- Barrett, L. 1859. On the atlas and axis of the *Plesiosaurus*. *Annals and Magazine of Natural History* 3:361–364.
- Benson, R. B. J., R. J. Butler, J. Lindgren, and A. S. Smith. 2010. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting vertebrates. *Proceedings of the Royal Society B* 277:829–834.
- Benson, R. B. J., H. F. Ketchum, L. F. Noë, and M. Gomez-Perez. In press. New information on *Hauffiosaurus* (Reptilia, Plesiosauria) based on a new species from the Alum Shale Member (Lower Toarcian: Lower Jurassic) of Yorkshire, UK. *Palaeontology*.
- Benton, M. J., and P. S. Spencer. 1995. *Fossil Reptiles of Great Britain*. Chapman and Hall, London, 386 pp.
- Blainville, H. D., de. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'Erpetologie et d'Amphibiologie. *Nouvelles Annales du Muséum (National) d'Histoire Naturelle*, Paris 4:233–296.
- Brown, D. S. 1981. The English Upper Jurassic Plesiosauroida (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum of Natural History, Geology Series* 35:253–347.
- Brown, D. S., and A. R. I. Cruickshank. 1994. The skull of the Callovian plesiosaur *Cryptoclidus eurymerus*, and the sauropterygian cheek. *Palaeontology* 37:941–953.
- Caldwell, M. W. 1997. Limb osteology and ossification patterns in *Cryptoclidus* (Reptilia: Plesiosauroida) with a review of sauropterygian limbs. *Journal of Vertebrate Paleontology* 17:295–307.
- Carpenter, K. 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 201:259–287.
- Carpenter, K. 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs; pp. 191–216 in J. M. Callaway and E. L. Nicholls (eds.), *Ancient Marine Reptiles*. Academic Press, San Diego, California.
- Cheng, Y.-N., T. Sato, X.-C. Wu, and C. Li. 2006. First complete pistosauroid from the Triassic of China. *Journal of Vertebrate Paleontology* 26:501–504.
- Conybeare, W. D. 1822. Additional notices on the fossil genera *Ichthyosaurus* and *Plesiosaurus*. *Transactions of the Geological Society of London*, series 2 1:103–123.
- Cruickshank, A. R. I. 1994a. Cranial anatomy of the Lower Jurassic plesiosaur *Rhomaleosaurus megacephalus* (Stutchbury) (Reptilia: Plesiosauria). *Philosophical Transactions of the Royal Society of London B* 343:247–260.
- Cruickshank, A. R. I. 1994b. A juvenile plesiosaur (Plesiosauria: Reptilia) from the Lower Lias (Hettangian: Lower Jurassic) of Lyme Regis, England: a pliosauroid-plesiosauroid intermediate? *Zoological Journal of the Linnean Society* 112:151–178.
- Cruickshank, A. R. I. 1996. The cranial anatomy of *Rhomaleosaurus thorntoni* Andrews (Reptilia, Plesiosauria). *Bulletin of the Natural History Museum, Geology Series* 52:109–114.
- Cruickshank, A. R. I. 1997. A Lower Cretaceous pliosauroid from South Africa. *Annals of the South African Museum* 105:207–226.
- Cruickshank, A. R. I., P. G. Small, and M. A. Taylor. 1991. Dorsal nostrils and hydrodynamically driven underwater olfaction in plesiosaurs. *Nature* 352:62–64.

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- Druckenmiller, P. S., and A. P. Russell. 2008a. A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews, 1922. *Zootaxa* 1863:1–120.
- Druckenmiller, P. S., and A. P. Russell. 2008b. Skeletal anatomy of an exceptionally complete specimen of a new genus of plesiosaur from the Early Cretaceous (Early Albian) of northeastern Alberta, Canada. *Palaeontographica Abteilung A* 283:1–33.
- Elliott, J. C., and S. D. Dover. 1982. X-ray microtomography. *Journal of Microscopy* 126:211–213.
- Evans, M. 1999. A new reconstruction of the skull of the Callovian elasmosaurid plesiosaur *Muraenosaurus leedsii* Seeley. *Mercian Geologist* 14:191–196.
- Gradstein, F. M., J. G. Ogg, and A. G. Smith. 2005. *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, U.K., 610 pp.
- Großmann, F. 2007. The taxonomic and phylogenetic position of the Plesiosauroidea from the Lower Jurassic Posidonia Shale of South-West Germany. *Palaeontology* 50:545–564.
- Hawkins, T. H. 1834. *Memoirs on Ichthyosauri and Plesiosauri*. Relfe and Fletcher, London, 58 pp.
- Hawkins, T. H. 1840. *The Book of the Great Sea-Dragons, Ichthyosauri and Plesiosauri, Gedolim Taninim of Moses*. William Pickering, London, 27 pp.
- Hulke, J. W. 1883. The anniversary address of the president. *Proceedings of the Geological Society* 39:38–65.
- Huxley, T. H. 1858. On a new species of the *Plesiosaurus* from Street, near Glastonbury; with remarks on the structure of the atlas and axis vertebrae, and of the cranium in that genus. *Quarterly Journal of the Geological Society, London* 14:281–294.
- International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature*. Fourth Edition. International Trust for Zoological Nomenclature, London, 306 pp.
- Kear, B. P. 2005. A new elasmosaurid plesiosaur from the Lower Cretaceous of Queensland, Australia. *Journal of Vertebrate Paleontology* 25:792–805.
- Kear, B. P. 2007. Taxonomic clarification of the Australian elasmosaurid genus *Eromangasaurus*, with reference to other austral elasmosaur taxa. *Journal of Vertebrate Paleontology* 27:241–246.
- Kear, B. P., N. I. Schroeder, and M. S. Y. Lee. 2006. An archaic crested plesiosaur in opal from the Lower Cretaceous high-latitude deposits of Australia. *Biology Letters* 2:615–619.
- Ketchum, H. F., and R. B. J. Benson. 2010. Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. *Biological Reviews* 85:361–392.
- Ketchum, H. F., and R. B. J. Benson. In press a. The cranial anatomy and taxonomy of *Peloneustes philarchus* (Sauropterygia, Plesiosauridae) from the Peterborough Member (Callovian, Middle Jurassic) of the UK. *Palaeontology*.
- Ketchum, H. F., and R. B. J. Benson. In press b. A new plesiosaurid (Sauropterygia, Plesiosauroidea) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early–Middle Jurassic plesiosaurids. *Special Papers in Palaeontology*.
- Ketchum, H. F., and A. S. Smith. 2010. The anatomy and taxonomy of *Macropata tenuiceps* (Sauropterygia, Plesiosauroidea) from the Hettangian (Lower Jurassic) of Warwickshire, United Kingdom. *Journal of Vertebrate Paleontology* 30:1069–1081.
- Lydekker, R. 1889. *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History)*. Part II. Containing the orders Ichthyopterygia and Sauropterygia. British Museum (Natural History), London, 307 pp.
- Maisch, M. W. 1998. Notes on the cranial osteology of *Muraenosaurus* Seeley, 1874 (Sauropterygia, Jurassic), with special reference to the neurocranium and its implications for sauropterygian phylogeny. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 207:207–253.
- Maisch, M. W., and M. Rücklin. 2000. Cranial osteology of the sauropterygian *Plesiosaurus brachypterygius* from the Lower Toarcian of Germany. *Paleontology* 43:29–40.
- Massare, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7:121–137.
- Mummery, P. M., B. Derby, P. Anderson, G. R. Davis, and J. C. Elliott. 1995. X-ray microtomographic studies of metal matrix composites using laboratory X-ray sources. *Journal of Microscopy* 177:399–406.
- Nichols, J. 1795–1815. *The History and Antiquities of the County of Leicestershire*. The author, London, 4 volumes.
- Noë, L. F., J. Liston, and M. Evans. 2003. The first relatively complete occipital-opisthotic from the braincase of the Callovian plesiosaur, *Liopleurodon*. *Geological Magazine* 140:479–486.
- O'Keefe, F. R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). *Acta Zoologica Fennica* 213:1–63.
- O'Keefe, F. R. 2002. The evolution of plesiosaur and plesiosaur morphotypes in the Plesiosauroidea (Reptilia: Sauropterygia). *Paleobiology* 28:101–112.
- O'Keefe, F. R. 2004a. Cranial anatomy of the polycotyloid plesiosaurs, including new material of *Polycotylus latipinnis*, Cope, from Alabama. *Journal of Vertebrate Paleontology* 24:326–340.
- O'Keefe, F. R. 2004b. Preliminary description and phylogenetic position of a new plesiosaur (Reptilia: Sauropterygia) from the Toarcian of Holzmaden, Germany. *Journal of Paleontology* 78:973–988.
- O'Keefe, F. R. 2006. Neoteny and the plesiomorphic condition of the plesiosaur basicranium; pp. 391–409 in M. T. Carrano, T. J. Gaudin, R. W. Blob, and J. R. Wible (eds.), *Amniote Paleobiology*. University of Chicago Press, Chicago, Illinois.
- O'Keefe, F. R. 2008. Cranial anatomy and taxonomy of *Dolichorhynchops bonneri* new combination, a polycotyloid (Sauropterygia: Plesiosauroidea) from the Pierre Shale of Wyoming and South Dakota. *Journal of Vertebrate Paleontology* 28:664–676.
- O'Keefe, F. R., and M. T. Carrano. 2005. Correlated trends in the evolution of the plesiosaur locomotor system. *Paleobiology* 31:656–675.
- Owen, R. 1838. A description of a specimen of the *Plesiosaurus macrocephalus*, Conybeare, in the collection of Viscount Cole, M.P., D.C.L., F.G.S., &c. *Transactions of the Geological Society of London, series 2* 5:515–535.
- Owen, R. 1860. On the orders of fossil and Recent Reptilia, and their distribution through time. *Report of the British Association for the Advancement of Science 1859*:153–166.
- Owen, R. 1865–1881. A monograph on the fossil Reptilia of the Liassic formations. Part III. *Plesiosaurus*, *Dimorphodon*, and *Ichthyosaurus*. Monograph of the Palaeontographical Society 35(166):1–134.
- Pinna, G. The cast of *Plesiosaurus hawkinsi* of the Lower Lias from Lyme Regis, England exhibited in the Natural History Museum of Milan, Italy. *Natura (Milan)* 65:49–52.
- Rieppel, O. 1994. The braincases of *Simosaurus* and *Nothosaurus*: monophyly of the Nothosauridae (Reptilia: Sauropterygia). *Journal of Vertebrate Paleontology* 14:9–23.
- Rieppel, O. 2000. Sauropterygia 1. *Encyclopedia of Paleoherpptology* 12A:1–134.
- Rieppel, O., and Werneberg, R. 1998. A new species of the sauropterygian *Cymatosaurus* from the Lower Muschelkalk of Thuringia, Germany. *Palaeontology* 41:575–589.
- Rieppel, O., P. M. Sander, and G. W. Storrs. 2002. The skull of the pistosaur *Augustasaurus* from the Middle Triassic of northwestern Nevada. *Journal of Vertebrate Paleontology* 22:577–592.
- Sander, P. M., O. Rieppel, and H. Bucher. 1997. A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of plesiosaurs. *Journal of Vertebrate Paleontology* 17:526–533.
- Sato, T. 2003. *Terminonatator pontiexensis*, a new elasmosaur (Reptilia: Sauropterygia) from the Upper Cretaceous of Saskatchewan. *Journal of Vertebrate Paleontology* 23:89–103.
- Sato, T. 2005. A new polycotyloid plesiosaur (Reptilia: Sauropterygia) from the Upper Cretaceous Bearpaw Formation in Saskatchewan, Canada. *Journal of Paleontology* 79:969–980.
- Sato, T., C. Li, and X.-C. Wu. 2003. Restudy of *Bishanplesiosaurus youngi* Dong, 1980, a fresh water plesiosaurian from the Jurassic of Chongqing. *Vertebrata Palasiatica* 41:17–33.
- Seeley, H. G. 1865a. On two new plesiosaurs, from the Lias. *Annals and Magazine of Natural History, series 3* 16:352–359.
- Seeley, H. G. 1865b. On *Plesiosaurus macropterus*, a new species from the Lias of Whitby. *Annals and Magazine of Natural History, series 3* 15:49–53.
- Seeley, H. G. 1874. Note on the generic modifications of the plesiosaurian pectoral arch. *Quarterly Journal of the Geological Society, London* 30:436–449.
- Smith, A. S., and G. J. Dyke. 2008. The skull of the giant predatory plesiosaur *Rhomaleosaurus cramptoni*: implications

- for plesiosaur phylogenetics. *Naturwissenschaften* 95:975–980.
- Smith, A. S., and P. Vincent. 2010. A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany. *Palaeontology* 53:1049–1063.
- Storrs, G. W. 1991. Anatomy and relationships of *Corosaurus alcovenensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. *Bulletin of the Peabody Museum of Natural History* 44:1–151.
- Storrs, G. W. 1994a. Fossil vertebrate faunas of the British Rhaetian (latest Triassic). *Zoological Journal of the Linnean Society* 112:217–259.
- Storrs, G. W. 1994b. A new Triassic plesiosaur based upon historical material from the lowermost Lias (Rhaetian) of Street, Somerset, England. *Journal of Vertebrate Paleontology* 14(3, Supplement):48A.
- Storrs, G. W. 1997. Morphological and taxonomic clarification of the genus *Plesiosaurus*; pp. 145–191 in J. M. Callaway and E. L. Nicholls (eds.), *Ancient Marine Reptiles*. Academic Press, San Diego, California.
- Storrs, G. W., and M. A. Taylor. 1996. Cranial anatomy of a new plesiosaur genus from the lowermost Lias (Rhaetian/Hettangian) of Street, Somerset, England. *Journal of Vertebrate Paleontology* 16:403–420.
- Sues, H.-D. 1987. Postcranial skeleton of *Pistosaurus* and interrelationships of the Sauropterygia (Diapsida). *Zoological Journal of the Linnean Society of London* 90:109–131.
- Tanner, L. H., S. G. Lucas, and M. G. Chapman. 2004. Assessing the record and causes of Late Triassic extinctions. *Earth Science Reviews* 65:103–139.
- Tarlo, L. B. 1960. A review of the Upper Jurassic pliosaurs. *Bulletin of the British Museum (Natural History), Geology* 14:145–189.
- Taylor, M. A. 1992. Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. *Philosophical Transactions of the Royal Society B* 335:247–280.
- Taylor, M. A., and A. R. I. Cruickshank. 1993a. A plesiosaur from the Linkfield Erratic (Rhaetian, Upper Triassic) near Elgin, Morayshire. *Scottish Journal of Geology* 29:191–196.
- Taylor, M. A., and A. R. I. Cruickshank. 1993b. Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 341:399–418.
- Warrington, G., and H.-C. Ivimey-Cook. 1990. Biostratigraphy of the Late Triassic and Early Jurassic: a review of type sections in southern Britain. *Cahiers Université Catholique du Lyon Séries Scientifiques* 3:207–213.
- Warrington, G., J. C. W. Cope, and H.-C. Ivimey-Cook. 1994. St. Audrie's Bay, Somerset, England: a candidate Global Stratotype Section and Point for the base of the Jurassic System. *Geological Magazine* 131:191–200.
- Wegner, T. 1914. *Brancaosaurus brancai* n. g. n. sp., ein Elasmosauride aus Wealden Westfalens; pp. 235–302 in F. Scheondorf (ed.), *Branca-Festschrift* 9. Verlag von Gebrüder Borntraeger, Leipzig, Germany.
- Welles, S. P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. *Memoirs of the University of California* 13:125–254.
- White, T. E. 1940. Holotype of *Plesiosaurus longirostris* Blake and classification of the plesiosaurs. *Journal of Paleontology* 14:451–467.
- Williston, S. W. 1903. North American plesiosaurs. Part 1. *Field Columbian Museum Publication (Geology)* 73(2):1–77.
- Wright, T. 1860. On the zone of *Avicula contorta*, and the Lower Lias of the south of England. *Quarterly Journal of the Geological Society, London* 16:374–411.

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APPENDIX 1. List of 25 works published since 1961 by at least 10 authors over a span of longer than 10 years employing *Plesiosaurus hawkinsii* Owen, 1838, *Thalsiodracon hawkinsii* (Owen, 1838), or an incorrect subsequent spelling of the same species (*P. hawkinsi* Owen, 1838, or *T. hawkinsi* [Owen, 1838]) as the presumed valid name for the plesiosaurian taxon based on NHMUK 2018*. This list indicates that *T. hawkinsii* Owen, 1838, is in prevailing usage (Article 23.9.1.2; International Commission on Zoological Nomenclature, 1999). As its objective senior synonym '*Plesiosaurus*' *triatarsostinus* Hawkins, 1834, has not been used since 1899 (Storrs and Taylor 1996), we designated *T. hawkinsii* Owen, 1838, as nomen protectum that supersedes *Plesiosaurus triatarsostinus* Hawkins, 1834 (Article 23.9.2; International Commission on Zoological Nomenclature, 1999).

Pinna (1974), Bakker (1993), Storrs (1994a, 1994b, 1997), Benton and Spencer (1995), Storrs and Taylor (1996), Caldwell (1997), Sander et al. (1997), Maisch (1998), Bardet et al. (1999), O'Keefe (2001, 2004b, 2006), Rieppel et al. (2002), Sato et al. (2003), O'Keefe and Carrano (2005), Cheng et al. (2006), Druckemiller and Russell (2008a), Smith and Dyke (2008), Ketchum and Smith (2010), Ketchum and Benson (2010, and in press b), Benson et al. (in press), Smith and Vincent (in press).