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Thaumatodracon wiedenrothi, a morphometrically and stratigraphically intermediate new rhomaleosaurid plesiosaurian from the Lower Jurassic (Sinemurian) of Lyme Regis

by

Adam S. Smith and Ricardo Araújo

with 2 plates, 13 text-figures, 1 table and 3 appendices

Abstract

An excellently preserved partial skeleton of a rhomaleosaurid plesiosaurian (NLMH 106.058) from the Sinemurian (Lower Jurassic) of Lyme Regis, England, is described. The material consists of a complete cranium, mandible, and articulated cervical vertebral column. It is noteworthy because large-headed rhomaleosaurids are rare from this stratigraphic horizon and it is taxonomically distinct. The material is referred to a new taxon, Thaumatodracon wiedenrothi gen. nov. et sp. nov, diagnosed by two autapomorphies: 1. a pronounced transverse trough on the posterior margin of the dorsal ramus of the squamosal; 2. possibly paired anteriorly tapering triangular basioccipital processes. It also possesses a unique combination of other characters including a 'short' premaxillary rostrum (length and width subequal), five premaxillary alveoli, premaxilla-maxilla sutures parallel anterior to the external nares, frontals contact on the midline, prefrontal-frontal suture convex and gently curved medially, mandibular symphyseal region spatulate and 'short' (length and width subequal), prominent dorsally concave medial flange anteromedial to the articular glenoid, robust rod-like axis neural spine with a circular transverse cross section, and cervical neural spines with a mediolaterally expanded apex. The taxon shares some of these characters with earlier Hettangian rhomaleosaurids (e.g. Atychodracon, Eurycleidus), and other characters with later Toarcian rhomaleosaurids (e.g. Rhomaleosaurus sensu stricto and Meyerasaurus). Inclusion of Thaumatodracon as an additional operational taxonomic unit in several existing cladistic analyses demonstrates that it occupies a relatively derived position within Rhomaleosauridae. A morphometric multivariate analysis of Lower Jurassic rhomaleosaurids shows that *Thaumatodracon* is also proportionally intermediate between known rhomaleosaurid taxa. Thaumatodracon is therefore a stratigraphically and anatomically intermediate taxon that fills a gap in our knowledge of the evolution of this macro-predatory plesiosaurian clade.

Key words: Plesiosauria - Sauropterygia - Rhomaleosauridae - Lower Jurassic - Lyme Regis

Contents

1. Intro	duction	90	3. Systematic Palaeontology	95
1.1	Institutional abbreviations	91	4. Comparative Description	96
2. Mate	erials and methods	91	4.1 Cranium	96
2.1	Material	91	4.1.1 Premaxilla	96
2.2	Methods	91	4.1.2 Maxilla	98
	2.2.1 Dataset	91	4.1.3 Frontal	98
	2.2.2 Principal component analysis	94	4.1.4 Prefrontal	98
	2.2.3 Agglomerative hierarchical clustering	94	4.1.5 Postfrontal	100
	2.2.4 Phylogenetic analysis	94	4.1.6 Postorbital	100
	2.2.5 3D laser scans	95	4.1.7 Jugal	100

Authors' addresses:

Adam S. Smith, Nottingham Natural History Museum, Wollaton Hall, Nottingham, NG8 2AE, UK;

e-mail: adam.smith@nottinghamcity.gov.uk

Ricardo Araújo, Instituto de Plasmas e Fusão Nuclear, Instituto Superior Técnico, Universidade de Lisboa, Portugal; Museum für Naturkunde, Berlin, Germany; Museu da Lourinhã, Portugal; Huffington Department of Earth Sciences, Southern Methodist University, Dallas, Texas, USA; e-mail: rmaraujo@smu.edu

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	4.1.8 Parietal	100
	4.1.9 Squamosal	100
	4.1.10 Quadrate	101
	4.1.11 Vomer	101
	4.1.12 Palatine	101
	4.1.13 Pterygoid	101
	4.1.14 Parabasisphenoid	102
	4.1.15 Basioccipital	103
	4.1.16 Exoccipital-opisthotic	103
4.2.	Mandible	103
	4.2.1 Dentary	103
	4.2.2 Splenial	107
	4.2.3 Surangular	107
	4.2.4 Angular	107
	4.2.5 Articular	107
	4.2.6 Prearticular	109
4.3.	Dentition	110

1. Introduction

The Plesiosauria is an extinct group of marine reptiles with a globally distributed fossil record that ranges from the Late Triassic (e.g. STORRS & TAYLOR 1996, SENNIKOW & ARKHANGELSKY 2010) to the Maastrichtian (Latest Cretaceous) (e.g. VINCENT et al. 2011, ARAÚJO et al. 2015). Plesiosaurians (also informally known as plesiosaurs) have a broad body, four wing-like flippers, and a short tail (Text-fig. 1) (STORRS 1993). However, there is much variation in the proportions of their cranium and cervical series (STORRS 1993, O'KEEFE 2002, O'KEEFE & CARRANO 2005). The Plesiosauria was once divided into two superfamilies: the short-necked Pliosauroidea and long-necked Plesiosauroidea (e.g. PERSSON 1963, BROWN 1981,

DRUCKENMILLER & RUSSELL 2008a), but recent studies have demonstrated that these traditionally defined groups have very different topologies that contain both long- and short-necked morphotypes (O'KEEFE 2001, KETCHUM & BENSON 2010, BEN-SON & DRUCKENMILLER 2013).

Rhomaleosaurids are a clade of medium to largebodied apex predators that are morphologically intermediate between the long-necked plesiosauromorphs and short-necked pliosauromorphs (CRUICKSHANK 1994a, SMITH & DYKE 2008, BENSON et al. 2012). The oldest rhomaleosaurids are from the latest Triassic/earliest Jurassic (?Rhaetian-Hettangian) of England, where they occurred alongside the earliest pliosaurids, plesiosauroids, and other plesiosaurians of uncertain



Text-fig. 1. Reconstructed skeleton of a rhomaleosaurid plesiosaurian to show the preserved parts (dark grey) and missing parts (light grey) in NLMH 106.058. The specimen consists of the complete skull and cervical series. Modified from SMITH & BENSON (2014).

affinity (STORRS & TAYLOR 1996, BENSON et al. 2011a, BENSON et al. 2012). The family is best known from the Hettangian (CRUICKSHANK 1994a) and the Toarcian (SMITH & BENSON 2014), whereas diagnostic rhomaleosaurid material from the intervening stages (Sinemurian, Pliensbachian) is sparse (SMITH 2008). Rhomaleosaurids survived into the Middle Jurassic where they are represented by two taxa, Maresaurus coccai from the Bajocian of Argentina (GASPARINI 1997), and Borealonectes russeli from the Callovian of Arctic Canada (SATO & WU 2008), but the clade became extinct in the late Middle Jurassic. The macropredatory niche occupied by the rhomaleosaurids in the Early Jurassic was repopulated by largeheaded, pliosauromorph thalassophonean pliosaurids in the Middle Jurassic and later (BAKKER 1993, KETCHUM & BENSON 2011a, BENSON et al. 2012).

Several plesiosaurian taxa are known from the famous fossil-bearing Lower Jurassic cliff exposures along the Dorset coast at Lyme Bay, between Lyme Regis and Seatown (MILNER & WALSH 2010). These represent a variety of morphotypes and diversity of taxa, but very few confirmed rhomaleosaurids (see discussion). This paper describes an excellently preserved partial skeleton of the first definite and diagnostic rhomaleosaurid from the Sinemurian of Lyme Regis, England, which helps to understand the anatomy of the clade and bridge a gap in the evolutionary history of rhomaleosaurids during this interval.

1.1 Institutional abbreviations

BRSMG, Bristol Museum and Art Gallery, Bristol; HALB, Halberstadt Museum, Halberstadt; LEICT, New Walk Museum, Leicester; NHMUK, The Natural History Museum (NHM), London; NLMH, Niedersächsisches Landesmuseum, Hannover; NMING, National Museum of Ireland, Dublin; SMNS, Staatliches Museum für Naturkunde, Stuttgart; WM, Whitby Museum, Whitby; WARMS, Warwickshire Museum, Warwick; YORYM, Yorkshire Museum, York.

2. Materials and methods

2.1 Material

NLMH 106.058 is an excellently preserved partial skeleton including much of the cranium (NLMH 106.058/A), mandible (NLMH 106.058/B), and articulated cervical series (NLMH 106.058/C) (SMITH & ARAÚJO 2012) (Text-figs 1, 2). The cervical vertebral column is complete and includes the atlas-axis. This material forms the basis for the anatomical de-

scription section of this paper. We collected measurements from NLMH 106.058 and 18 other Lower Jurassic plesiosaurian specimens for inclusion in several morphometric multivariate analyses (see below). This material includes the type specimens of the following valid species: Anningasaura lymense (NHMUK OR 49202), Archaeonectrus rostratus (NHMUKOR38525), Attenborosaurus conybeari (NHMUK OR1339), Eurycleidus arcuatus (NHMUK OR2028* etc.), Macroplata tenuiceps (NHMUK OR5488), Meyerasaurus victor (SMNS 12478), 'Plesiosaurus' macrocephalus (NHMUK OR1336), Rhomaleosaurus cramptoni (NMING F8785), Atychodracon megacephalus (the holotype BRSMG Cb 2335, and the neotype LEICT G221.1851, were coded separately), Rhomaleosaurus thorntoni (NHMUK OR4853), Rhomaleosaurus zetlandicus (YORYM G503, and a referred specimen WM 851.S, the type of 'Rhomaleosaurus propinguus', was coded separately), and Thalassiodracon hawkinsii (NHMUK OR2018*). In addition, data from the following unnamed specimens were included: HALB uncatalogued, NMING F10194, NMING F8749, and WARMS G10875. All of these operational taxonomic units (OTUs) represent individual specimens of rhomaleosaurid plesiosaurians or taxa closely related to that clade, and the material was observed first hand by ASS (SMITH 2007) with the exception of HALB uncatalogued. Measurements for the latter were derived from BRANDES (1914).

2.2 Methods

Linear measurements of vertebrae were taken in triplicate using a Mitutoyo 500-762-10 IP67 Digimatic Digital Caliper (length: 150 mm, minimum measurement: 0.01 mm). Table 1 presents the average of these measurements and corresponding standard deviations.

2.2.1 Dataset

We constructed a morphometric multivariate dataset consisting of 128 morphometric variables (absolute measurements) and 19 operational taxonomic units (listed above) including NLMH 106.058. OTUs can be interpreted statistically as integers in multivariate analyses because each is a discrete entity. The morphometric variables were mostly taken from the skull and appendicular skeleton (as opposed to the axial skeleton) to allow for direct comparison between equivalent elements in different OTUs. Measurements less than 150 mm were taken with callipers and these are

Table 1. Measur measurements. '	rements of t Measurem	he cervical ' ent done in	vertebrae and the posterio	l correspor r side of th	nding standar e vertebra. **	rd deviatio Estimated	ns of NLMH 1 measurement.	106.058. P	lease refer to Appendix 3 for a diag	ammatic k	cey to the various linea	r vertebral
	Anterior width	SD	Anterior height	SD	Ventral length	SD	Neural arch height	SD	Maximum width at dorsalmost point of neural arch	SD	Maximum width of zygapophysis	SD
Cervical #4	54,22	0,16	46,24	0,34	46,24	0,07	75,56	0,43	14,81	0,04	44,38	0,02
Cervical #5	53,76	0,27	51,37	0,24	30,65	0,29	73,94	0,10	14,18	0,28	45,39	0,33
Cervical #6	52,68	0,32	46,53	0,03	30,77	0,15	68,01	0,25	14,94	0,37	36,54	0,37
Cervical #7	56,94	0,17	51,13	0,16	32,29	0,12	۸.		~-		۸.	
Cervical #8	64,59	0,28	55,46	0,05	34,05	0,73	۸.		~-		۸.	
Cervical #9	57,55	0,42	49,94	0,33	28,56	0,06	17,33	0,96	~-		۸.	
Cervical #10	62,12	0,09	56,30	0,39	34,74	0,08	۸.		~-		۸.	
Cervical #11	58,76	0,05	62,62	0,50	37,50	0,06	۸.		~-		51,78	
Cervical #12	62,99	0,49	55,86	0,22	32,07	0,02	۰.		~-		53,81	0,52
Cervical #13	66,82	0,26	62,40	1,01	36,81	1,28	۰.		~-		۸.	
Cervical #14	72,79	0,09	56,56	1,30	38,05	0,76	۰.		~-		52,19	0,68
Cervical #15	70,56	0,36	57,64	0,41	38,49	0,09	114, 14	0,36	11,45	0,11	60,82	0,14
Cervical #16	66,69	0,44	62,42	1,05	38,11	0,04	۸.		~-		60,45	0,66
Cervical #17	71,84	0,14	69,11	0,03	41,38	0,17	۸.		~-		۸.	
Cervical #18	73,74	0,11	69,38	0,59	39,46	0,75	۸.		۰.		64,34	0,16
Cervical #19	72,05	0,67	69,60	0,12	41,51	0,61	۸.		~-		۸.	
Cervical #20	75,44	0,15	69,47	1,02	43,37	0,17	۸.		~-		۸.	
Cervical #21	79,36	0,25	70,68	1,96	46,91	0,02	135,56	1,19	10,99	0,11	70,64	0,26
Cervical #22	78,04	0,51	80,62	0,08	43,65	0,05	140,71	0,57	11,96	0,58	71,63	0,29
Cervical #23	80,37	0,23	74,30	1,31	48,68	0,38	134,31	0,00	۸.		73,40	0,08
Cervical #24	۸.		84,54	0,14	44,24	0,81	۸.		۰.		70,79	0,01
Cervical #25	۸.		77,53	0,25	47,05	0,46	131,94	$0,\!78$	18,80	0,02	69,20	0,20
Cervical #26	85,39	0,06	67,50	0,62	46,02	0,74	130,66	5,26	21,97	0,19	69,92	0,32
Cervical #27	۸.		73,79	1,34	45,45	0,04	۰.		~-		60,45	0,66

Adam S. Smith and Ricardo Araújo 92

SD	0,65	0,29	0,48	0,56	0,46	0,50	0,48	0,47	1,22	0,44	0,72	0,68	0,15	1,40	0,34	0,18	0,29	0,24	2,10	0,95		1,18	0,46	0,15
Rib facet length	21,00	23,55	22,09	18,41	21,95	21,12	21,62	24,70	17,03	24,70	24,25	25,75	23,96	24,31	24,63	25,77	28,64	28,44	30,21	31,51	۸.	17,10	27,79	23,96
SD	0,06			0,06	0,51	0,01		0,59	0,13	0,56	0,06		0,20	0,13	0,43	0,13		0,25	0,14	0,25	0,05			0,20
Minimum width of the neural arch	32,36	۸.	۸.	36,48	33,15	36,23	۸.	35,19	36,63	36,85	44,38	۸.	47,90	49,99	49,10	52,16	۸.	54,25	55,04	10,54	57,72	۸.	Λ.	47,90
SD	0,14		0,63	0,33	0,19	0, 41		0,48	0,23	0,08		0,38	0,83	0,05	0,48	0,02		0,45	0,70		0,66			0,83
Height of the neural canal	12,89	۸.	16,46	13,16	18,76	16,02	۸.	15,44	20,41	10,56	۸.	24,68	20,45	22,19	20,77	25,40	۸.	21,54	31,60	۸.	35,93	Λ.	۸.	20,45
SD	1,00			1,62	1,00	0,02		0,56	1,62	0,64		0,66	0,21	0,87	1,11	0,38		0,29	0,17	0,69	0,74			0,21
Width of the neural canal	14,35	۸.	۸.	17,52	11,00	16,02	۸.	13,08	16,16	13,36	۸.	27,99	22,55	18,29	17,59	34,12	۸.	20,70	29,20	32,55	28,25	۸.	۸.	22,55
SD	0,37			0,55	0,10	0,05		0,20	0,29	0,27		0,00	0,06	0,42	0,10	0,17		0,31	0,48	1,61	17,71			0,06
Thickness of the pedicles	10,47	Λ.	Λ.	10,41	11,71	9,72	Λ.	9,89	11,67	8,51	Λ.	27,33	12,49	18,12	16,36	20,46	۸.	18,20	11,33	8,75	17,71	۸.	Λ.	12,49
SD	0,10	0,12	0,16								0,07	0,28	0,23		0,21	0,57		0,16	0,66	0,25	0,02	0,25	1,09	0,23
Minumum width of neural spine	10,51	8,73	8,49	۸.	۸.	۸.	۸.	۸.	۸.	۸.	9,49	8,39	48,70	۸.	9,59	53,64	۸.	96,99	10,17	10.54	12,00	12,19	11,24	48,70
	Cervical #4	Cervical #5	Cervical #6	Cervical #7	Cervical #8	Cervical #9	Cervical #10	Cervical #11	Cervical #12	Cervical #13	Cervical #14	Cervical #15	Cervical #16	Cervical #17	Cervical #18	Cervical #19	Cervical #20	Cervical #21	Cervical #22	Cervical #23	Cervical #24	Cervical #25	Cervical #26	Cervical #27

accurate to the nearest 0.1 mm; larger measurements were taken with a tape measure and are accurate to the nearest 5 mm (SMITH 2007). The most incomplete OTU in the dataset is HALB uncatalogued (13.3%) (BRANDES 1914) while the most complete is *Meyera*saurus victor (76.6%). The dataset is incomplete (43.1%), so we conducted three different analyses: 1) with all data (43.1% complete); 2) with pruned variables with less than 10 entries (63.4% complete); and 3) with pruned morphometric variables with less than 10 entries for skull data only (64.4% complete). Such high levels of incompleteness would hinder a multivariate analysis unless some method is used to estimate the missing data. To complete the missing data with estimates to allow first principal components to be calculated we used a non-linear iterative partial least squares algorithm (NIPALS, WOLD 1966a, b, run in XLSTAT 2014.1.01). The NIPALS algorithm was specifically designed for principal component analysis (PCA) but it is also used for other multivariate analysis tools. To test the quality of the estimates generated by the NIPALS algorithm we deleted 16 known measurements for NLMH 106.058 and then compared the estimates with the actual values. The average error was only 13% with a minimum error of 0.18% (Appendix 1). This demonstrates the power of the NIPALS algorithm for providing confident estimates for missing data.

2.2.2 Principal component analysis

We applied two methods of multivariate analysis to our morphometric dataset: principal component analysis (PCA) and agglomerative hierarchical clustering (AHC) (see below). Both methods were applied (in XLSTAT 2014.1.01) to the complete datasets with missing data generated with the NIPALS algorithm. The PCA was used to understand the variability within the dataset and to provide information on correlated morphometric variables. PCA was used in favour of correspondence analysis (HAIR et al. 2010, MURTAGH & HECK 2012) because it is more appropriate for absolute measures (rather than relative measures, where correspondence analysis would be more adequate). We used Spearman type PCA and AHC because it is best used for non-normally distributed data. We performed normality tests (Shapiro-Wilk, Anderson-Darling, Lilliefors and Jarque-Bera tests) to all 128 morphometric variables using XLSTAT 2014.1.01. Some of the morphometric variables failed at least one of the tests to normality or had a high risk of being a non-normal sample (see Appendix 1). Furthermore,

Spearman PCA type and AHC dissimilarity are better for continuous variables (absolute measurements), applied to integers (in this case, individual OTUs).

2.2.3 Agglomerative hierarchical clustering

The AHC was used to identify OTU clusters based on morphometric similarity (see Appendix 1). We used unweighted pair-group averages for this analysis because this is an appropriate method for classification of sampling units (such as OTUs) on the basis of their pairwise similarities in relevant variables (such as morphometric measurements).

2.2.4 Phylogenetic analysis

To test the phylogenetic position of NLMH 106.058 we coded it as an additional OTU in three different cladistic analyses of plesiosaurians: SMITH & DYKE (2008), BENSON et al. (2012), and BENSON & DRUCKENMILLER (2013).

The data matrix of SMITH & DYKE (2008) was selected because its character codings and OTUs were compiled specifically to resolve the relationships among Rhomaleosauridae. The data matrix of SMITH & DYKE (2008) contains 93 characters and 39 taxa. *Cymatosaurus* was used as outgroup and we ordered characters 8, 21, 47, 54, 62, 65, and 78 (as per SMITH & DYKE 2008). We also trimmed *Sthenarosaurus* and *Leptocleidus clemai* from the final analysis because they were identified as wildcard taxa in early analyses.

The data matrix of BENSON et al. (2012) was selected because it focusses particularly on Lower Jurassic taxa. The data matrix of BENSON et al. (2012) contains 207 characters and 34 taxa. We used *Yunguisaurus*, *'Pistosaurus* postcranium', *'Pistosaurus* skull', and *Augustasaurus* as outgroups.

The data matrix of BENSON & DRUCKENMILLER (2013) was selected because it is the most recent comprehensive phylogenetic analysis of Plesiosauria as a whole. The data matrix of BENSON & DRUCKENMILLER (2013) contains 207 characters and 81 taxa. *Yunguisaurus* was defined as the outgroup. We did not eliminate any of the wildcard taxa suggested by the BENSON & DRUCKEN-MILLER (2013) because these did not affect the resolution of the relationships with the closest related OTU's (i.e. *Rhomaleosaurus* sensu stricto).

The resulting matrices were run in TnT 1.1 (no taxon limit) December 2013 version for Windows (GOLOBOFF et al. 2008). We applied the same methodology to all three different data matrices. TnT found the most parsimonious trees for the dataset with 20 independent hits to the best score ("xmult" plus ten cycles of tree drifting; GOLOBOFF 1999), then we calculated a strict consensus by TBR-collapsing using "rule 3" (i.e. no possible support).

For SMITH & DYKE (2008) the tree search algorithm (FUSE) calculated a total of 52,076,757 rearrangements with a best score (tree length) of 372 and a total of 47 MPTs (most parsimonious trees). The synapomorphies shown are common to the 47 trees (Appendix 2). For BENSON et al. (2012) there were 36,715,636 rearrangements with a best score (tree length of 618) and a total of 46 MPT's (Appendix 2). The synapomorphies shown are common to the 46 trees. For BENSON & DRUCKENMILLER (2013) there were 325,344,700 rearrangements with a best score (tree length) of 1337 and a total of 125 MPTs (Appendix 2). The synapomorphies shown are common to the 125 trees.

Group support was calculated for the cladistic analyses by TBR-swapping (tree bisection reconnection) the trees to find the number of steps required to lose each group. Resampling scores were calculated using 100 replications of symmetric resampling (GOLO-BOFF et al. 2003), analysing each data set with a single addition, and then collapsing the resulting tree with tree bisection reconnection (TBR, GOLOBOFF & FAR-RIS 2001). Both absolute (BREMER 1994) and relative Bremer (GOLOBOFF & FARRIS 2001) are presented. Bremer support is the difference of number of steps between the MPT and other suboptimal trees that did not recover a particular node (BREMER 1994). Whereas relative Bremer support is, in other words, also a way to collapse branches considering suboptimal trees but by weighting favourable and contradicting evidence (GOLOBOFF & FARRIS 2001). Symmetric resampling avoids the underestimation and overestimation of nodes when characters have a priori weights because it is calculated in a way that the probability of overweighing a character is the same as underweighing it (GOLOBOFF et al. 2003). GC (i.e., group present / contradicted) varies between -100 and 100 and is a form of relative symmetric resampling in which -100 means maximum contradiction, 0 indifference and 100 maximum support (GOLOBOFF et al. 2003).

2.2.5 3D laser scans

We scanned all substantial parts of NLMH 106.058 with a Next Engine 3D laser scanner. The scanned material includes all skull fragments over 150 mm long

and all cervical vertebrae. The individual scans (.scn files) were trimmed, aligned, and fused in Scanstudio and exported as .obj files. These files therefore represent virtual models of the bones.

3. Systematic Palaeontology

Class Reptilia LINNAEUS, 1758

Superorder Sauropterygia Owen, 1860 Order Plesiosauria DE BLAINVILLE, 1835

Family Rhomaleosauridae KUHN, 1961

Genus *Thaumatodracon* gen. nov. urn:lsid:zoobank.org:act:97FB2FDB-09F4-4A60-8DE1-A21DEAFEDC17

Genus etymology: The genus name derives from the greek θαύμα (= thávma), meaning 'wonder', and δράκων (= drákon), meaning 'dragon'.

Type species: *Thaumatodracon wiedenrothi* gen. nov. et sp. nov., urn:lsid:zoobank.org:act:5EEDDBD4-E7DE-4D0F-96A2-5F404D9F87B8

Species etymology: The species name honours Kurt Wiedenroth, the amateur fossil hunter who discovered and collected the specimen.

Holotype: NLMH 106.058, a partial skeleton comprising a complete cranium, mandible, articulated cervical series, and indeterminate fragmentary remains (Text-figs 2–10; Pls 1–2).

Horizon and Location: Black Ven Mudstone Member of the Charmouth Mudstone Formation (Sinemurian, Lower Jurassic), on the stretch of coast between Lyme Regis and Charmouth (Lyme Bay), UK.

Diagnosis: As for the type and only species, *Thauma-todracon wiedenrothi*.

Autapomorphies: 1. a pronounced pit on the posterior margin of the dorsal ramus of the squamosal; 2. paired anteriorly tapering triangular basioccipital processes, although it is possible these are a taphonomic artefact (see Comparative Description). The taxon is also distinguished by the following unique combination of characters: Premaxilla-maxilla suture parallel immediately anterior to the external nares, frontals contact on the midline, premaxillary rostrum short, five teeth in the premaxilla, gently rounded medially convex prefrontal-frontal suture, articular with prominent dorsally concave medial flange anteromedial to the articular glenoid, robust rod-like axis neural spine with circular cross section, neural spines expanded distally.

Notes: NLMH 106.058 was discovered in early 1969 by amateur fossil hunter Kurt Wiedenroth in Lyme Bay, on the stretch of coast between Lyme Regis and Charmouth. It was purchased in 1969 by the Nied-



Text-fig. 2. Thaumatodracon wiedenrothi (NLMH 106.058), photograph of articulated skull and neck. Scale bar represents 200 mm.

ersächsisches Landesmuseum, Hannover, where it was prepared in the 1990s by Elijah Widmann.

4. Comparative Description

4.1 Cranium

The cranium is almost complete, but it is dorsoventrally compressed due to taphonomic processes, and preserved in several fragments (Text-fig. 3). Although the dorsal margin of the orbital opening and medial portion of the postorbital is incompletely preserved, it is possible to estimate the anteroposterior length of the orbit (100 mm), which is approximately half the length of the supratemporal fenestra (approx. 200 mm).

4.1.1 Premaxilla

The premaxillae comprise a short rounded spatulate rostrum and a broad posterior process that extends posteriorly along the midline (Text-fig. 3). Although the posterior parts of the premaxillae are incompletely preserved, a fragment of the left premaxilla contacts the frontal and represents the posterior-most extension of the process. In *Rhomaleosaurus* and *Meyerasaurus* the premaxilla contacts the parietal (SMITH & DYKE 2008, SMITH & VINCENT 2010), separating the frontals on the midline, whereas it does not in *Thaumatodracon* or *Atychodracon megacephalus* (CRUICKSHANK 1994a). The width of the posterior process of the premaxilla remains constant for most of its length so that the premaxilla/maxilla sutures run parallel to each other anterior to the external nares. This is also seen in Meyerasaurus and Rhomaleosaurus, but not in Atychodracon. The dorsal surface of the premaxilla is ornamented by numerous irregularly distributed anteriorly opening nutritive foramina. The external naris is not preserved on the left side, and only partially preserved on the right, where it is clear that the premaxilla contacts its anteromedial margin. However, the posterior extent of this contact is unknown. The external naris is positioned approximately 35 mm posteriorly relative to the internal nares. There is a mediolateral constriction between the premaxilla and maxilla that coincides with a diastema between the last tooth of the premaxilla and the first tooth of the maxilla. This constriction is widespread in plesiosaurians, including rhomaleosaurids (SMITH & BENSON 2014), but is absent in OUM J.28585, also from Lyme Regis (CRUICKSHANK 1994b). Due to damage it is impossible to determine if a dorsomedian foramen was situated on the midline between the posterior margins of the external nares as in Rhomaleosaurus (SMITH & DYKE 2008), but not in Atychodracon megacephalus (Sмітн 2015).

Each premaxilla bears five tooth alveoli (Text-fig. 3C, D), a character shared with *Rhomaleosaurus thorntoni* (CRUICKSHANK 1996, SMITH & BENSON 2014), *Atychodracon* (CRUICKSHANK 1994a), *Maresaurus* (GASPARINI 1997), and *Borealonectes* (SATO & WU 2008; "five to six" p. 311), but in contrast with other Lower Jurassic pliosauroids: *Anningasaura* has



Text-fig. 3. *Thaumatodracon wiedenrothi* (NLMH 106.058); cranial elements articulated in life position. A. Photograph in dorsal view. B. Interpretation of dorsal view. C. Photograph in ventral view. D. Interpretation of ventral view. Abbreviations: ang: angular; atax: atlas-axis complex; bo: basioccipital; bo?: possible anterior process of basioccipital; bs: basisphenoid; c3: third cervical vertebra; cor: facet for coronoid; dpmx: dorsal process of maxilla; exn: external naris; exop: exoccipital-opisthotic; fr: frontal; in: internal naris; jug: jugal; mw: medial wall of premaxilla; mx: maxilla; mx13: thirteenth maxillary alveolus; oc: olfactory canal; pal: palatine; par: parietal; pin: pineal foramen; piv: posterior interpterygoid vacuity; pmx: premaxilla; pmx1: first premaxillary alveolus; pmx5: fifth premaxillary alveolus; ps: parabasisphenoid; pf: postfrontal; po: postorbital; pt: pterygoid; pt?: possible pterygoid; prf: prefrontal; q: quadrate; sa: surangular; sof: suborbital fenestra; sq: squamosal; vom: vomer. Diagonal lines represent broken surfaces; stippling represents matrix; grey areas in **B**. represent the dorsal surface of the palate; grey areas in **D**. represent the ventral surface of the skull roof. Scale bar represents 100 mm.

four premaxillary alveoli (VINCENT & BENSON 2012), Macroplata has six (KETCHUM & SMITH 2010), and Hauffiosaurus has seven – ten (BENSON et al. 2011b). In Thaumatodracon the first alveolus in the premaxilla is the smallest and the fourth is the largest. The first alveolus is significantly smaller than the third alveolus and the dentition can be regarded as heterodont. Several primary alveoli, some of which contain small teeth, are situated medial to the functional tooth alveoli. A raised medial wall articulates loosely with the vomer. This wall is separated from the vomer anteriorly and forms the lateral margin of an anteroposteriorly oriented channel. The left and right channels meet on the midline to form an arrow-shaped structure. The premaxilla-maxilla suture on the palate is transversely orientated and follows a gently anteriorly convex path from the lateral notch to the vomer medially.

4.1.2 Maxilla

The maxilla is a large triradiate element that contacts the premaxilla anteromedially, the jugal posteriorly, and contributes to the whole lateral margin of the external naris and anterolateral margin of the orbital opening (Text-fig. 3). There is no trough or depressed region anterior to external naris, as is present in, for example, Atychodracon megacephalus (SMITH 2015). The maxilla is mediolaterally expanded at the level of the third, fourth and fifth teeth. The posteromedial portion of the maxilla is damaged on both elements, so its exact relationship to the prefrontal and frontal is unclear. However, a distinct process of bone contacts the prefrontal and frontal and this is interpreted as the short triangular dorsal flange of the maxilla, as described in *Rhomaleosaurus* (SMITH & DYKE 2008), Atychodracon megacephalus (SMITH 2007), and Macroplata (KETCHUM & SMITH 2010). The orbital bar bears a raised anteroposteriorly oriented ridge that divides a laterally facing surface from a medially facing surface. The maxilla-jugal contact is clearest on the left side of the skull at the anterolateral margin of the orbital opening. On the palatal surface the maxilla contacts the anterior and lateral margins of the internal naris, and contributes to the entire lateral margin of a suborbital fenestra. On the palate, the maxilla forms a smooth band that extends from the internal naris to the suborbital fenestra.

4.1.3 Frontal

The frontals are elongate bones positioned between the orbital openings and contact each other on the midline (Text-fig. 3). They are similar to Atychodracon megacephalus (CRUICKSHANK 1994a, SMITH 2007) and Hauffiosaurus tomistomimus in this regard (BEN-SON et al. 2011b), but different to *Rhomaleosaurus* and derived plesiosaurians, in which the frontals are separated on the midline by a contact between the premaxillae and parietals (SMITH & DYKE 2008). Each frontal has a broad anterior process but this is broken so its anterior extent and relationship to the external naris is unknown. The dorsal margin of the orbital opening is incomplete so it is not possible to determine whether or not the frontal contributed to the orbital margin. The frontal does not participate to the margin of the supratemporal fenestra, whereas it does in *Atychodracon megacephalus* (CRUICKSHANK 1994a).

A well-preserved fragment representing the dorsal roof between the orbits provides information on the ventral surface of the cranium (Text-figs 3C, D; 4K). There is a broad oval midline fossa – the olfactory canal – and posteriorly, a smaller oval midline fossa separated from the large fossa by a narrow channel (Text-fig. 4K). The small fossa is asymmetrical, with a more deeply concave left margin and flatter right margin. The frontals contact on the midline posterior to this channel. A deeply concave fossa is situated anterolateral to the olfactory canal and anteromedial to the orbital opening, bordered laterally by a strong ventrally projecting longitudinally oriented flange that also comprises the medial wall off the orbital opening. A lower longitudinal flange separates this fossa from the olfactory canal, but anteriorly this flange transforms into a low longitudinally oriented ridge. The sutures in this region are unclear but most of the preserved portion seems to consist of the frontals and prefrontals. This region compares closely with the same region in Peloneustes as figured and described by ANDREWS (1913, text-fig. 13) and KETCHUM & BENSON (2011b, text-fig. 5).

4.1.4 Prefrontal

The prefrontal contributes to the anteromedial margin of the orbit and contacts the maxilla anteriorly and the frontal medially (Text-fig. 3A, B). The prefrontalfrontal contact curves gently posterolaterally. Both prefrontals are damaged and only a small fragment of the left prefrontal is preserved. Therefore the posterior and anterior extent of the prefrontal is unknown. It is



Text-fig. 4. *Thaumatodracon wiedenrothi* (NLMH 106.058), cranial elements. A. Photograph of the posterior surface of the squamosals. B. Interpretation. C. Photograph of the left jugal and surrounding bones in lateral view. D. Interpretation. E–F. Photographs of left exoccipital-opisthotic in posterior (E) and lateral (F) views. G–H. Interpretations. I. Photograph of possible posterolateral fragment of right pterygoid showing the rugose 'ectopterygoid boss'. J. Interpretation. K. Stereo pair of the ventral surface of frontals (derived from a three-dimensional laser scan) showing the shape and extent of the olfactory canal. Abbreviations: axns: axis neural spine; ec: rugose boss – probably the 'ectopterygoid' flange; cen: centrum; cr3: left cervical rib of third cervical vertebra; fo: foramina; jug: jugal; mx: maxilla; nc: neural canal; paro; paraoccipital process; fac: facet for posterior extension of postorbital; q: quadrate; qpf: quadrate-ptergoid flange; sq: squamosal; ttr: transverse trough; ?: unknown element. Diagonal lines represent broken surfaces, stip-pling represents matrix. Scale bar in A–D represents 50 mm; in E–K represents 10 mm.

unclear whether the prefrontal contacted the posterior margin of the external naris.

4.1.5 Postfrontal

The postfrontal contacts the frontal anteriorly and the parietal posteromedially (Text-fig. 3A, B). Both postfrontals are damaged laterally so their relationship to the postorbitals is unknown. The postfrontal contacts the parietal along a posterolaterally inclined interdigitating suture, and contributes to the anterior margin of the posttemporal fenestra.

4.1.6 Postorbital

The postorbital extends posteriorly along the dorsal surface of the jugal as a narrow 'footplate' that contacts and extends along the dorsal surface of the squamosal (Text-figs 3C, D; 4C, D). The left postorbital is missing but the right postorbital is almost complete. The medial portion of the right postorbital is damaged but it is still possible to estimate the anteroposterior length of the orbit, which is little more than a third that of the supratemporal fenestra. The anterior surface of the right postorbital is dorsoventrally thin and forms a sharp and slightly crenulated edge that protrudes into the orbital opening. Two nutritive foramina are located on the dorsal surface of the right postorbital close to the orbital opening.

4.1.7 Jugal

The jugal is a dorsoventrally narrow and anteroposteriorly elongate element that contacts the maxilla anteriorly, the squamosal posteriorly, and the postorbital dorsally (Text-figs 3; 4C, D). It extends about halfway along the anteroposterior length of the orbital opening of which it forms the posterolateral and lateral margins, and extends posteriorly to form the anteriormost portion of the delicate temporal bar. A raised orbital margin runs the entire length of the orbital opening and separates the concave medially facing surface of the jugal from the convex dorsolaterally facing convex surface. The lateral surface of the jugal, below the postorbital, is pierced by numerous large foramina (five on the left jugal, four on the right, each 1-3 mm in diameter) and bears a sculptured ornamentation of deep anteroposteriorly oriented grooves and ridges (Text-fig. 4C, D). Similar ornamentation is also present in *Rhomaleosaurus* (SMITH & BENSON 2014).

4.1.8 Parietal

The parietal is a large element that separates the temporal fenestrae on the midline (Text-fig. 3A, B). It contacts the frontal and postfrontal anteriorly along an interdigitating suture, and the squamosal posteriorly, though the parietal-squamosal suture is unclear and probably fused. The dorsal part of the parietal is damaged so the extent of the sagittal crest is unknown. The parietal vault is expanded to approximately onethird the mediolateral width of the skull, and the lateral surfaces are weakly convex (= 'lateral angle', SMITH & DYKE 2008). The oval pineal foramen is situated anteriorly, approximately level with the anterior margin of the temporal fenestra, and is completely enclosed by the parietals. Several pits and sulci are present around the pineal foramen. A mediolaterally narrow pointed anterior projection of the parietal extends between the frontals to about one third of the orbit length. This resembles the condition in Atychodracon megacephalus (CRUICKSHANK 1994a) but contrasts with *R. cramptoni* (SMITH & DYKE 2008), where the parietal extends about halfway along the anteroposterior length of the orbital openings.

4.1.9 Squamosal

The squamosal is a large triradiate element that forms all of the posterior and lateral margin of the large temporal fenestra (Text-figs 3; 4A, B). The anterior ramus comprises most of the lower temporal bar, a part of the skull prone to taphonomic damage in plesiosaurians. It is delicate, dorsoventrally shallow for most of its length, and strongly mediolaterally compressed. It contacts the jugal anteriorly along an interdigitating 'V' shaped suture with the apex facing anteriorly on the lateral surface (Text-fig. 4C, D). The dorsal rami of the squamosals meet on the midline along a strongly interdigitating suture, and a posterior bulb is formed by the squamosals on the midline. The suture between the squamosals and the parietal is unclear. There is a pronounced transverse trough on the posterior surface of the dorsal ramus of the squamosal (Text-fig. 4A, B), present on both elements, and therefore a natural biological character. A weakly developed trough is present in this position in R. zetlandicus (TAYLOR 1992), but in *Thaumatodracon* it is deeper and more pronounced, so we consider it an autapomorpy of the taxon. In cross-section through the middle of the dorsal ramus the anterior surface of the squamosal is deeply excavated and produces a pronounced, curved overhanging anterodorsal crest. This rounded crest diminishes medially into a shallow ridge, but is sharp

laterally, where it forms the posterior margin of the temporal fenestra. Another rounded ridge extends along the dorsal surface of the dorsal ramus, dividing its surface into two flattened areas, the posterior of which becomes slightly concave as it approaches the quadrate ventrally.

4.1.10 Quadrate

The right quadrate is roughly in life position in articulation with the right articular glenoid of the mandible (Text-figs 3, 8). It contacts the squamosal along a straight suture, with no sign of a quadrate-squamosal foramen, as present in OUM J.28585 (CRUICKSHANK 1994b) and *Rhomaleosaurus* (SMITH & DYKE 2008). However, the main body of the right quadrate is crushed and its articular surface is not visible. The left quadrate (together with the presumed quadrate ramus of the pterygoid) is well exposed (Text-fig. 3C, D). It has broken off at the proximal base of the flange and appears to have flipped during taphonomy into a displaced position below the dorsal ramus of the right squamosal. The ventral end of the quadrate is slightly mediolaterally expanded and forms the rounded ventral condyle for articulation with the mandibular glenoid. The glenoid articulation is kidney-shaped in outline with a cupped anterior and convex posterior surface that matches the shape of the mandibular glenoid. The medial part of the condyle is anteroposteriorly longest and the condyle is not divided into two by a notch (as it is in *Peloneustes*, KETCHUM & BENSON 2011b).

4.1.11 Vomer

The vomer is a single ossified element situated on the midline of the anterior surface of the palate (Text-fig. 3C, D). It contacts the premaxilla, maxilla, and palatine laterally, but it is damaged posteriorly, so its relationship to the pterygoid is unclear. It has convex lateral margins for most of its length and is slightly constricted mediolaterally between the internal nares. The internal nares are therefore situated very close to each other (the mediolateral width of the vomer between the internal nares is 14.5 mm). The anterior portion of the vomer is mediolaterally narrow and tapers to a pointed tip that extends anteriorly between the slightly displaced premaxillae. A transverse section through the vomer at midlength is gently convex, whereas between the internal nares it is flat and forms the vertical medial walls of the internal narial openings. The left internal naris is complete (17 mm long and 9.4 mm wide) and oval in outline. A narrow process of the vomer wraps around the posterior margin of the internal naris and contacts the maxilla on the posterolateral margin, excluding the palatine from the internal naris. This condition is also present in *Rhomaleosaurus* (SMITH & BENSON 2014) and *Meyerasaurus* (SMITH & VINCENT 2010). In contrast, the palatine contacts the posterior margin of the naris, separating the vomer from the maxilla, in *Atychodracon* (CRUICK-SHANK 1994a, SMITH 2007) and *Anningasaura* (VIN-CENT & BENSON 2012). The vomer extends posterior to the internal nares but the posterior extremity is damaged. The vomer-palatine suture extend posteromedially from the palatine-maxilla-vomer contact but it becomes unclear posteriorly.

4.1.12 Palatine

The palatines are mostly damaged but the anteriormost portion of the left element is preserved in situ (Text-fig. 3C, D) and a displaced fragment of palate located in the right subtemporal fenestra may represent part of the pterygoid or palatine. The palatinemaxilla-vomer contact is located posterolateral to the internal naris. The palatine is separated from the maxilla posteriorly by a suborbital vacuity, but only the anteriormost portion of the suborbital vacuity is preserved, so it is unknown if the opening was mediolaterally constricted around two-thirds of its length to resemble the shape of a bowling pin, as in Rhomaleosaurus (SMITH & BENSON 2014). The palatine-maxilla contact is a weakly interdigitating suture that extends posterolaterally from the palatine-maxillavomer contact to the anterior margin of the suborbital vacuity. The isolated palatal fragment located in the subtemporal opening has almost entirely damaged margins except for a short concave section that could represent part of the margin of the suborbital vacuity.

4.1.13 Pterygoid

The pterygoids are damaged and their anterior rami are missing, but the posterior rami surrounding the posterior interpterygoid vacuities are preserved in situ (Text-figs 3C, D; 5) There are several isolated fragments of bone that probably also belong to the pterygoids or palatines, but their exact original position in the skull is unclear. Posterior to the posterior interpterygoid vacuities the pterygoids appear to contact for more than two-thirds of their anteroposterior length (Text-fig. 5). However, this region is damaged and cracked so no clear sutures are visible. The pterygoids also meet behind the posterior interpterygoid vacui-



Text-fig. 5. *Thaumatodracon wiedenrothi* (NLMH 106.058), close up view of the posterior part of palate showing the region around the posterior interpterygoid vacuities. **A.** Photograph. **B.** Interpretation. **Abbreviations:** ba: basal articulation; bo?: possible anterior process of basioccipital; bs: basisphenoid; fo: foramina; piv: posterior interpterygoid vacuity; ps: parabasisphenoid; pt: pterygoid; Diagonal lines represent broken surfaces, stippling represents matrix, dashed lines represent uncertain sutures. Scale bar represents 20 mm.

ties in most derived rhomaleosaurids, but not in Anningasaura (VINCENT & BENSON 2012), NHMUK OR39514 (VINCENT 2012), or OUM J.28585 (CRUICKSHANK 1994b). The pterygoid is crushed and only slightly mediolaterally dished as in most other rhomaleosaurids, although it is possible that this is a preservational artefact. The posterior interpterygoid vacuities are short broad ovals, 37 mm long anteroposteriorly and 16 mm wide mediolaterally (Text-fig. 5). The long axes of the vacuities converge anteriorly and the combined width of the vacuitiues is greatest posteriorly (43 mm) (length of vacuity:combined width of posterior interpterygoid vacuities ratio = 0.9). A robust medial pterygoid process, visible through the anterior end of the interpterygoid vacuity, extends medially to form the basal articulation between the basioccipital and pterygoid. A damaged and disarticulated fragment of sheet-like bone bears a distinct ectopterygoid/pterygoid boss and can therefore be identified as the posterolateral surface of the right side of the palate, including part of the lateral ramus of the right

pterygoid (Text-fig. 4I, J) This fragment is absent from Text-fig. 3 because its exact relationship to the rest of the skull is unclear. The posteroventrally inclined pterygoid boss is a mediolaterally broad and anteroposteriorly narrow oval with a rugose surface. It is similar to *Atychodracon megacephalus* (CRUICKSHANK 1994a) but more weakly developed than *Rhomaleosaurus* (SMITH & DYKE 2008).

4.1.14 Parabasisphenoid

The parasphenoid is situated between the posterior interpterygoid vacuities and extends anteriorly between a 'V'-shaped notch in the pterygoids to form a short (12.5 mm) triangular, asymmetrical cultriform process on the surface of the palate (Text-figs 3C, D; 5). A similar cultriform process is present in most rhomaleosaurids, and is also asymmetrical in some specimens of *Atychodracon megacephalus* (SMITH 2007). In contrast, a cultriform process is absent in *Meyerasaurus* (SMITH & VINCENT 2010), and it extends far anteriorly in *Peloneustes* (KETCHUM & BEN-

SON 2011b). The parasphenoid is flat anteriorly but bears a ventral keel posteriorly (Text-fig. 5). The parasphenoid lies superficial to the basisphenoid and tapers posteriorly to a point. The parasphenoid-basisphenoid contact is unclear but it probably extends posteromedially from the anterior margin of the posterior interpterygoid vacuity, to the posterior extent of the ventral keel. The basisphenoid bears several foramina on its ventrolateral surface. The largest is on the right side adjacent to the ventral keel (Text-fig. 5). A similar large foramen is present on the basisphenoid in Thalassiodracon (BENSON et al. 2011a), Hauffiosaurus tomistomimus (BENSON et al. 2011b), OUM J.28585 (CRUICKSHANK 1994b, O'KEEFE 2006), and the basal pistosaurian Yunguisaurus (CHENG et al. 2006), but in these taxa it is located in the left side, not the right. A pair of foramina is present on the basisphenoid in Dolichorhynchops (O'KEEFE 2004a). In all of these taxa this opening is regarded as the internal carotid foramen, an interpretation we follow here for Thaumatodracon. A row of three smaller foramina is also present on the left side of the basisphenoid in Thaumatodracon, but these are situated more posteriorly and laterally.

4.1.15 Basioccipital

A sharp rim separates the hemispherical occipital condyle from the main body of the basioccipital (Text-fig. 3C, D). The maximum width of the occipital condyle (at its base) is 40 mm and it is 18 mm long anteroposteriorly (as measured from the rim to the posterior margin). A notocordal pit is present on the occipital condyle, situated slightly ventrally, and an additional pair of shallow notches, or foramina, is situated on the ventrolateral surface of the condyle. This pair of ventrally positioned notches is absent in most plesiosaurians, but is also present in Meyerasaurus (SMITH & VINCENT 2010), and may therefore be of systematic value. The ventral aspect of the basioccipital is obscured by the pterygoids, but paired anteriorly tapering triangular processes appear to extend anteriorly along the ventral surface of the basisphenoid between the interpterygoid vacuities (Text-fig. 5). This region is compressed and cracked, so this could be a taphonomic artefact. If natural, these triangular processes have not been described in any other plesiosaurian, and we therefore tentatively consider them as an autapomorphy of Thaumatodracon.

4.1.16 Exoccipital-opisthotic

Both exoccipital-opisthotics are partially preserved but displaced in rough life position adjacent to the basicranium (Text-figs 3, 4E-H). The suture between the exoccipital and opisthotic is not visible and presumably closed. Both paraoccipital processes are broken so only their bases are preserved, but they were apparently circular in cross section at their base and oriented posteroventrally (Text-fig. 4E-H). The medial surfaces are obscured by matrix but the lateral and posterior surfaces are clear in the left element. There is a matrix-filled depression on the posterolateral surface immediately below the base of the paraoccipital process, which houses the foramen (or foramina) for the exiting cranial nerves or vessels, namely the jugular foramen and the hypoglossal nerve foramen (SACHS et al. 2016).

4.2 Mandible

The mandible is essentially complete although the middle portion of each ramus (the posterior-most parts of the dentary) is broken into fragments and difficult to interpret. The mandible is preserved in close association with the cranium, but the jaws are not occluded, allowing an excellent view of the ventral surface of the premaxilla and dorsal surface of the symphyseal region of the dentary (Text-figs 6-8). The mandibular rami appear bowed (sensu DRUCKEN-MILLER & RUSSELL 2008a) and there is a prominent longitudinal trough that occupies much of the lateral surface anterior to the glenoid (dentary, angular, surangular): bounded ventrally by a robust longitudinal, ventrolateral ridge, as in other rhomaleosaurids (BENSON et al. 2012), leptocleidians (BENSON et al. 2013a), and Hauffiosaurus (BENSON et al. 2011b) (Textfigs 7, 8).

4.2.1 Dentary

The region of the mandibular symphysis is mediolaterally expanded (Text-fig. 6). In ventral view there is no midline keel and this differs from *Atychodracon* and *Rhomaleosaurus* which have a sharp low keel (CRUICKSHANK 1994a, TAYLOR 1992, SMITH 2015). The dorsal surface of the spatulate mandibular symphysis bears the primary and replacement alveoli (Text-fig. 6A, B). There are five teeth adjacent to the mandibular symphysis. TARLO (1960) considered the number of symphyseal teeth an important character in plesiosaurian taxonomy. Among rhomaleosaurids and



Text-fig. 6. *Thaumatodracon wiedenrothi* (NLMH 106.058), region of the mandibular symphysis. A. Photograph in dorsal view. B. Interpretation. C. Photograph in ventral view. D. Interpretation. E. Photograph in right lateral view. F. Interpretation. Abbreviations: bos: raised bosses; ch: diagonal channels; den: dentary; d1: first dentary alveolus; d5: fifth dentary alveolus; d10: tenth dentary alveolus; d15: fifteenth dentary alveolus; sp: splenial; sp?: possible fragment of splenial. Diagonal lines represent broken surfaces, stippling represents matrix. Scale bar represents 50 mm.

basal pliosauroids, *Anningasaura* has approximately four (VINCENT & BENSON 2012), and *Macroplata* has seven – eight (KETCHUM & SMITH 2010), while all other rhomaleosaurid taxa have five (TAYLOR 1992, CRUICKSHANK 1996, SMITH 2007). A gently rounded diamond-shaped platform occupies the posterior half of the mandibular symphysis on the midline (Text-fig. 6A, B). A narrow platform in this region was considered to be an autapomorphy for *Peloneustes* (KETCHUM & BENSON 2011b), so this character may also have systematic implications. The interdigitating interdentary suture is visible on the surface of this



Text-fig. 7. *Thaumatodracon wiedenrothi* (NLMH 106.058), posterior part of left mandible. A. Photograph of dorsomedial surface. B. Interpretation. C. Photograph of lateral surface. D. Interpretation. E. Photograph in ventromedial view. F. Interpretation. G. Photograph of posterior surface. H. Interpretation. Abbreviations: ang: angular; art: articular; cl: cleft between surangular and articular; gl: mandibular glenoid; mf: medial flange; pra?: possible posterior process of prearticular; ret: retroarticular process; sa: surangular; ?: unknown element. Scale bar in A–F represents 50 mm, in G–H represents 20 mm.



Text-fig. 8. *Thaumatodracon wiedenrothi* (NLMH 106.058), posterior part of right mandible. A. Photograph of medial surface. B. Interpretation. C. Photograph of ventral surface. D. Interpretation. E. Photograph of lateral surface. F. Interpretation. G. Photograph of dorsal surface. H. Interpretation. Abbreviations: ang: angular; art: articular; cor: facet for coronoid; den?: possible fragment dentary; dmc: dorsomedian crest; fo: foramina; gl: mandibular glenoid; pra: prearticular; q: quadrate; ret: retroarticular process; sa: surangular; saf: surangular foramen; sp?: possible facet for splenial; sq: squamosal; vlc: ventrolateral crest. Diagonal lines represent broken surfaces, stippling represents matrix, grey areas represent cranial elements associated with the mandible. N.B. The squamosal has been artificially removed in A, B, E & F. Scale bar represents 50 mm.

platform posteriorly, but appears to be fused anteriorly. Immediately posterior to this rounded platform is a distinct but shallow transverse channel oriented anterolaterally on each ramus. A small raised boss is situated on the posterior surface of this channel on both sides, and an additional raised boss is present on the right side only, on the posterolateral margin of the diamond-shape raised platform just anterior to the channel (Text-fig. 6A, B). The dorsal surface of the mandibular symphysis is poorly known in rhomaleosaurids, known only in *Rhomaleosaurus thorntoni* (SMITH & BENSON 2014) and *Eurycleidus* (NHMUK OR2030*, pers obs.). Channels are present in this region in both taxa, and similar channels are widespread among plesiosaurians (SMITH & BENSON 2014).

4.2.2 Splenial

The splenial is a mediolaterally narrow splint of bone that forms the ventromedial surface of the mandible behind the mandibular symphysis (Text-fig. 6). The splenials contact anteriorly on the midline and extend for a short distance along the mandibular symphysis. The splenials are damaged posteriorly and the right element is displaced, so their posterior extent is unclear.

4.2.3 Surangular

Posteriorly the mandible becomes mediolaterally compressed and the lateral surface of the mandible is deeply concave, as in other rhomaleosaurids (SMITH & BENSON 2014). The surangular forms most of the dorsal part of the mandibular ramus posterior to the coronoid process and anterior to the mandibular glenoid (Text-figs 7, 8). On the lateral surface of the mandible, the dorsoventrally deep posterolateral wall of the mandible is formed by the surangular dorsally and the angular ventrally, and it is deeply concave. The angular-surangular contact on the lateral surface is straight and horizontal anteriorly, but becomes sigmoid posteriorly, with a dorsally convex arch anteroventral to the glenoid fossa and a dorsally concave arch immediately below it (Text-figs 7C, D; 8E, F). This morphology is also present in Meyerasaurus (SMITH & VINCENT 2010), Rhomaleosaurus (SMITH & BENSON 2014), and to a lesser degree in OUM J.28585 (CRUICKSHANK 1994b), but contrasts with the condition in pliosaurids where the contact is almost straight for its entire length (BENSON et al. 2013b). Posteriorly this contact wraps around the glenoid fossa and becomes almost vertically oriented. Several distinct foramina are present on the lateral surface of the surangular posteriorly, as in Meyerasaurus (SMITH & VINCENT 2010) and Rhomaleosaurus (TAYLOR 1992). Such foramina are absent in pliosaurids (Benson et al. 2013b, Ketchum & Benson 2011b). Stratesaurus also bears a lateral surangular foramen but it is positioned more anteriorly (BENSON et al. 2015). The surangular contributes to the dorsal half of the medial surface of the mandible between the coronoid process and the mandibular glenoid, and contacts the coronoid anteriorly, angular anteroventrally, and articular posteroventrally. A distinct rugose boss is present on the medial surface of the surangular which corresponds to the dorsomedial crest of Rhomaleosaurus (TAYLOR 1992, SMITH & BENSON 2014) (Text-fig. 8A, B). A widely spaced row of three

foramina, which decrease in size posteriorly, is present on the ventral margin of the medial surface of the surangular. The largest of these foramina is situated directly below the coronoid process, as in *Stratesaurus* (which has three foramina figured in this position, BENSON et al. 2015, fig. 9) and OUM J.28585 (CRUICKSHANK 1994b). Two relatively small foramina are figured in this position in Pliosaurus kevani (BENSON et al. 2013b), and one is present posteriorly in *Peloneustes* (KETCHUM & BENSON 2011b). A longitudinal cleft is present on the dorsomedial surface of the mandible anterior to the articular glenoid, between the surangular and articular, as in Rhomaleosaurus (TAYLOR 1992, VINCENT & SMITH 2009, SMITH & BENSON 2014), NMING F8749 (SMITH 2007), and Leptocleidus capensis (CRUICKSHANK 1997) (Text-fig. 7A, B).

4.2.4 Angular

The angular is a large element that forms the ventral surface of the posterior half of the mandible. It extends anteriorly as a tapering narrow splint between the dentary (laterally) and splenial (medially), and it extends posteriorly below the glenoid fossa to form almost all of the ventral surface of the short retroarticular process (Text-figs 7C-H, 8A-F). The angular appears to be exposed on the medial surface both ventral to and dorsal to the prearticular, as in many plesiosaurians including Peloneustes (KETCHUM & BENSON 2011b), Hauffiosaurus (BENSON et al. 2011b) and Stratesaurus (BENSON et al. 2015) (Text-fig. 8A, B). The dorsomedial surface of the angular bears a longitudinal depression to accommodate the posterior process (Text-figs 7C-H, 8A-F)". of the splenial or anterior process of the prearticular.

4.2.5 Articular

The articular forms the mandibular glenoid, all of the dorsal surface of the retroarticular process, and extends anterior to the glenoid on the dorsal surface (Text-figs 7, 8). A small part of the articular is also visible in ventral view extending beyond the posterior extent of the angular (Text-fig. 8C, D). The articular bears a prominent dorsally concave medial flange anteromedial to the articular glenoid (Text-fig. 7A, B). This is similar to the condition in *Peloneustes* (KETCH-UM & BENSON 2011b) but unlike the 'squared-off' morphology in other rhomaleosaurids (SMITH & BENSON 2014), and so we consider this a local auta-



Text-fig. 9. *Thaumatodracon wiedenrothi* (NLMH 106.058), selected disarticulated teeth. A–H: Tooth 1. Photographs in A. Axial. B. Labial. C. Axial. D. Lingual. E–H: Interpretations. I–P: Tooth 2. Photographs in I. Axial. J. Labial. K. Axial. L. Lingual. M–P. Interpretations. Q–X: Tooth 3. Photographs in Q. Axial. R. Labial. S. Axial. T. Lingual. U–X. Interpretations. Y–FF: Tooth 4. Photographs in Y. Axial. Z. Labial. AA. Axial. BB. Lingual. CC–FF. Interpretations. GG–NN: Tooth 5. Photographs in GG. Axial. HH. Labial. II. Axial. JJ. Lingual. KK–NN. Stippling represents matrix or areas of missing enamel from the tooth crown, grey areas represent unenamelled bases ('roots'). Scale bar represents 10 mm.

pomorphy. A shallow longitudinal trough occupies much of the lateral surface anterior to the glenoid (including the dentary, angular, surangular), and this is bounded ventrally by a robust longitudinal, ventrolateral ridge, as in other rhomaleosaurids (SMITH & BENSON 2014). The anteriorly concave posterior rim of articular glenoid is continuous and bears no cleft. The retroarticular process is nearly horizontal and there is a tenuous anteroposterior inclination of the retroarticular process, but this contrasts clearly with the posteriorly sloping condition of *Yunguisaurus*. The transverse long axis of the retroarticular is inclined to face dorsomedially and it terminates posteriorly in a flattened slightly posterodorsally facing surface. The medial part of the glenoid is anteroposteriorly longest, as is also the case in *Rhomaleosaurus zetlandicus* (VIN-CENT & SMITH 2009).



Text-fig. 10. *Thaumatodracon wiedenrothi* (NLMH 106.058), atlas-axis complex and third cervical vertebra (first postaxial vertebra). A. photograph in left lateral view. B. interpretation; C: photograph in ventral view. D. interpretation. Abbreviations: atc?: atlas centrum (or dorsal projection of the axis intercentrum); ati: atlas intercentrum; axc: axis centrum; axi: axis intercentrum; axna: axis neural arch; axns: axis neural spine; axpz: axis postzygapophysis; axr: axis rib; c3: third cervical vertebra (first postaxial vertebra); cr3: left cervical rib of third cervical vertebra; crf3: cervical rib facet of third cervical rib; fo: foramina; na3: neural arch of third cervical vertebra; qpf: quadrate-pterygoid flange; sq: squamosal; ?: unknown element. Stippling represents matrix. Scale bar represents 20 mm.

4.2.6 Prearticular

The prearticular is visible as a dorsoventrally narrow and anteroposteriorly elongate element situated on the medial surface of the mandible anteroventral to the articular glenoid (Text-fig. 8A, B). It is a mediolaterally compressed splint-like element that sits superficial to the angular. In medial view it contacts the angular both ventrally and anterodorsally along straight horizontal contacts, and posterodorsally it contacts the anterior process of the articular. The anterior extent of the prearticular is unclear because on the left ramus it is broken away and on the right ramus the anterior sutures are obscured by a rugosity. The posterior extent is also ambiguous because this region is covered by the quadrate on the right side, and obscured by an unknown fragment of bone, possibly the displaced anterior process of the prearticular, on the left side. The preservation is not good enough to be certain but a tentatively identified posterior termination of the prearticular is visible immediately ventral to the glenoid, posterior to the unidentified fragment (Text-fig. 7E, F). In this case the prearticular terminates posteriorly in the same position as Rhomaleosaurus (Smith & Benson 2014) and OUM J.28585 (CRUICKSHANK 1994b). In rhomaleosaurids a lingual mandibular fenestra (= Meckelian foramen) is usually present on the medial surface of the mandible at the junction of the prearticular, splenial and angular (SMITH & VINCENT 2010), but this region is not preserved in NLMH 106.058.

4.3 Dentition

The preserved alveoli indicate five tooth positions in each premaxilla, a minimum of 13 teeth in each maxilla, and 28 teeth in each dentary. The variation in size of the alveoli along the jaw indicates that the dentition was heterodont, with large caniniform teeth situated adjacent to the mandibular symphysis in the mandible, in most of the premaxilla, and anteriorly in the maxilla, with smaller teeth posterior in the jaws. The posterior extent of the tooth row is unknown but probably extended beyond the anterior margin of the temporal fenestra as in other rhomaleosaurids (SMITH & BENSON 2014). Several disarticulated complete and fragmentary teeth are preserved (Text-fig. 9). They are robust and circular in cross section with recurved crowns that terminate in a pointed but blunt apex. The enamel crowns bear closely spaced apicobasally oriented striations on the concave (lingual) and axial (lateral) surfaces whereas the convex (labial) surfaces are smooth. Most of the striations extend from the base of the crown and extend two thirds the length of the crown, but only three extend all the way to the apex. The striations are slightly more densely distributed compared to Rhomaleosaurus (TAYLOR 1992, SMITH & BENSON 2014) and more similar to Atychodracon (CRUICKSHANK 1994a). Some teeth have some possible natural apical wear facets (Text-fig. 9I-X). The unenamelled bases ('roots') of the teeth are subequal in length to the enamelled crowns.



Text-fig. 11. Plots of vertebral proportions. **A.** Vertebral dimensions through the preserved cervical vertebral column with corresponding error bars (see Table 1, Appendix 3). Note that the height and width is always significantly greater than the length, and the width is usually slightly greater than the height. Note also that the height and width (m = 1,3972) increases posteriorly more rapidly than the length (m = 0,8802). **B.** The vertebral length index through the vertebral column. Note that the vertebral length index maintains relatively constant through the preserved column at around 50–60.

4.4 Axial skeleton

4.4.1 Atlas-axis

The atlas-axis complex is partially exposed in left lateral and ventral views, and includes the entire axis neural arch and spine (Text-fig. 10). The anterior elements of the atlas-axis are obscured by matrix and the squamosal, so it is not possible to determine if the atlas centrum contributed to the lateral rim of atlantal cotyle. The atlas neural arch is obscured by an indeterminate fragment of bone so its anatomy is also unknown. The visible elements show clear contacts indicating that they have not fused. The ventral surface of the atlas intercentrum is poorly visible but the axis intercentrum is well exposed ventrally and has no ornamentation. The atlas centrum (or possibly this is a dorsal projection of the axis intercentrum) contacts the axis centrum on the lateral surface along an anteriorly concave suture (Text-fig. 10 A, B). The neurocentral suture between the axis centrum and axis neural arch is 'U' shaped and extends halfway down the lateral surface of the axis centrum body. The axis centrum bears a pair of small nutritive foramina on its ventral surface (Text-fig. 10C, D), however, these foramina are not set in squared depressions or separated by a midline keel as they are in the postaxial cervical vertebrae. There is also no hypophyseal ridge or bulge on the axis centrum. Both axial ribs are preserved in rough life position on the ventrolateral surface of the axis centrum, close to the atlas intercentrum. The axis neural arch lacks prezygapophyses but has large postzygapophyses with almost horizontally oriented facets preserved in articulation with the prezygapophyses of the third cervical vertebra. The axis neural spine is anteroposteriorly long (76.1 mm) with an anterior process with a narrow circular transverse cross section that extends over the body of the atlas, and a mediolaterally and dorsoventrally broader posterior process, also circular in transverse section. The dorsal surface of the neural spine is gently inclined posterodorsally. The altas-axis is poorly known in rhomaleosaurids but the general morphology in Thaumatodracon compares well with *Macroplata* (KETCHUM & SMITH 2010) and Meyerasaurus (SMITH & VINCENT 2010), and the leptocleidid Nichollssaura (DRUCKENMILLER & RUSSELL 2008b). The axis intercentrum differs from WARMS G10875 which bears a midline ventral keel (pers. obs.).

4.4.2 Cervical vertebrae

There are 27 cervical vertebrae preserved including the atlas axis (Text-figs 2, 10; Pls 1, 2). In vertebra 27 the rib facet is almost in contact with the neural arch (Pl. 2, fig. 8), so this is regarded as the last cervical vertebra and the cervical series is therefore complete. 27 cervical vertebrae is typical for rhomaleosaurids, which have between 26 and 30. For example, 26 cervical vertebrae are present in *Macroplata* (KETCHUM & SMITH 2010), 28 are present in *Rhomaleosaurus* (SMITH & DYKE 2008, VINCENT & SMITH 2009), 28–29 are present in *Atychodracon megacephalus* (SMITH 2007), and approximately 30 are present in *Meyerasaurus* (SMITH & VINCENT 2010).

Vertebral measurements and proportions are given in Table 1, Appendix 3 and Text-fig. 11.

In all cervical vertebrae the centrum is higher dorsoventrally than long anteroposteriorly, and the mediolateral width is subequal to the dorsoventral height. In the posterior cervical vertebrae the centra become relatively wider mediolaterally.

The articular surfaces of the cervical vertebrae are strongly concave with rounded margins in longitudinal cross-section, as in Rhomaleosaurus thorntoni (SMITH & BENSON 2014). A notochord pit is present on the articular surface of the centrum situated slightly ventral to the centre of the face (Pl. 1, figs 9, 13). The anterior cervical centra have a small, semi-oval 'lip' that extends ventrally from the anterior articular surface, as also described in Anningasaura (VINCENT & BENSON 2012). The lateral surface of the centrum in anterior vertebrae is rugose and the neurocentral suture is 'U' shaped in lateral view and not connected to the cervical rib facet (Pl. 1, figs 2, 7, 8, 10, 14, 18). This contrasts with the condition in *R. thorntoni*, which has a smooth, well-defined vertical groove between the neural arch and cervical rib facet (SMITH & BEN-SON 2014). The neurocentral suture is more 'V' shaped in some posterior cervical vertebrae (Pl. 2, fig. 4), and the lateral surfaces are smoother. The neural arches are centra are fused along the entire cervical vertebral column (although the neurocentral sutures remain visible), which indicates that NLMH 106.058 is a mature individual (sensu BROWN 1981).

The cervical rib facets are obscured by the cervical ribs in many vertebrae, but where visible, they are dorsoventrally tall and occupy the lower one-third of the centrum (Pl. 1, figs 8, 10, 18; Pl. 2, figs 1, 4). Each rib facet consists of a subrectangular lower facet (parapophysis) and an equally sized triangular upper facet (diapophysis). These are divided by a narrow anteroposteriorly oriented ridge. This longitudinal ridge represents the medial wall of a channel between the rib heads (see Cervical ribs). The surface of both the upper and lower rib facets is concave, with slightly raised rims (Pl. 1: fig. 9). The rib facets in the more posterior cervical vertebrae also consist of two conjoined facets but the lower facet becomes relatively larger than the upper facet (Pl. 2, fig. 8). The ventral surface of the centrum bears paired nutritive foramina surrounded by smooth, depressed rectangular regions, either side of a low, rounded, anteroposteriorly oriented, midline ridge (Text-fig. 10C, D; Pl. 1: 12, 17, 21; Pl. 2: figs 3, 7, 11). The foramina are positioned slightly posterior to centrum midlength. The depressed rectangular regions and the nutritive foramina are relatively larger in more anterior vertebrae and less pronounced in posterior cervical vertebrae (Pl. 2, fig. 11).

The neural arch is dorsoventrally high (subequal to the centrum) and the anterior and posterior openings of the neural canal are subcircular (Pl. 1: figs 1, 3, 13, 19; Pl. 2: fig. 5). The neural arch has broken off in vertebra 10 exposing the base of the neural canal, which is slightly constricted around midlength, resulting in an hourglass shape (Pl. 1: fig. 11). A shallow ridge on the lateral surface of the neural arch in vertebrae 3-13 extends posteroventrally for a short distance from the prezygapophysis, delimiting a fossa on the neural arch peduncle between the pre- and postzygapophyses, and forming a buttress-like support for the prezygapophysis. The mediolateral width of the combined prezygapophyses is slightly greater than that of the centrum (Pl. 1: figs 4, 6, 16, 20), as in *Rhomaleo*saurus, some non-plesiosaurian pistosaurians and other rhomaleosaurids such as Archaeonectrus (NHMUK PV OR 38525) and Eurycleidus (SMITH & DYKE 2008, BENSON et al. 2012). As in other non-cryptoclidian plesiosaurians, the prezygapophyses of R. thorntoni are separated across the midline and thus do not contact each other. They are anteroposteriorly longer than half the anteroposterior length of the centrum (Pl. 1: figs 4, 6), and have large, flat facets that face dorsomedially, whereas those of the postzygapophyses face ventrolaterally. The planar articular facets of the zygapophyses are inclined at approximately 40 degrees throughout the cervical series (Pl. 1: figs. 1, 3, 13, 19;



Text-fig. 12. Plot of morphometric multivariate analysis of rhomaleosaurids and closely related taxa, including *Thaumatodracon*. This is a principal component analysis (PCA) (Spearman type) with the groupings (highlighted in grey) derived from the agglomerative hierarchical clusterings analysis (AHC). The key differentiates the data points into three categories, Hettangian, Sinemurian, and To-arcian. Note the *Atychodracon/Eurycleidus/Macroplata* cluster close to the mean variance of the dataset, mostly composed of Hettangian taxa (see discussion). Note also the intermediate position along the x-axis of *Thaumatodracon*, located between the *Atychodracon/Eurycleidus/Macroplata* cluster close.

Pl. 2: fig. 5). The lateral surface of the prezygapophysis is ornamented by fine ridges oriented anterodorsally, perpendicular to the facet edge, as in *R. thorntoni* (SMITH & BENSON 2014). A prominent, anteroposteriorly oriented ridge on the dorsolateral surface of the neural arch connects the pre- and postzygapophyses. The postzygapophyses extend far posteriorly beyond the articular surface of the centrum.

The base of the neural spine is situated posteriorly relative to the centrum, so its anteriormost extent is at approximately centrum midlength, and the posterior half of the spine is situated over the intervertebral space and anterior portion of the succeeding vertebra (Pl. 1: figs. 2, 14, 18; Pl. 2: figs. 1, 4, 8, 9). In the anterior vertebrae the neural spines are dorsoventrally short, strongly recurved and inclined posterodorsally (Pl. 1, fig. 2). The neural spines gradually become relatively larger and more vertically inclined in more posterior cervical vertebrae (Pl. 1: fig. 18; Pl. 2: figs 4, 8, 9). The anterior and posterior margins of the neural spines converge in the anterior vertebrae, whereas they are parallel in more posterior vertebrae, and in vertebra 22 they diverge so the distal end of the spine is expanded. In the anterior cervical vertebrae the apex of the neural spine has a subtriangular transverse cross section with a flat anterodorsal surface and pointed ventral surface (Pl. 1: figs 2, 4). The termination of the neural spine is flat and inclined posterodorsally in the anterior vertebrae, whereas it is anteroposteriorly convex and faces dorsally in the posterior cervical vertebrae (Pl. 2: figs 1, 4, 8, 9). The neural spines are mediolaterally compressed at their bases and for most of their dorsoventral length (Pl. 1: figs 16, 20; Pl. 2: fig. 10), but the apex is mediolaterally expanded in the anterior vertebrae (Pl. 1: figs 1, 3) and to a lesser degree in the posterior vertebrae (Pl. 2: fig. 5), as in Eurycleidus arcuatus (NHMUK OR1318) (pers. obs.).

4.4.3 Cervical ribs

Several cervical ribs are preserved in situ in the anterior cervical vertebrae, but only weakly fused to the cervical centrum. Their proximal ends are dorsoventrally deep for articulation with the tall rib facets, and their distal ends are dorsoventrally compressed, with prominent anterior and posterior projections (Textfig. 10). A wide vascular channel runs anteroposteriorly through the base of the rib and opens as a distinct foramen on the anterior and posterior surfaces, as seen most clearly in the left rib of cervical vertebra 12 (Pl. 1, fig. 15). This channel separates the proximal end of the rib into two equally sized heads, one dorsal and one ventral. However, the dorsal and ventral heads approach each other proximally and almost contact each other where they join the cervical rib facet, so the ribs are functionally single-headed. This cervical rib morphology is very similar to *R. cramptoni* (SMITH 2007), but differs from derived plesiosaurians, which have anatomically single-headed ribs and lack an anteroposteriorly oriented channel (PERSSON 1963).

4.5 Other material

A large unprepared block of matrix (350 x 350 x 200 mm) from the pectoral region may contain additional vertebrae and pectoral girdle elements. In addition, hundreds of small (< 30 mm) indeterminate fragments are also associated with this skeleton, and probably represent parts of the cranium, mandible, and postcranium. A thorough investigation of this material may result in their identification and them being reunited, but such an undertaking was beyond the scope of the current study.

5. Results

5.1 AHC results

The AHC analysis found five significantly different clusters, i.e., beyond the dissimilarity threshold level of 0.02. The following significant clusters were retrieved: 1) Meyerasaurus victor, HALB uncatalogued and Anningasaura lymense; 2) Thaumatodracon, R. cramptoni, R. thorntoni, R. zetlandicus; 3) A. megacephalus, Attenborosaurus, E. arcuatus, Macroplata, NMING F8749, NMING F10194, WARMS G10875, and '*R. propinguus*' (the latter is problematic, see Discussion; $\overline{4}$) Archaeonectrus; 5) Thalassiodracon and 'P'. macrocephalus. These clusters are also present in the PCA analysis results (Text-fig. 12). The AHC analysis shows a variance decomposition of the optimal classification of 24.34% within class and 75.66% between classes. When all data was included (AHC Analysis 1) the first two factors accounted for 81.46% of the data variance. When all the variables with less than ten data entries were pruned from the dataset (AHC Analysis 2) the two first factors accounted for 83.98% of the variance. When all of the skull variables with less than ten entries were pruned from the dataset (AHC Analysis 3) the two first factors accounted for 84.98% of the variance. Appendix 1 provides ad-

A Benson & Druckenmiller 2013



B Benson et al. 2012



C Smith & Dyke 2008



Text-fig. 13. Pruned cladograms to show the interrelationships of Rhomaleosauridae and the position of *Thaumatodracon* (for the complete cladograms see Appendix 2). The same methodology was applied to all the data matrices. Note that the interrelationships in the cladograms derived from A: BENSON & DRUCKENMILLER (2013) and B: BENSON et al. (2012) lack resolution, while C: SMITH & DYKE (2008), results from a matrix focused specifically on Rhomaleosauridae has resulted in a well-resolved cladogram. Note the intermediate position of *Thaumatodracon* in C and the consistent presence of this taxon among rhomaleosaurids in all three analyses. Numbers above nodes represent Bremer support / relative Bremer support, and those below nodes represent symmetric resampling / GC values.

ditional results of the AHC analysis including node statistics, class centroids, distances between class centroids, central objects, distances between the central objects, and results by class.

5.2 PCA Results

The results in all three different PCA analysis we ran are similar independent of the number of variables used. In Analysis 1 (Text-fig. 12) the variables that contribute the most to the variance of Factor 1 (> 1%contribution, with a squared cosine greater than 0.9), i.e. variables with high quality of representation were: maximum width of the glenoid, width of the preglenoid process, posterior coracoid cornua, length to midglenoid, length to fenestra, scapular maximum width, radius facet, ulna facet, ulna distance of minimum width, ischium distal flare width, fibula width, tibia length, fibula postaxial distance, fibula flare, ulna preaxial distance, ulna flare, total length (see Appendix 1). Factor 1 therefore consists entirely of postcranial characters. The most significant variables that contribute to Factor 2 are: length of the dorsomedian foramen, overlap between nares and dorsomedian foramen, radius facet, ulna facet, tibia facet length (dorsal view), fibula facet length (dorsal view). Factor 2 therefore consists of a mixture of cranial and postcranial characters.

In Analysis 2 the variables that contributed the most (> 2.5%) to Factor 1 are: skull length to the squamosal bulb, mandible length and total length. In Analysis 3 the variables that contributed the most (> 3.7%) to the construction of Factor 1 are: skull length to the squamosal bulb, length of premaxilla, premaxilla tip to pineal foramen, mandible length, symphysis width, diagonal length to symphysis. For Factor 2 is width across the glenoid. This shows that postcranial characters contribute a significant amount of variance in the dataset and may therefore also contain a phylogenetic signal. The OTUs that are closest to the mean of the sample in both Factors 1 and 2 are all Hettangian taxa: *E. arcuatus*, specimens of *Atychodracon* and *Macroplata*.

Appendix 1 provides additional results of the PCA analyses such as summary statistics, correlation matrix with a significance level of 5%, Bartlett's sphericity test, eigenvalues, eigenvectors, factor loadings, correlations between variables and factors, contribution of the variables, squared cosines of the variables with a significance level of 5%, factor scores, contribution of the observations: OTUs (%), and squared cosines.

5.3 Phylogenetic analysis results

Strict consensus trees resulting from three cladistic analyses are presented in Text-fig. 13. All three analyses resolved Thaumatodracon as a rhomaleosaurid. In the cladograms resulting from the reanalyses of BEN-SON et al. (2012) and BENSON & DRUCKENMILLER (2013) the ingroup relationships of the Rhomaleosauridae are poorly resolved (Text-fig. 13A, B). In the reanalysis of Benson & Druckenmiller (2013) Thaumatodracon wiedenrothi forms a sister relationship with R. thorntoni within the clade Rhomleosaurus, while in the reanalysis of BENSON et al. (2012) it forms an unresolved polytomy alongside all rhomaleosaurids. In the reanalysis of SMITH & DYKE (2008) the ingroup relationships of Rhomaleosauridae are almost completely resolved and Thaumatodracon occupies a derived position within Rhomaleosauridae in an unresolved polytomy with Maresaurus and Rhomaleosaurus (Text-fig. 13C). This greater resolution in the cladogram resulting from the reanalysis of SMITH & DYKE (2008) demonstrates the importance of coding characters specifically to resolve more restricted clades. Thaumatodracon presents a combination of characters present in both older Rhetian/Hettangian rhomaleosaurids (Atychodracon, Eurycleidus (sensu stricto) and younger Toarcian rhomaleosaurids (Rhomaleosaurus sensu stricto, Meyerasaurus). For example, Thaumatodracon shares with Atychodracon a contact between the frontals on the midline, and a flat parasphenoid anteriorly, while it shares with Rhomaleosaurus and Meyerasaurus a short premaxillary rostrum and mandibular symphysis, and parallel premaxilla-maxilla sutures.

6. Discussion

6.1 Diversity of plesiosaurians from Lyme Regis

At least seven distinct plesiosaurian species, including *Thaumatodracon wiedenrothi*, are currently known from the Lower Jurassic deposits between Lyme Regis and Seatown (MILNER & WALSH 2010). This includes two plesiosauroid taxa of the long-necked plesiosauromorph type. *Plesiosaurus dolichodeirus* is well known from several skeletons from the Sinemurian (STORRS 1997), while fragmentary material of a second long-necked plesiosaurian taxon from younger Pliensbachian strata has been referred to cf. *Microcleidus homalospondylus* (MILNER & WALSH 2010).

Attenborosaurus conybeari (BRSMG Cb2479, holotype lost but known from casts e.g. NHMUK R1339, BAKKER 1993) is a basal plesiosaurian of unknown affinity with a relatively long neck and a relatively large head (BAKKER 1993). Different authors have regarded it as a basal plesiosaurian situated outside of Rhomaleosauridae, Pliosauridae and Plesiosauroidea (e.g. KETCHUM & BENSON 2011a, SMITH & DYKE 2008), or as a basal pliosaurid (O'KEEFE 2001, 2004b).

The other plesiosaurians from Lyme Bay generally have shorter necks and larger heads, and some of them may be rhomaleosaurids. Anningasaura lymense (NHMUK OR49202, previously referred to 'Plesiosaurus' macrocephalus, ANDREWS 1896) is a basal plesiosaurian from Lyme Regis consisting of a skull and partial cervical series (VINCENT & BENSON 2012). It has been resolved as a basal rhomaleosaurid in some cladistic analyses (KETCHUM & BENSON 2011a, Benson & Druckenmiller 2014, Benson et al. 2013a) but has also been regarded as a basal pliosauroid (SMITH & DYKE 2008) and as a basal plesiosaurian (BENSON et al. 2012). The long-snouted form Archaeonectrus rostratus is another valid taxon (contra O'KEEFE 2001, MILNER & WALSH 2010) known from a single complete skeleton from the Sinemurian between Lyme Regis and Charmouth (NOVOZHILOV 1964). It has been resolved as a rhomaleosaurid by several authors (summarised in SMITH & BENSON 2014). The holotype (NHMUK OR38525) needs to be described in detail, however, the cranium is poorly preserved (pers. obs.) and the postcranium is currently inaccessible. The holotype of 'Plesiosaurus' macrocephalus (NHMUK OR1336) is a complete skeleton from Lyme Regis of unknown stratigraphic age that represents a juvenile individual of a large-headed plesiosaurian. It is probably an immature rhomaleosaurid but its early ontogenetic state precludes a confident systematic review of this specimen (SMITH 2007).

A partial skull (NHMUK OR39514) collected from the same location as the holotype of *Archaeonectrus* (between Lyme Regis and Charmouth) was described by VINCENT (2012) and represents a largeskulled plesiosaurian. It is distinct from *Attenborosaurus* and *Archaeonectrus*, but it is currently regarded as Plesiosauria indet. because it lacks diagnostic anatomical information (VINCENT 2012). The large absolute size of the skull and expanded mandibular symphyseal region are similar to *Thaumatodracon*, but the parabasisphenoid is flat and the pterygoids do not contact posterior to the interpterygoid vacuities as they do in *Thaumatodracon*. Therefore, NHMUK OR39514 cannot be referred to *Thaumatodracon wiedenrothi*.

CRUICKSHANK (1994b) referred a partial skeleton of another plesiosaurian from Lyme Regis to the rhomaleosaurid taxon *Eurycleidus*, but this specimen is distinct from *Eurycleidus* (SMITH 2007). This body of evidence shows that several rhomaleosaurids, or close relatives of rhomaleosaurids, were indeed present during this interval.

6.2 Morphometrics provide insights into the evolutionary history of Rhomaleosauridae

In both the PCA and AHC, Thaumatodracon shows a close similarity with Rhomaleosaurus sensu stricto, but in the PCA analysis *Thaumatodracon* is closer to the mean variance of the dataset than is Rhomaleosaurus sensu stricto (Text-fig. 12). This observation correlates with the derived rhomaleosaurid phylogenetic position identified in the cladistic analysis, but also differentiates it statistically from other Sinemurian OTUs. The distance to the class centroid containing Archaeonectrus is 157.28, and to Anningasaura it is 407.187 (see Appendix 1). Specifically, the new taxon plots midway between the Atychodracon/Eurycleidus/Macroplata cluster and the Rhomaleosaurus sensu stricto cluster. Thaumatodracon can therefore be regarded as morphometrically intermediate between these groups. The combination of plesiomorphic and derived anatomical characters in Thaumatodracon, together with its intermediate morphometric and phylogenetic position, is consistent with its intermediate stratigraphic position.

BENSON et al. (2012) identified high diversity and low disparity in Hettangian plesiosaurians and we reproduce similar results for early rhomaleosaurids using a different methodology and dataset. BENSON et al. (2012) used Principal Co-ordinates Analysis based on a character matrix, while we used a Principal Component Analysis based on a morphometric multivariate dataset. Although the disparity results presented by BENSON et al. (2012) are relatively weak (the large error bars potentially allow for non-increasing disparity through the Lower Jurassic) our results show a similar trend for increasing disparity through time, specific to the Rhomaleosauridae. With the exception of *Thalas*siodracon, which is a non-rhomaleosaurid (SMITH & Dyke 2008, Benson et al. 2011a, Benson & Druck-ENMILLER 2013), all Hettangian OTUs in the analysis plot close to the mean of the variance of the dataset (i.e., near the origin of the PCA plot) (Text-fig. 12,

Appendix 1). This cluster of 'average' rhomaleosaurids includes a relatively high diversity of at least four valid Hettangian taxa. These include *Macroplata tenuiceps* (NHMUK OR5488), *Eurycleidus arcuatus* (NHMUK OR2028* etc.), *Atychodracon megacephalus* (BRSMG Cb2335, LEICT G221.1851), as well as three unnamed Hettangian specimens, of which at least one (WARMS G10875) represents a distinct species (Smith 2015). The other unnamed specimens (NMING F10194, NMING F8749) may be referred to *Atychodracon megacephalus* (SMITH 2015).

This cluster situated close to the mean variance also includes two non-Hettangian taxa, but one of these is a non-rhomaleosaurid (Attenborosaurus) and the other is an anomaly ('R. propinquus'). The position of the 'R. propinguus' (a specimen referred to R. zetlandicus by VINCENT & SMITH 2009) within a cluster of mainly Hettangian OTUs in both the PCA and AHC, is unusual because 1: It is from the Toarcian, and 2: It plots far from the Rhomaleosaurus sensu stricto cluster to which it belongs phylogenetically (SMITH & DYKE 2008). This anomaly can be explained by one or more of the following factors: 1: The specimen is a juvenile (VINCENT & SMITH 2009) and so it possesses immature proportions, which are different to the adult proportions. Another juvenile specimen in this analysis, 'P' macrocephalus, also plots significantly negatively in Factor 1 relative to its stratigraphic contemporaries (Archaeonectrus, Attenborosaurus, Thaumatodracon, Anningasaura), so a positive shift along this axis may occur with ontogeny. The holotype of Anningasaura is also regarded as immature (VINCENT & BENSON 2012), which might explain why in Factor 1 Anningasaura also plots relatively negatively. 2: The specimen is highly incomplete. In particular, the tip of the premaxilla is missing (VIN-CENT & SMITH 2009), and therefore the majority of the original skull measurements were estimates. Most elements of the girdles are also missing and these form key components of the PCA. This might have been a source for error. 3: The specimen is possibly a composite and some parts are certainly poorly restored (the coracoid). The measurements may therefore be artificial or might reflect more than one individual. Given these possible sources of error, little significance should be attached to the anomalous position of this specimen in the morphometric analyses.

Thaumatodracon also differs morphometrically from all other Sinemurian taxa from Lyme Regis. For example, Anningasaura is morphometrically distinct in the analysis and this supports its generic separation (VINCENT & BENSON 2012). *Anningasaura* has morphometric similarities to the Toarcian *Meyerasaurus* and HALB uncatalogued, with which it forms a weak cluster (slightly above the threshold level of 0.02) in the AHC analysis. *Archaeonectrus rostratus* is also morphometrically distinct from the rest of the OTUs, plotting significantly distant (0.607 squared cosine with 5% significance level) from the mean of the variance and with a dissimilarity level of 0.06 in the AHC. In contrast, all other rhomaleosaurid OTUs are below 0.04 Spearman dissimilarity index. This supports the generic separation of *Archaeonectrus* from all other Sinemurian rhomaleosaurids.

The PCA analysis indicates a greater range of disparity among Toarcian rhomaleosaurid taxa compared to their Hettangian relatives. *Meyerasaurus victor* (SMITH & VINCENT 2010) is consistently retrieved close to HALB uncatalogued (Brandes 1914) and equidistant from *Rhomaleosaurus* sensu stricto and the Hettangian rhomaleosaurid cluster. This supports its generic separation. HALB uncatalogued is a poorly studied specimen that, in light of this analysis, may be closely related to or congeneric with *Meyerasaurus*.

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References

- ANDREWS, C.W. (1896): On the structure of the plesiosaurian skull. – Quarterly Journal of the Geological Society, London **52**: 246–253.
- ANDREWS, C.W. (1913): A descriptive catalogue of the marine reptiles of the Oxford Clay, based on the Leeds Collection in the British Museum (Natural History), London, Part II.
 British Museum (Natural History), London, xxiv + 206 pp., 13 pls.

- ARAÚJO, R., POLCYN, M.J., SCHULP, A.S., MATEUS, O. & JACOBS, L.L. (2015): A new Elasmosaur from the early Maastrichtian of Angola and the implications of girdle morphology on swimming style in plesiosaurs. – Netherlands Journal of Geosciences – Geologie en Mijnbouw: 1–12, doi: 10.1017/njg.2014.44.
- BAKKER, R.T. (1993): Plesiosaur extinction cycles events that mark the beginning, middle and end of the Cretaceous. – Special Papers of the Geological Association of Canada **39**: 641–664.
- BENSON, R.B.J. & DRUCKENMILLER, P.S. (2013): Faunal turnover of marine tetrapods during the Jurassic-Cretaceous transition. – Biological Reviews 89: 1–23, doi: 10.1111/brv.12038.
- BENSON, R.B.J., BATES, K.T., JOHNSON, M.R. & WITHERS, P.J. (2011A): Cranial anatomy of *Thalassiodracon hawkinsi* (Reptilia, Plesiosauria) from the Early Jurassic of Somerset, United Kingdom. – Journal of Vertebrate Paleontology 31: 562–574.
- BENSON, R.B.J., KETCHUM, H.F., NOÈ, L.F. & GOMEZ-PEREZ, M. (2011b): New information on *Hauffiosaurus* (Reptilia, Plesiosauria) based on a new species from the Alum Shale Member (lower Toarcian: Lower Jurassic) of Yorkshire, UK. – Palaeontology 54: 547–571.
- BENSON, R.B.J., EVANS, M. & DRUCKENMILLER, P.S. (2012): High diversity, low disparity and small body size in plesiosaurs (Reptilia, Sauropterygia) from the Triassic-Jurassic boundary. – PLoS ONE 7: e31838.
- BENSON, R.B.J., KETCHUM, H.F., NAISH, D. & TURNER, L.E. (2013a): A new leptocleidid (Sauropterygia, Plesiosauria) from the Vectis Formation (early Barremian – early Aptian; Early Cretaceous) of the Isle of Wight and the evolution of Leptocleididae, a controversial clade. – Journal of Systematic Palaeontology 11: 233–250.
- BENSON, R.B., EVANS, M., SMITH, A.S., SASSOON, J., MOORE-FAYE, S., KETCHUM, H.F. & FORREST, R. (2013b): A giant pliosaurid skull from the Late Jurassic of England. – PLoS ONE 8: e65989.
- BENSON, R.B.J., EVANS, M. & TAYLOR, M.A. (2015): The anatomy of *Stratesaurus* (Reptilia, Plesiosauria) from the lowermost Jurassic of Somerset, United Kingdom. – Journal of Vertebrate Paleontology, (doi:10.1080/02724634.2014.93 3739).
- BLAINVILLE, H.M.D. DE (1835): Description de quelques espèces de reptiles de la Californie, précédé de l'analyse d'un système général d'Herpétologie et d'Amphibiologie. – Nouvelles Annales du Muséum National d'Histoire Naturelle, Paris 4: 233–296.
- BRANDES, T. (1914). Die Plesiosauriden aus dem Unteren Lias von Halberstadt. – Palaeontographica 61: 41–55.
- BREMER, K. (1994): Branch support and tree stability. Cladistics 10: 295–304.
- BROWN, D.S. (1981): The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. – Bulletin of the British Museum (Natural History), Geology Series 35: 253–347.
- CHENG, Y.N., SATO, T., WU, X.C. & LI, C. (2006): First complete pistosauroid from the Triassic of China. – Journal of Vertebrate Paleontology **26**: 501–504.

- CRUICKSHANK, A.R.I. (1994a): Cranial anatomy of the Lower Jurassic pliosaur *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 *Rhomale-osaurus thorntoni* Andrews (Reptilia, Plesiosauria). Bulletin of the Natural History Museum of London, 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.
- DRUCKENMILLER, P.S. & RUSSELL, A.P. (2008a): A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews, 1922. – Zootaxa **1863**: 1–120.
- DRUCKENMILLER, P.S. & RUSSELL, A.P. (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.
- GASPARINI, Z. (1997): A new pliosaur from the Bajocian of the Neuquen Basin, Argentina. Palaeontology **40**: 135–147.
- GOLOBOFF, P.A. (1999): Analyzing large data sets in reasonable times: solutions for composite optima. – Cladistics 15: 415–428.
- GOLOBOFF, P.A. & FARRIS, J.S. (2001): Methods for Quick Consensus estimation. – Cladistics 17: S26–S34.
- GOLOBOFF, P.A., FARRIS, J.S., KÄLLERSJÖ, M., OXELMAN, B., RAMÍREZ, M.J. & SZUMIKA, C.A. (2003): Improvements to resampling measures of group support. – Cladistics 19: 324–332.
- GOLOBOFF, P.A., FARRIS, J.S. & NIXON, K.C. (2008): TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786.
- HAIR, J.F., BLACK, W.C., BABIN B.J. & ANDERSON R.E. (2010). Multivariate data analysis. – Pearson College Division.
- KETCHUM, H.F. & BENSON, R.B.J. (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. & BENSON, R.B.J. (2011a): A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early-Middle Jurassic pliosaurids. – Special Papers in Palaeontology 86: 109–129.
- KETCHUM, H.F. & BENSON, R.B.J. (2011b): The cranial anatomy and taxonomy of *Peloneustes philarchus* (Sauropterygia, Pliosauridae) from the Peterborough Member (Callovian, Middle Jurassic) of the United Kingdom. Palaeontology 54: 639–665.
- KETCHUM, H.F. & SMITH, A.S. (2010): The anatomy and taxonomy of *Macroplata tenuiceps* (Sauropterygia, Plesiosaur-

ia) from the Hettangian (Lower Jurassic) of Warwickshire, United Kingdom. – Journal of Vertebrate Paleontology **30**: 1069–1081.

- КИНN, O. (1961): Die Familien der Rezenten und fossilen Amphibien und Reptilien. – Verlagshaus Meisenbach, 79 pp., Bamberg.
- LINNAEUS, C. (1758): Systema Naturae per Regna tria Naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. – Editio decima, reformata, 824 pp., Laurentii Salvii, Stockholm.
- MILNER, A.C. & WALSH, S.A. (2010): 18. Reptiles. In: LORD, A.R. & DAVIS, P.G. (eds): Fossils from the Lower Lias of the Dorset coast. – The Palaeontological Association 13: 372–394.
- MURTAGH, F. & HECK, A. (2012): Multivariate data analysis (Vol. 131). – Springer Science & Business Media.
- NOVOZHILOV, N.J. (1964): Order Sauropterygia. In: ORLOV, J.A. (ed.): Osnovy Paleontologii **12:** 309 – 332.
- 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 pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). – Paleobiology **28**: 101–112.
- O'KEEFE, F.R. (2004a): On the cranial anatomy of the polycotylid 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): 12. Neoteny and the plesiomorphic condition of the plesiosaur basicranium. – In: Carrano, M.T., GAUDIN, T.J., BLOB, R.W. & WIBLE, J.R. (eds): Amniote Paleobiology: Perspectives on the evolution of mammals, birds, and reptiles. – The University of Chicago Press: 391– 409.
- O'KEEFE, F.R. & CARRANO, M.T. (2005): Correlated trends in the evolution of the plesiosaur locomotor system. – Paleobiology **31**: 656–675.
- 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 **29**: 153–166.
- PERSSON, P.O. (1963): A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. – Lunds Universitets Årsskrift, ser. 2 (59): 1–59.
- SACHS, S., HORNUNG J.J. & KEAR, B.P. (2016): Reappraisal of Europe's most complete Early Cretaceous plesiosaurian: *Brancasaurus brancai* Wegner, 1914 from the "Wealden facies" of Germany. – PeerJ 4: e2813 (https://doi.org/ 10.7717/peerj.2813).
- SATO, T., LI, C. & WU, X.-C. (2003): Restudy of *Bishanoplio-saurus youngi* Dong, 1980, a fresh-water plesiosaurian from the Jurassic of Chongqing. – Vertebrata PalAsiatica 41: 17–33.

- SATO, T. & WU, X.C. (2008): A new Jurassic pliosaur from Melville Island, Canadian Arctic Archipelago. – Canadian Journal of Earth Sciences 45: 303–320.
- SENNIKOV, A.G. & ARKHANGELSKY, M.S. (2010): On a typical Jurassic sauropterygian from the Upper Triassic of Wilczek Land (Franz Josef Land, Arctic Russia). – Paleontological Journal 44: 567–572.
- SMITH, A.S. (2007): Anatomy and systematics of the Rhomaleosauridae (Sauropterygia: Plesiosauria). – Unpublished Ph.D. Thesis, 278 pp., University College Dublin.
- SMITH, A.S. (2008): Plesiosaurs from the Pliensbachian (Lower Jurassic) of Bornholm, Denmark. – Journal of Vertebrate Paleontology 28: 1213–1217.
- SMITH, A.S. (2015): Reassessment of 'Plesiosaurus' megacephalus (Sauropterygia: Plesiosauria) from the Triassic-Jurassic boundary, UK. – Palaeontologia Electronica 18.1.20A: 1–19.
- SMITH, A.S. & DYKE, G.J. (2008): The skull of the giant predatory pliosaur *Rhomaleosaurus cramptoni*: implications for plesiosaur phylogenetics. – Naturwissenschaften 95: 975–980.
- SMITH, A.S. & VINCENT, P. (2010): A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany. – Palaeontology 53: 1049–1063.
- SMITH, A.S. & ARAÚJO, R. (2012): A new rhomaleosaurid pliosaur from the Sinemurian (Lower Jurassic) of Lyme Regis, UK. – Program and abstracts, 72nd Annual Meeting of the Society of Vertebrate Paleontology. – Supplement to the online Journal of Vertebrate Paleontology, p. 174.
- SMITH, A.S. & BENSON, R.B.J. (2014): Osteology of *Rhomaleosaurus thorntoni* (Sauropterygia: Rhomaleosauridae) from the Lower Jurassic (Toarcian) of Northamptonshire, England. – Monograph of the Palaeontographical Society, London 168 (642): 1–40.
- STORRS, G.W. (1993): Function and phylogeny in sauropterygian (Diapsida) evolution. – American Journal of Science 293-A: 63–90.
- STORRS, G.W. (1997): Morphological and taxonomic clarification of the genus *Plesiosaurus*. – In: CALLAWAY, J.M. & NICHOLLS, E. (eds): Ancient Marine Reptiles. – Academic Press: 145–190.
- STORRS, G.W. & TAYLOR, M.A. (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.
- TARLO, L.B. (1960): A review of the Upper Jurassic pliosaurs. Bulletin of the British Museum (Natural History), Geology Series 4: 1–189.
- 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 of London B 335: 247–280.
- VINCENT, P. (2012): Re-description of a basal plesiosaur (Reptilia, Sauropterygia) from the Lower Jurassic of England. – Journal of Paleontology **86**: 167–176.
- VINCENT, P. & SMITH, A.S. (2009): A redescription of *Plesio-saurus propinquus* Tate & Blake, 1876 (Reptilia, Plesiosauria), from the Lower Jurassic (Toarcian) of Yorkshire, Eng-

land. – Proceedings of the Yorkshire Geological Society **57**: 133–142.

- VINCENT, P., BARDET, N., PEREDA SUBERBIOLA, X., BOUYA, B., AMAGHZAZ, M. & MESLOUH, M.S. (2011): Zarafasaura oceanis, a new elasmosaurid (Reptilia: Sauropterygia) from the Maastrichtian Phosphates of Morocco and the palaeobiogeography of latest Cretaceous plesiosaurs. – Gondwana Research 19: 1062–1073.
- VINCENT, P. & BENSON, R.B.J. (2012): Anningasaura, a basal plesiosaurian (Reptilia, Plesiosauria) from the Lower Jurassic of Lyme Regis, United Kingdom. – Journal of Vertebrate Paleontology 32: 1049–1063.
- WOLD, H. (1966a): Nonlinear estimation by iterative least squares procedures. – In: NEYMAN, J. & DAVID, F. (eds): Research papers in statistics. – Wiley: 411–444, New York.
- WOLD, H. (1966b): Estimation of principal components and related models by iterative least squares. – In: KRISHNAIAH, P.R. (ed.): Multivariate Analysis. – Academic Press: 391–420, New York.

Note

The following appendices are available under https://doi.pangaea. de/10.1594/PANGAEA.870543

Appendix 1. Morphometric dataset and multivariate analysis. For clarification of anatomical measurements used in these analyses see figure 5.1 in SMITH (2007) Sheet #1: the complete morphometric dataset (Analysis 1); Sheet #2, normality tests of the morphometric dataset; Sheet #3, sensitivity test to the NIPALS estimation; Sheet #4, missing entries of the dataset estimated with the NIPALS algorithm; sheet #5, normality test including the missing entries; Sheet #6: Spearman type principal component analysis; Sheet #7: Spearman type agglomerative hierarchical clustering; Sheet #8, pruned dataset, all measurements with less than ten entries were pruned (Analysis 2); Sheet #9, missing entries of the Analysis 2 dataset estimated with the NIPALS algorithm; Sheet #10, Spearman type principal component analysis with the Analysis 2 dataset; Sheet #11, pruned dataset with only skull measurements (Analysis 3); Sheet #12, missing entries of the Analysis 3 dataset estimated with the NIPALS algorithm; sheet #13, Spearman type principal component analysis with the Analysis 3 dataset.

Appendix 2. Results and data for the phylogenetic analysis, including matrix codings for *Thaumatodracon*, complete trees, group frequencies results, apomorphies, and Bremer support results for the SMITH & DYKE (2008), BENSON et al. (2012) and BENSON & DRUCKENMILLER (2013) data matrices.

Appendix 3. Diagram showing the various linear measurements taken for the cervical vertebrae in lateral, anterior and dorsal view.

Explanation of the plates

Plate 1

Thaumatodracon wiedenrothi (NLMH 106.058), selected anterior cervical vertebrae.

Figs 1–5. Vertebrae four-six. 1. v4 in anterior view, 2. v4–6 in left lateral view. 3. v6 in posterior view. 4. v4–6 in dorsal view (anterior towards top). 5. v4–6 in ventral view (anterior towards top).

Figs 6–8. Vertebra seven. 6. in dorsal view. 7. in left lateral view. 8. in right lateral view.

Figs 9–12. Centrum of vertebra ten. 9. in anterior view. 10. in left lateral view. 11. in dorsal view (anterior towards top). 12. in ventral view (anterior towards top).

Figs 13–17. Vertebrae 11 and 12. 13. v11 in anterior view. 14. v11–12 in left lateral view. 15. close-up of the left cervical rib of v12 in posterior view. 16. v11–12 in dorsal view (anterior towards top). 17. v11–12 in ventral view (anterior towards top).

Figs 18–21. Vertebrae 18 and 17. 18. v17-18 in right lateral view. 19. v17 in anterior view. 20. v17–18 in dorsal view (anterior towards top). 21. v17–18 in ventral view (anterior towards top).

Scale bars represents 20 mm.



Plate 2

Thaumatodracon wiedenrothi (NLMH 106.058), selected posterior cervical vertebrae.

Figs 1–3. Vertebrae 19–21. 1. v19–21 in left lateral view. 2. v19–21 in dorsal view (anterior towards top). 3. v19–21 in ventral view (anterior towards top).

Figs 4–7. Vertebrae 23 and 24. 4. v22–23 in right lateral view. 5. v22 in anterior view. 6. v22–23 in dorsal view (anterior towards top). 7. v22–23 in ventral view (anterior towards top). Figs 8–11. Vertebrae 24–27. 8. v24–27 in left lateral view. 9. v24–27 in right lateral view. 10. v24–27 in dorsal

Figs 8–11. Vertebrae 24–27. 8. v24–27 in left lateral view. 9. v24–27 in right lateral view. 10. v24–27 in dorsa view (anterior towards left). 11. v24–27 in ventral view (anterior towards right).

Scale bar represents 20 mm.

