A basal elasmosaurid plesiosaur from the upper Albian–lower Cenomanian? Cambridge Greensand

JOSE P. O'GORMAN and ROGER B.J. BENSON

O'Gorman, J.P. and Benson, R.B.J. 2025. A basal elasmosaurid plesiosaur from the upper Albian–lower Cenomanian? Cambridge Greensand. *Acta Palaeontologica Polonica* 70 (4): 613–628.

An historical indeterminate elasmosaurid specimen CAMSM X50356 (CAMSM = Sedgwick Museum) collected during the 19th century is described. The specimen comes from the Cenomanian Cambridge Greensand although the possibility of an Albian–lower Cenomanian age is discussed. CAMSM X50356 is recovered within the Elasmosauridae. Our phylogenetic analysis indicates that elongated cervical centra with absence of the lateral ridge are the basal condition of elasmosaurids. The lateral ridge is present in almost all other elasmosaurids with the exception of some taxa that have secondarily shortened the cervical centra such as the aristonectines and *Nakonanectes bradti*. The lack of correlation between cervical elongation and the lateral ridge is thus recorded here for the first time as CAMSM X50356 is the only elasmosaurid with cervical centra longer than high but without the lateral ridge.

Key words: Sauropterygia, Elasmosauridae, Cambridge Greensand, Albian, Cenomanian, Cretaceous.

Jose P.O'Gorman [joseogorman@fcnym.unlp.edu.ar; ORCID: https://orcid.org/0000-0001-9279-6314], División Paleontología Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina. CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina.
Roger B.J. Benson [rbenson@amnh.org; ORCID: https://orcid.org/0000-0001-8244-6177], American Museum of Natural History, New York, New York, USA. Department of Earth Sciences, University of Oxford, Oxford, UK.

Received 25 October 2024, accepted 7 July 2025, published online 30 Octobeber 2025.

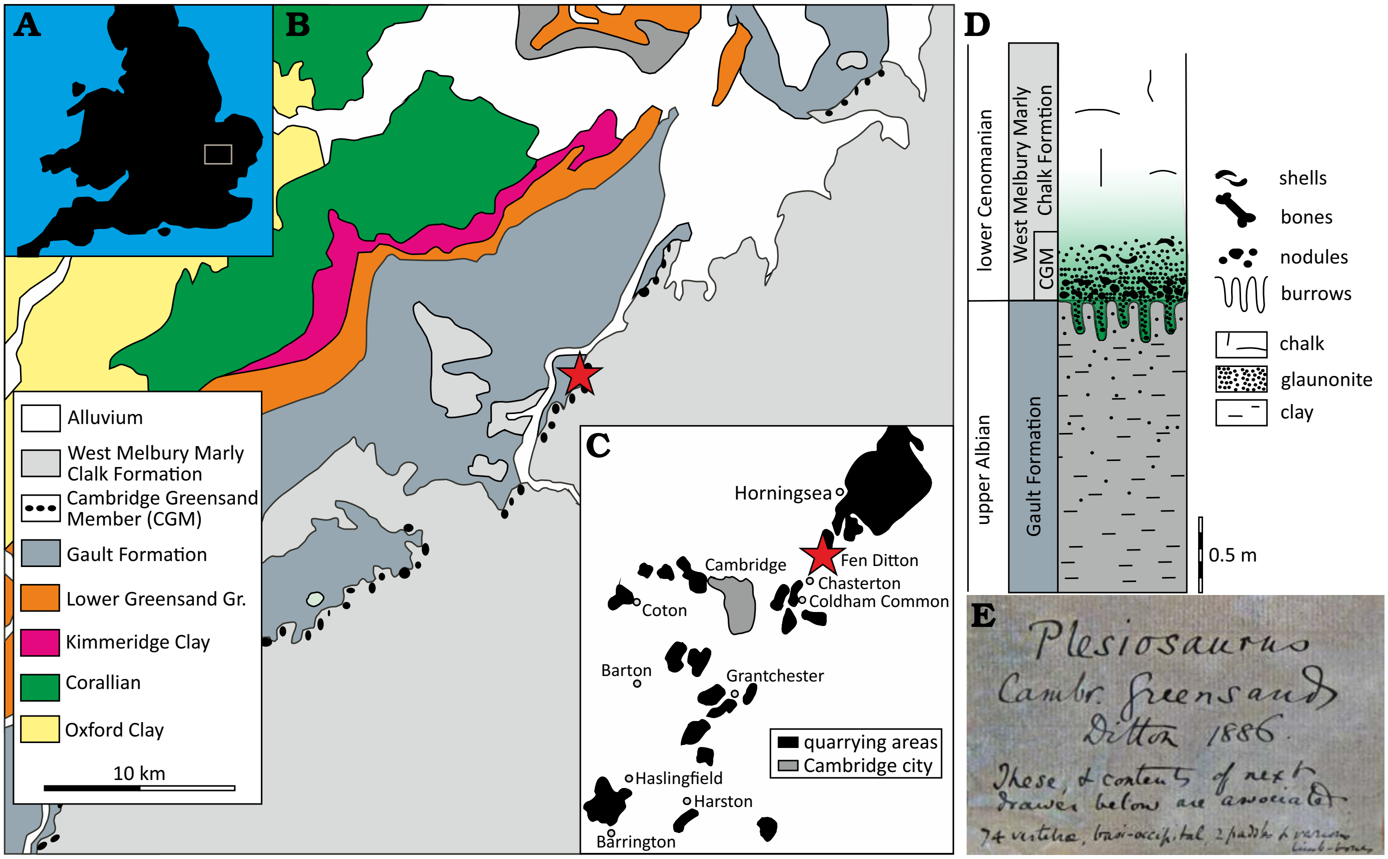
Introduction

Plesiosaurians are a group of diapsid marine reptiles whose biochron extends from the Rhaetian (Late Triassic) to the K/Pg mass extinction event (Gasparini et al. 2003; Vincent et al. 2011; Wintrich et al. 2017). Throughout their long history, plesiosaurians showed substantial diversification in body proportions (O'Keefe 2002; Soul and Benson 2017; Gutarra et al. 2022), while retaining a conservative bauplan based on four-limbed propulsion and a stiff trunk. Several distinct intervals marked important episodes of diversification or turnover for plesiosaurians, including the initial diversification of the group in the earliest Jurassic (Bardet 1994; Benson et al. 2012), the diversification of thalassophonean pliosaurids and cryptoclidian plesiosaurians early in the Middle Jurassic (e.g., Sachs et al. 2023), and the rise of the xenopsarian groups Leptocleidia and Elasmosauridae around the Jurassic/Cretaceous transition (Benson and Druckenmiller 2014).

The transition from the Early to Late Cretaceous, around the Albian–early Turonian marked an important episode of faunal change that substantially altered the composition of marine reptile assemblages during a protracted interval of approximately 14 Ma. This interval saw the decline and final extinction of ichthyosaurs (Fischer et al. 2014; McGowan 1972) and the radiation of mosasaurs, beginning in the Early Cretaceous (Madzia and Cau 2020; Polcyn et al. 2014). It was also important for plesiosaurians, with the diversification of Euelasmosaurida, increases in polycotylid diversity, and the extinction of pliosaurids (Fischer et al. 2018; O'Gorman 2019). Understanding Albian–Cenomanian marine reptile faunas is extremely important in order to understand this process, but so far these are poorly understood compared to younger faunas.

Among the groups of plesiosaurians that radiated around the Albian–Cenomanian are Elasmosauridae (O'Gorman 2019). Elasmosaurids are characterized by an elongated neck and small skull (Benson and Druckenmiller 2014; Serratos et al. 2017; O'Gorman 2019). The cervical centra of elasmosaurids are usually elongate and bear a lateral keel but there are exceptions that lack both centrum elongation and lateral keel (O'Gorman 2016b, 2019; Serratos et al. 2017).

The Albian–early Cenomanian (see Geological setting for age discussion) vertebrate fauna of the Cambridge Greensand of the West Melbury Marly Chalk Formation is among the richest fossil vertebrate assemblages in England (Unwin 2001), and has great potential to shed light on this important



Plesiosaurus
Cambr. Greensand
Ditton 1886.
These, & contents of next
drawer below are associated
74 vertebrae, basi-occipital, 2 paddles & various
limb-bones

Fig. 1. **A**. Location of the study area in the UK. **B**. Geological map of eastern England showing the distribution of the Cambridge Greensand (red star). **C**. Cambridge Greensand phosphate quarrying areas near Cambridge (adapted from Unwin 2001; Grove 1976; Worssam and Taylor 1969). **D**. Lithologic and stratigraphic scheme of the Albian/Cenomanian boundary interval in Cambridgeshire (taken from Machalski 2018). **E**. Original inked label of CAMSM X50356.

interval of biotic turnover. Despite difficulties resulting from the fragmentary nature of the specimens and the complexity of their stratigraphy, revisions of several vertebrate groups, such as pterosaurs (Unwin 2001), turtles (Evers et al. 2019; Joyce 2025), ichthyosaurs (Fischer et al. 2014), and dinosaurs (Barrett and Bonsor 2021), have been undertaken in the past few decades. However a revision of plesiosaurians as a whole has not yet been undertaken.

Here, we describe CAMSM X50356, which is exceptionally complete compared to other plesiosaurians from the Cambridge Greensand. The specimen was collected and catalogued by Ditton (1886) as is seen in the original label (Fig. 1E).

We evaluate its phylogenetic relationships and discuss the implications for the early diversification of elasmosaurids.

Institutional abbreviations.—CAMSM, Sedgwick Museum, Cambridge, UK; NHMUK, Natural History Museum, London, UK; SCARB, Rotunda Museum, Scarborough, UK.

Other abbreviations.—CGS, Cambridge Greensand; cap, capitulum; cf, coracoid foramen; di, diapophysis; exf, exoccipital facet; opf, opisthotic facet; OTUs, operational taxonomic units; pa, parapophysis; pez, prezygapophysis; pf, pedicellar facet; pf+pa, pedicellar facet + parapophysis; poz, postzygapophysis; vf, ventral foramina; VLI, vertebral length index.

Geological setting

The Cambridge Greensand crops out in the region of Cambridge, extending to north to Soham and south to Harlington (Unwin 2001; Fig. 1A–C). The most representative outcrops of the Cambridge Greensand were exposed during phosphate quarrying in the nineteenth century, but were largely covered after the cessation of quarrying activity (Grove 1976) and are now inaccessible. This circumstance underscores the importance of the collections made at that time, which today constitute a significant part of the paleontological holdings of the Sedgwick Museum. It is also noteworthy that some specimens of the Cambridge Greensand have been recovered from other types of outcrops (Codrington 1864, 1908).

Stratigraphically the Cambridge Greensand is located at the basal level of the Lower Chalk (White 1932; Worssam and Taylor 1969), also called the West Melbury Marly Chalk Formation (Machalski 2018; Fig. 1D). The Cambridge Greensand is a thin unit (thickness between 0.6 m to 1.5 m, Worssam and Taylor 1969) of micaceous, glauconitic, silt marl with a basal lag of reworked phosphatic nodules usually associated with vertebrate fossils and exotic clasts, often encrusted in small oysters and other epibionts (Sedgwick 1846; Seeley 1866). The rich vertebrate fossil assemblage of the Cambridge

Table 1. Measurements (in mm) of vertebrae (c, cervical; ca, caudal; d, dorsal; p, pectoral; s, sacaral) length (L), height (H), breadth (B) and indexes height/length ratio (HI = 100*H/L), breadth/length ratio (BI = 100*B/L), breadth/height ratio (BHI = 100*B/H) and vertebral length index [VLI = 100*L/(0.5*(H + B))]. The order given is relative because the skeleton was found disarticulated.

Vertebra	L	H	B	HI	BI	BHI	VLI
1c	24	22	32	92	133	145	89
2c	26						
3c	26	25		96			
4c	30	27	38	90	127	141	92
5c	31	27		87			
6c	30	28	39	93	130	139	90
7c	30	28		93			
8c	31	30	42	97	135	140	86
9c	33						
10c	34	34	44	100	129	129	87
11c	35	34	47	97	134	138	86
12c	34	35	45	103	132	129	85
13c	39	38	51	97	131	134	88
14c	37	39	51	105	138	131	82
15c	37	39	52	105	141	133	81
16c	39	41	52	105	133	127	84
17c	39	41	51	105	131	124	85
18c	38	42	52	111	137	124	81
19c	37	43	52	116	141	121	78
20c	40	45	50	113	125	111	84
21c	37	45	56	122	151	124	73
22c	40	45	57	113	143	127	78
23c	41	47	58	115	141	123	78
24c	42	47	56	112	133	119	82
25c	41	48	59	117	144	123	77
26c	41	48	60	117	146	125	76
27c	42	49	59	117	140	120	78
28c	42	49	60	117	143	122	77
29c	41	50	60	122	146	120	75
30c	42	50	61	119	145	122	76
31c	40	50	66	125	165	132	69
32c	41	50	65	122	159	130	71
33c	41	50	67	122	163	134	70
34c	42	51	62	121	148	122	74
35c	41	51	64	124	156	125	71
36c	41	51	64	124	156	125	71
37c	41	51	69	124	168	135	68
1p	41	49	67	120	163	137	71
2p	41	52	70	127	171	135	67
3p	44	51	71	116	161	139	72
1d	44	54	68	123	155	126	72
2d	45	55	66	122	147	120	74
3d	45	56	68	124	151	121	73
4d	42	59	68	140	162	115	66
5d	43	61	67	142	156	110	67
6d	43	61	64	142	149	105	69
7d	43	60	66	140	153	110	68
8d	45	61	65	136	144	107	71
9d	45	60	67	133	149	112	71
10d	45	58	65	129	144	112	73
11d	40	59	63	148	158	107	66
12d	45	58	65	129	144	112	73
13d	40	54	64	135	160	119	68
14d	42	50	62	119	148	124	75
15d	36	54	63	150	175	117	62
16d	39	46	64	118	164	139	71
17d	36	52	59	144	164	113	65
18d	35	46	60	131	171	130	66
19d	34	46	57	135	168	124	66
20d	34	49	58	144	171	118	64
1s	31	44		142			
2s	31	45	62	145	200	138	58
3s	27	47	55	174	204	117	53
4s	25	45	56	180	224	124	50
5s	27	43	56	159	207	130	55
1ca	25	44	53	176	212	120	52
2ca	23	39	49	170	213	126	52
3ca	25	41	53	164	212	129	53

Greensand may originate mostly as reworked material from the underlying Gault Formation (Reed 1897). Therefore this is a typical fossil “Konzentrat-Lagerstatte” (sensu Seilacher 1970). Regarding the stratigraphic age, the Cambridge Greensand were deposited very early in the Cenomanian (Hart 1973). However, most of the fossils may be reworked from the underlying Gault Clay Formation (Albian) (Unwin 2001; Gallois et al. 2016; Hart and Lyndsey 2020). The presence of some reworked phosphatised Cenomanian ammonites in recent studies indicates that at least some of the reworked fossils are also early Cenomanian in age (Gallois et al. 2016).

Material and methods

Measures.— Linear measurements were taken using a mechanical calliper with an accuracy of 0.1 mm. Both width and height were measured on the posterior articular surface of the vertebral centra. The vertebral indices considered in this contribution are those proposed by Welles (1952), which take into account the ratio between the centrum length length (L) and height (H) (HI = 100 * H/L) and the ratio between centrum width breadth (B) and length (BI = 100 * B/L). The ratio between the centrum breadth and height (BHI = 100 * B/H was also considered. The vertebral length index VLI = 100 * L/(0.5 * (H + B)) proposed by Brown (1981) was also used for comparison.

Taxon sampling and characters.—A phylogenetic analysis was conducted to clarify the evolutionary relationships of CAMSM X50356. This analysis makes use of the data set of Ketchum (2010) modified by Benson and Druckenmiller (2014) and Serratos et al. (2017), modified by rescoring and addition of new OTUs (O’Gorman 2019; O’Gorman et al. 2021; for references see O’Gorman et al. 2023). The result-

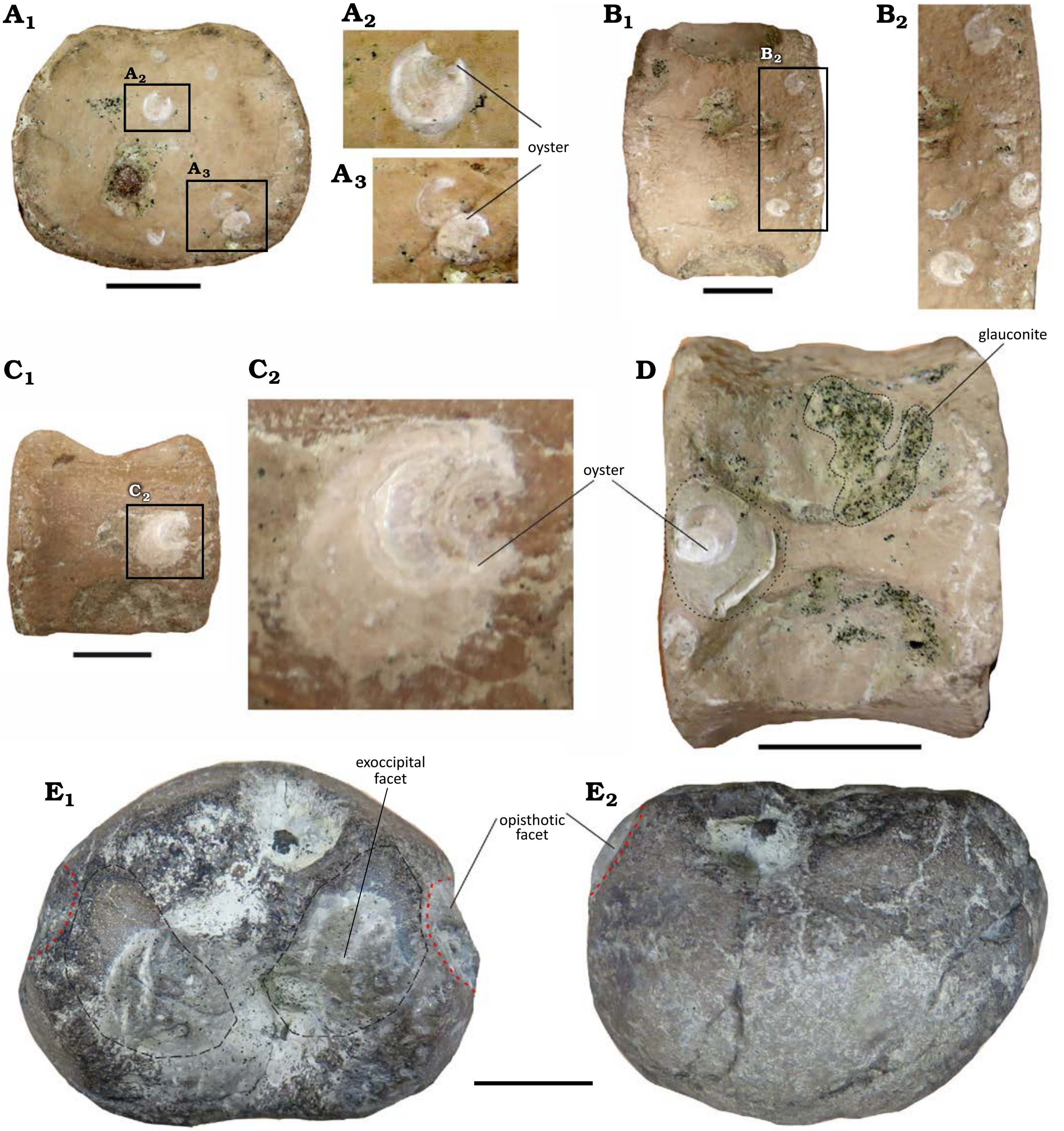


Fig. 2. **A**–**D**. Taphonomic features of four cervical centra of CAMSM X50356 (Elasmosauridae indet.) from Fen Ditton, near Cambridge, UK, upper Albian–lower Cenomanian, oyster encrustations. A_1, cervical cetrum in posterior view; A_2 and A_3, details of incrusted oysters; B_1, cervical centrum in ventral view; B_2, detail of incrusted oyster; C_1, cervical centrum in left lateral view; C_2, detail of incrusted oyster. **D**. Cervical centrum in dorsal view. **E**. Platypterygiinae indet. CAMSM X50356 (Elasmosauridae indet.) from Fen Ditton, near Cambridge, UK, upper Albian–lower Cenomanian, basioccipital in dorsal (E_1) and posterior (E_2) views. Scale bars 20 mm.

ing matrix includes 290 characters and 120 OTUs, including 33 elasmosaurid OTUs. The complete data set was compiled using Mesquite (Maddison and Maddison 2011) and given as SOM 1 (Supplementary Online Material available at http://app.pan.pl/SOM/app70-OGorman_Benson_SOM.pdf). The percentage of missing data of CAMSM X50356 is 88.3%.

Phylogenetic analysis.—The complete data set was analyzed with the TNT 1.5 software package (Goloboff and

Catalano 2016). Only character 155 was considered ordered. Initial tree searches were conducted using new technology searches (1000 random addition sequence and default setting). The resulting trees were then reanalyzed using TBR (tree bisection-reconnection) to generate the full set of most parsimonious trees (MPTs).

To detect OTUs that act as wild card taxa, we used the command pcrprune of TNT.1.5 (Goloboff and Catalano 2016). To test clade robustness, Bremer Support values were calculated for some nodes using TNT.1.5 (Bremer 1994).

Systematic palaeontology

Subclass Sauropterygia Owen, 1860
Order Plesiosauria de Blainville, 1835
Clade Xenopsaria Benson & Druckenmiller, 2014
Family Elasmosauridae Cope, 1869
Elasmosauridae indet.

Figs. 2A–D, 4–8.

Material.—CAMSM X50356, 37 cervical centra, 3 pectoral centra, 20 dorsal centra, 5 sacral centra, 3 caudal centra, isolated neural arches, fragmentary ribs, part of a scapula, one almost complete propodial, and propodial fragments; from locality "Ditton", probably referring to Fen Ditton, near Cambridge. Probably from the West Melbury Marly Chalk Formation, a unit that was historically referred to as the Cambridge Greensand (Joyce 2025). Most of the vertebrate materials from these levels are reworked from the underlying Gault Clay Formation that is upper Albian (Unwin 2001; Hart and Lyndsey 2020). However the specimen described could also be deposited simultaneously with the Cambridge Greensand matrix, representing the *carcitanensis* Subzone, at the very base of the Cenomanian (Hart 1973). Therefore the possible stratigraphic range is upper Albian–lower Cenomanian.

Description.—*Taphonomic condition of the specimen*: CAMSM X50356 is the disarticulated skeleton of an osteologically immature individual (sensu Araújo et al. 2015). Neural arches are detached from the vertebral centra, likely due to incomplete ossification during growth. The centra exhibit possible oyster encrustations (Fig. 2A–D). Some elements display signs of abrasion and fracturing, while the neural arches and girdles are fragmentarily preserved.

Cervical region: The cervical region comprises the centra of thirty-seven preserved vertebrae. The cervical cen-

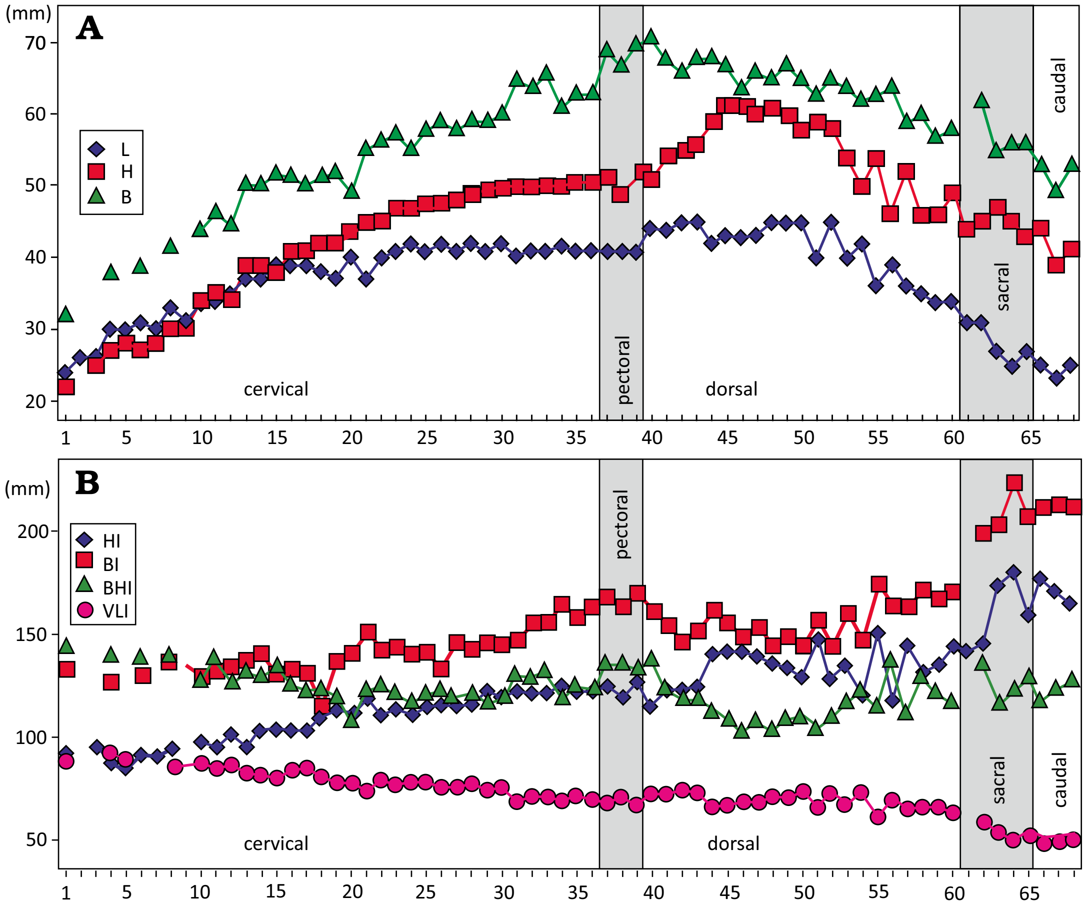


Fig. 3. CAMSM X50356 (Elasmosauridae indet.) from Fen Ditton, near Cambridge, UK, upper Albian–lower Cenomanian, vertebral centra measurements and indexes. **A**. Values (in mm) of length (L), height (H), and centrum width (B). **B**. Indexes HI (100*H/L), BI (100*B/L), BHI (100*B/H), VLI [100 *L/(0.5*(H + B))].

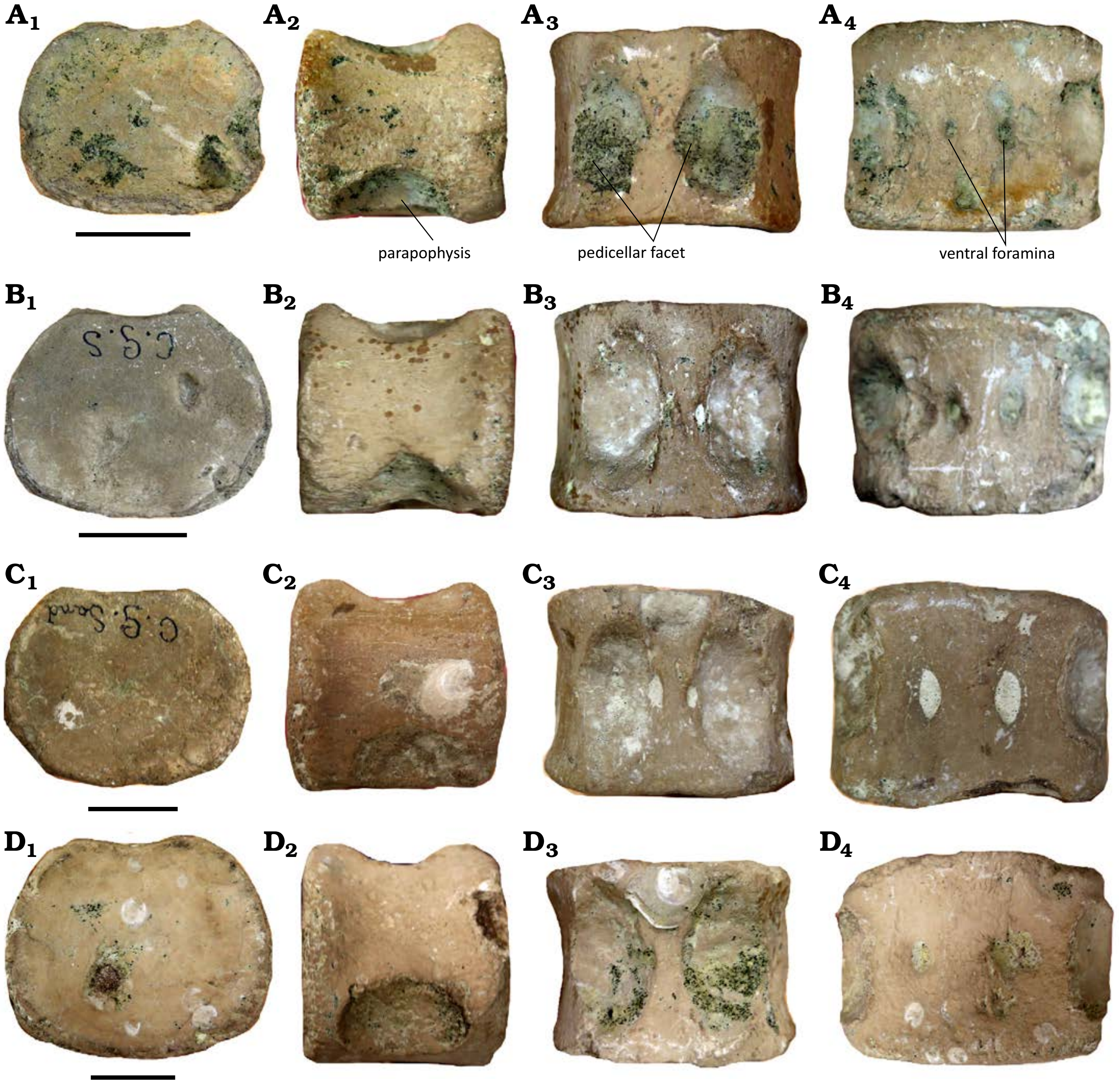


Fig. 4. CAMSM X50356 (Elasmosauridae indet.) from Fen Ditton, near Cambridge, UK, upper Albian–lower Cenomanian, anterior and middle cervical centra. **A**. 10th cervical centrum in posterior (A_1), right lateral (A_2), dorsal (A_3), and ventral (A_4) views. **B**. 13th cervical centrum in posterior (B_1), right lateral (B_2), dorsal (B_3), and ventral (B_4) views. **C**. 23rd cervical centrum in posterior (C_1), right lateral (C_2), dorsal (C_3), and ventral (C_4) views. **D**. 30th cervical centrum in posterior (D_1), right lateral (D_2), dorsal (D_3), and ventral (D_4) views. Scale bars 20 mm.

tra are identified by the presence of ventrolateral parapophysys. However, the sequence is clearly not complete as it lacks the atlas, axis, and possibly other individual vertebrae. Therefore the original number of cervical vertebrae was at least thirty-nine, and possibly more. The cervical centra are proportionally wide, being broader mediolaterally than the diameters of their articular surfaces (Fig. 3, Table 1). The articular surfaces are elliptical and slightly concave. The vertebral centra are longer than high in anterior cervicals but higher than long in middle to posterior cervicals. VLI is less than 100 in all cervical centra (Fig. 3B). The pedicellar facets are elongated and strongly concave (Fig. 4). A pair of dorsal foramina is located on the medial limit of each pedicellar facet (Fig. 4A_3–D_3). The lateral surface lacks any trace of a lateral keel or ridge (Fig. 4A_2–D_2). The ventrolateral margins of anterior and medial vertebrae show deep parapophyses without any trace of cervical ribs attached. The parapophyses of the most posterior cervical centra are less concave or even slightly laterally projected (Fig. 4A_2–D_2). The ventral surface of each cervical centrum is pierced

Fig. 5. CAMSM X50356 (Elasmosauridae indet.) from Fen Ditton, near Cambridge, UK, upper Albian–lower Cenomanian. Neural arches. **A**. Posterior cervical neural arches in left lateral (A_1) and anterior (A_2) views. **B**. Caudal? neural arch in anterior view. **C**. Caudal neural arches in posterior (C_1) and left lateral (C_2) views. **D**, **E**. Caudal neural arches in left alterl view; dash line indicate suposed morphology. **F**, **G**. Diapophyses. **H**. Proximal end of dorsal rib. Scale bars 20 mm.

Fig. 6. CAMSM X50356 (Elasmosauridae indet.) from Fen Ditton, near Cambridge, UK, upper Albian–lower Cenomanian, two posteriormost cervical and the three pectoral centra in dorsal (A_1), right lateral (A_2), and ventral (A_3) views. Abbreviations: c, cervical; p1, p2, p3, pectoral 1, 2, and 3.

by a pair of subcentral foramina with a broad, almost flat surface between them (Fig. $4A_4$–D_4).

The neural arches are not well preserved but some features are evident. The prezygapophyses are mediolaterally narrow compared to the centrum width. They have slightly curving articular surfaces that are inclined to face dorsomedially, and are fused in the midline, as are the postzygapophyses. A low median ridge is present between the prezygapophyseal facets (Fig. $5A_2$) that fits into a median sulcus between the postzygapophyses (Fig. $5A_3$).

Pectoral region: Three pectoral centra are preserved, identified based on the confluence of pedicellar and parapophyseal facets (Welles 1943). The proportions of the pectoral centra are similar to those of posterior cervical centra (Fig. 3). However, the ventral surfaces of pectoral centra are more convex and bear a pair of additional, smaller foramina (Fig. $6A_3$).

Dorsal region: Twenty dorsal centra are preserved, identified based on the absence of parapophysis (Welles 1943). The pedicellar facets are deeply concave and elliptical in shape (Fig. 7). The dorsal centra are wider mediolaterally than high dorsoventrally, and are higher dorsoventrally than long anteroposteriorly. Anterior middle dorsal centra are larger than other vertebrae (Fig. 3). The lateral surfaces of dorsal centra are anteroposteriorly concave (Fig. 7). The ventrolateral and ventral surfaces are pierced by 2–4 fo-

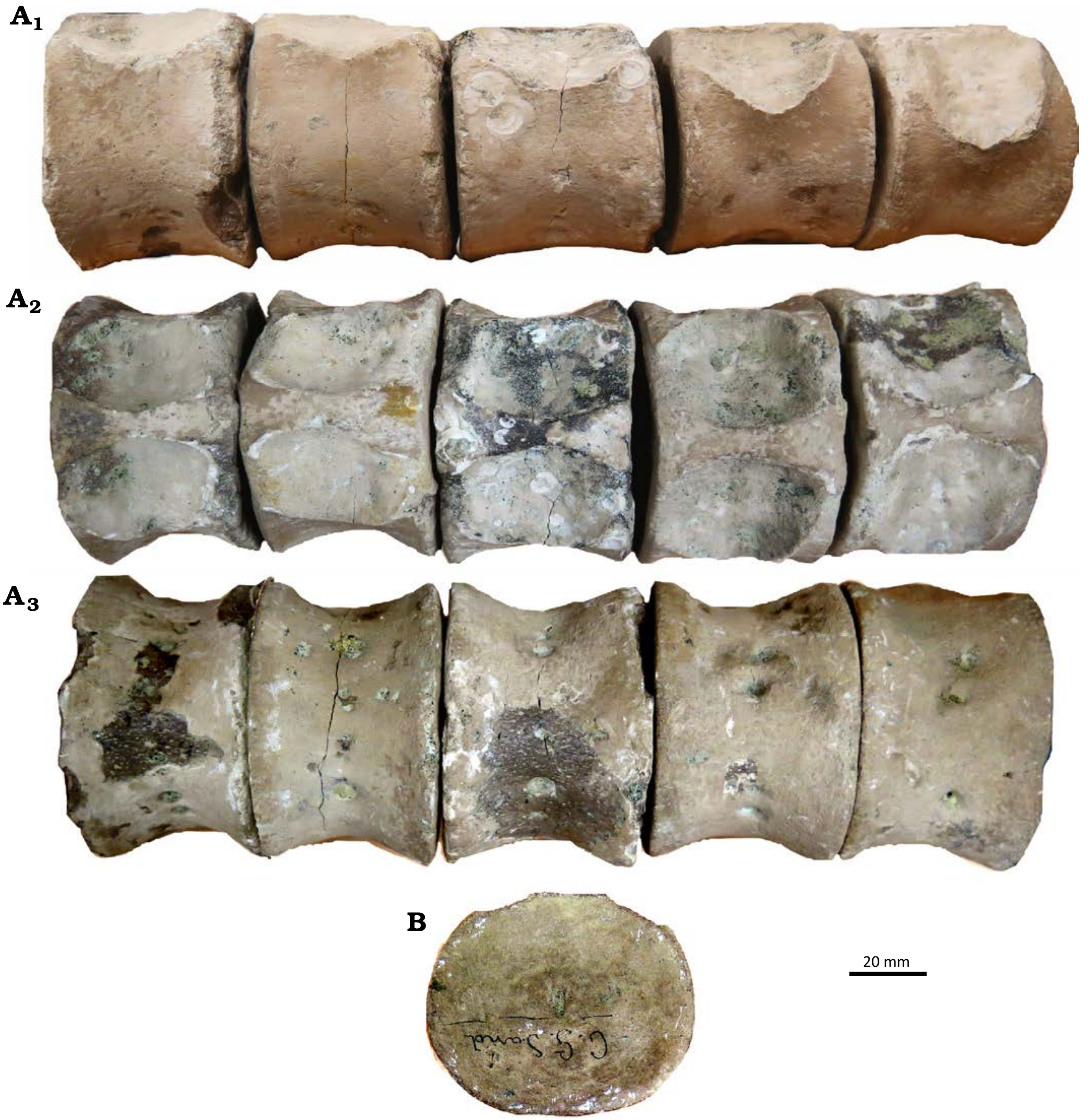


Fig. 7. CAMSM X50356 (Elasmosauridae indet.) from Fen Ditton, near Cambridge, UK, upper Albian–lower Cenomanian. **A**. 41–45th dorsal centra in right lateral (A_1), dorsal (A_2), and ventral (A_3) views. **B**. Dorsal centrun in anterior view.

ramina (Fig. 7A_3). The diapophyses show a rounded cross section (Fig. 5F, G).

Sacral region: The sacral region comprises five vertebrae (Fig. 8A_2–A_4) identified by the presence of laterally projected transverse processes (Welles 1943). Their articular surfaces are more depressed than those of the dorsal and caudal vertebrae (Fig. 8A_1). The ventral part of the rib facet is anteroposteriorly short and dorsoventrally elongated (Fig. 8A_2).

Caudal region: Two caudal centra are preserved, identified by lateral parapophysis and haemal facets (Welles 1943). The caudal centra are broader than high and higher than long (Figs. 3A, 8B). The parapophyses are lateral in position and circular in shape. Ventrally there is one single foramen and low haemal facets are located both anteroventrally and posteroventrally (Fig. 8B_3).

Scapula: Only the glenoid ramus of the left scapula is preserved that shows the margin elevated and progressively

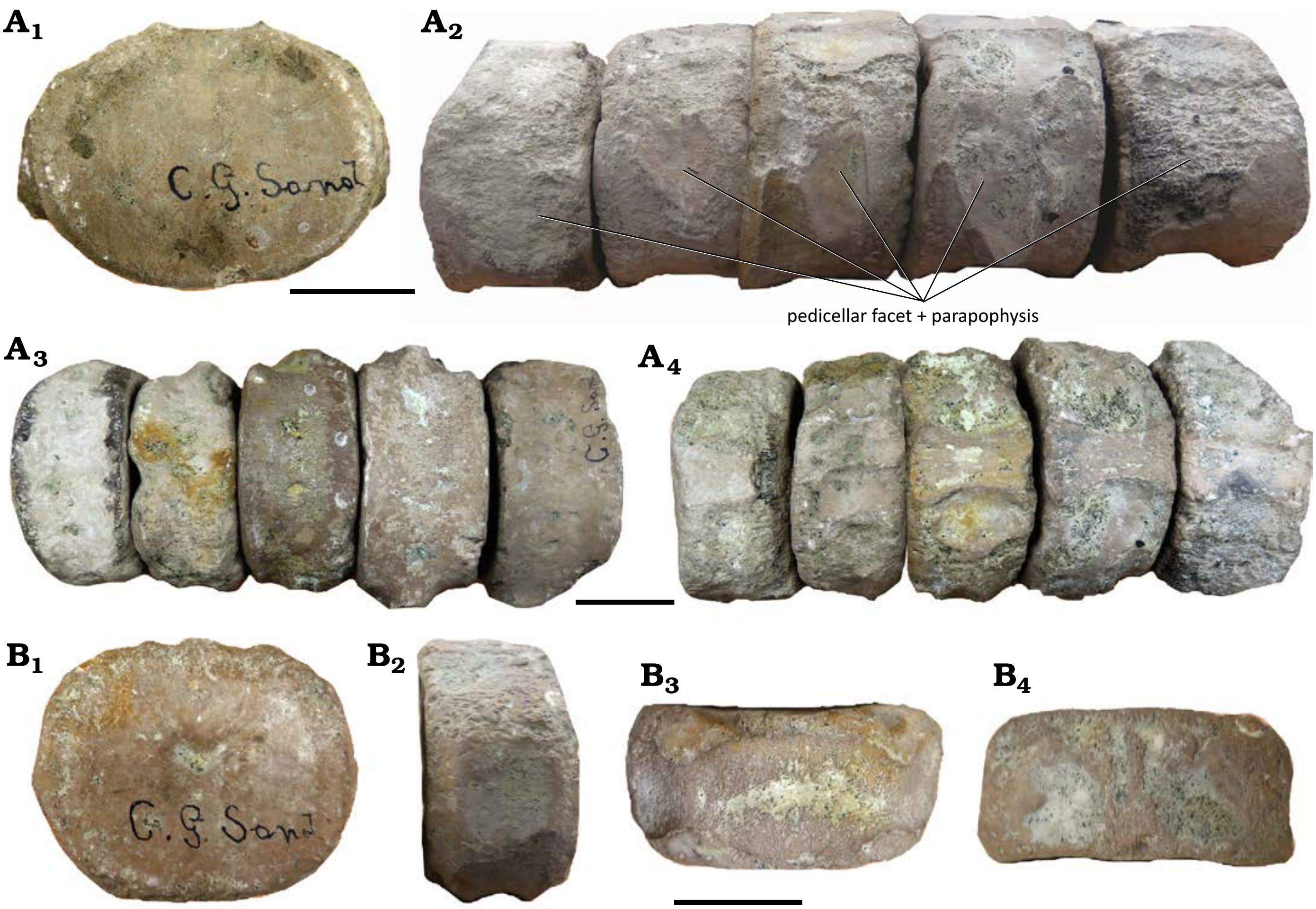


Fig. 8. CAMSM X50356 (Elasmosauridae indet.) from Fen Ditton, near Cambridge, UK, upper Albian–lower Cenomanian. **A**. Sacral centra in posterior (A_1), right lateral (A_2), ventral (A_3), and dorsal (A_4) views. **B**. Caudal centra in posterior (B_1), left lateral (B_2), ventral (B_3), and dorsal (B_4) views. Scale bars 20 mm.

displaced relative to the plane determined by the main axes of the coracoids and glenoid facet. This portion is interpreted as the proximal part of the dorsolateral process. The glenoid facet is as long as the coracoid facet in dorsal view (Fig. 9A).

Propodium: Two propodials are preserved. One is represented only by the proximal end (Fig. 9B) and the other preserves most of the element (Fig. 9C), with substantial damage. Due to the state of preservation, it is not possible to determine whether these propodials are humeri or femora. In both elements the fracture shows an internal structure that follows the limit between perichondral and endochondral ossification, a feature associated with specimens that have not achieved full osteological maturity as the absence of secondary remodelling has not affected the perichondral–endochondral boundary (O'Gorman et al. 2014; Fig. 9C_3). The more complete of the two propodials provides more complete evidence of morphology. It is 205 mm in length and has more than 102 mm of distal expansion (complete distal expansion can not be measured due to incompleteness) (Fig. 9C). This is similar to the propodial proportions of many other elasmosaurids. The tuberosity/trochanter is not well developed but it is visible as a small lip in the ventral surface of the propodial (Fig. 9C_2).

Remarks.—The only element with the original elements that clearly does not belong to a plesiosaurian is a basioccipital bone, listed on the original label (Fig. 1E). The basioccipital differs from the morphology observed in elasmosaurids (Sato 2003; Zverkov et al. 2017; O'Gorman 2019, 2021) consistent with that of a platypterygiine ichthyosaur, based on the extremely reduced extracondylar area (Fig. 2E), which is not visible ventrally in posterior view (Fischer et al. 2012).

Phylogenetic results

Our initial tree search using new technologies recovered 50 MPTs of 1942 steps. After TBR branch swapping, a much larger set of 20 000 MPTs of 1942 steps was recovered. Three OTUs were recovered as wild card taxa *Wapuskanectes betsynicholsae*, *Fluvionectes sloanae*, and *Alexandronectes zealandiensis*. After pruning them from the consensus the CAMSM X50356 ("Cambridge Elasmosauridae") is recovered as the basalmost member of Elasmosauridae (Fig. 10).

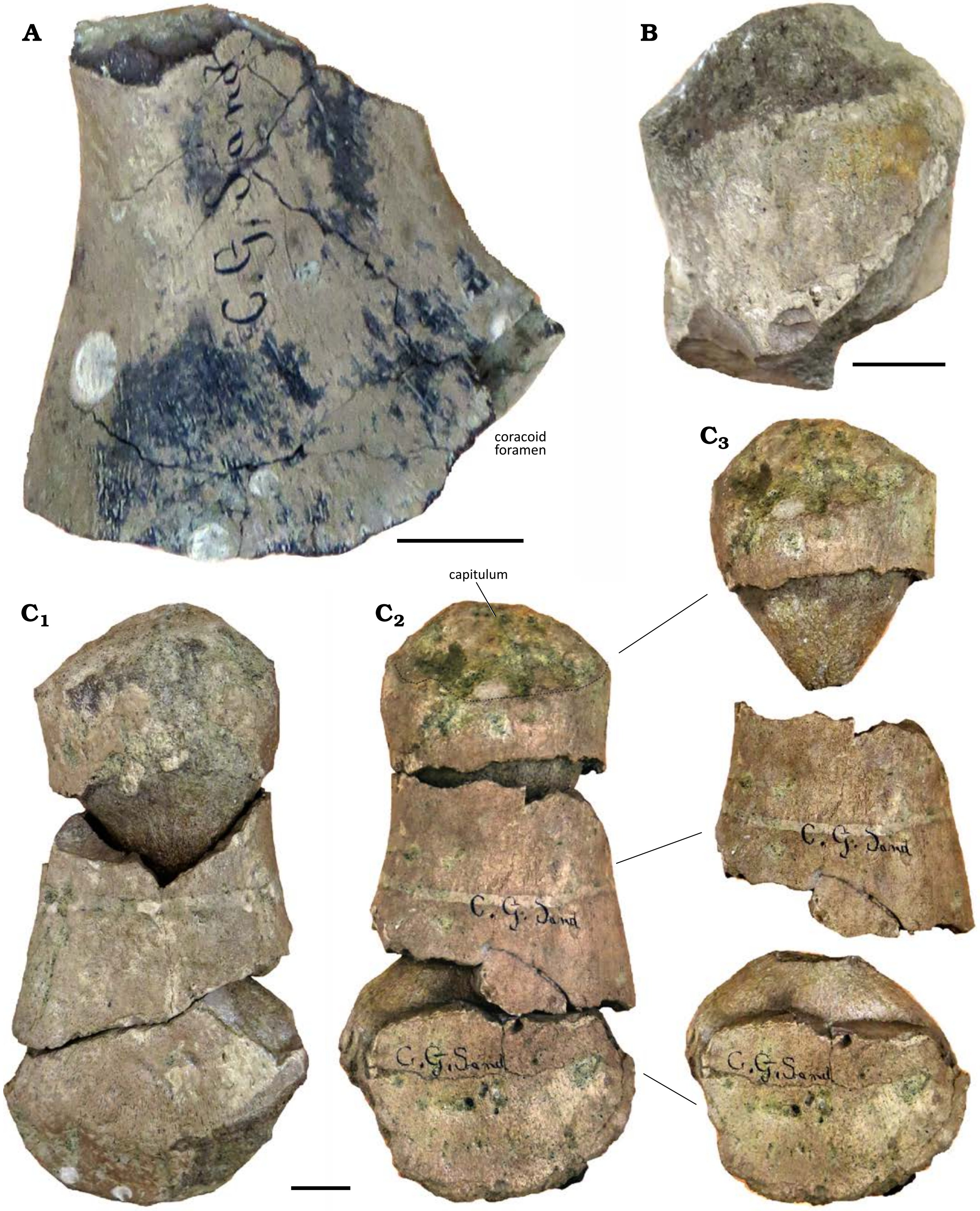


Fig. 9. CAMSM X50356 (Elasmosauridae indet.) from Fen Ditton, near Cambridge, UK, upper Albian–lower Cenomanian. **A**. Proximal half of left scapula. **B**. Part of propodium. **C.** Propodium in ventral (C_1) and dorsal (C_2) views; propodium separated in three sectors (C_3), showing the separation between perichondral and endochondral ossification. Scale bars 20 mm.

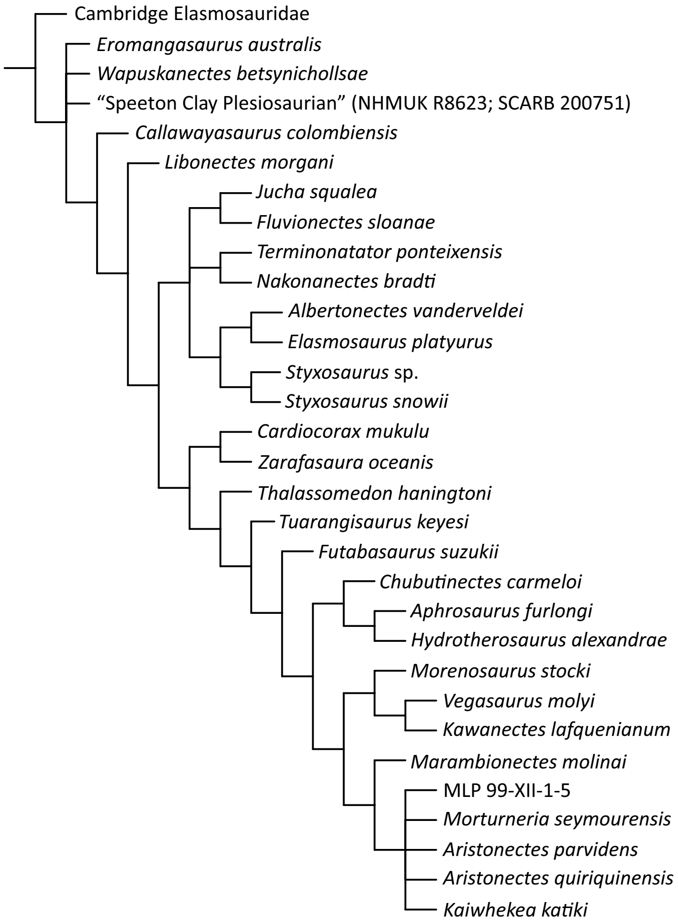


Fig. 10. Reduced consensus tree derived from 20 000 MPTs of length 1942 steps, after pruning *Wapuskanectes betsynicholsae*; *Fluvionectes sloanae*, and *Alexandronectes zealandiensis*. We show relationships within Elasmosauridae only, excluding other groups of plesiosaurs from this diagram. Bremer support below some nodes.

Discussion

The nature of CAMSM X50356.—It is very likely that most of the material accessioned as CAMSM X50356 belongs to a single individual (with the clear exception of the ichthyosaur basioccipital; Fig. 2E). Because no record of the original state of CAMSM X50356 is available the only evidence for this is indirect. However: (i) all elements of CAMSM X50356 described here are stored together, and are listed on the original specimen label, suggesting they represent a single episode of collection or acquisition (Fig. 1E); (ii) all vertebral elements have consistent and gradational morphology, and all elements bear features consistent with placement as an early-diverging elasmosaurid; (iii) all elements are consistent in size (Fig. 3); (iv) the vertebral sequence shows no anomalies in relative size; (v) all material belongs to an osteologically immature specimen, including vertebrae and propodials; (vi) there are no duplicated elements; and (vii) the preservation is consistent among all elements, showing abrasion and oyster encrustations. The only element that clearly does not belong to a plesiosaur is the basioccipital bone, listed on the original label (Fig. 1E) but more consisntent with the one of platypterygiine ichthyosaur (see above, Fischer et al. 2012).

Although most other vertebrate fossils from the Cambridge Greensand are isolated elements, associated remains were also found. For example, Seeley (1879: 592) reported seeing associated remains of plesiosaur and ichthyosaurs: "Then, in the cases of some Plesiosaurs and Ichthyosaurs, I have been present at the workings when associated portions of skeletons have been found, so that I can state from my own knowledge that naturally associated portions of single animals are met with; and often we have had to wait for months for the neck of an animal of which the body has been found, until the overlying rock was removed so that the bones could be collected".

Therefore CAMSM X50356 is considered part of a single specimen. It is currently not clear how complete the vertebral sequence is, but the gradational nature of our measurements suggests that there are not large series of missing elements (Fig. 3A).

Phylogenetic analysis and comparison.—Our phylogenetic analysis recovered CAMSM X50356 in Elasmosauridae (sensu Benson and Druckenmiller 2014). Therefore detailed comparisons are made with members of this clade. The phylogeny of elasmosaurids have much attention recently (Vincent et al. 2011; O'Gorman et al. 2015; Serratos et al. 2017; Sachs et al. 2018; O'Gorman 2019; Fischer et al. 2021). The general results, the monophyly of Elasmosauridae and the recovering of Aristonectinae after removing the wild card taxa are shared by previous studies (O'Gorman et al. 2015; Serratos et al. 2017; O'Gorman 2019; Sachs et al. 2021).

The record of Albian–Cenomanian elasmosaurids is quite scarce and usually comprises isolated vertebrae (Bardet et al. 2016; Latil et al. 2021). However, a partially preserved elasmosaurids was collected from the Albian of the Marnes Bleues Formation, France. The specimen differs from CAMSM X50356 in having lateral keel and dorsal projections on dorsal surface of neural spines (Vincent et al. 2020).

First, CAMSM X50356 differs from the all the post Cenomanian elasmosaurids with the exception of *Zarafasaura oceanis* Vincent et al., 2011, and *Traskasaura sandrae* O'Keefe et al., 2025 (O'Gorman 2019) by lacking the ventral notch on articular surfaces of the cervical centra (Welles 1943, 1962; Cruickshank and Fordyce 2002; Sato 2003; Sato et al. 2006; O'Gorman et al. 2015; O'Gorman 2016a, b, 2019; Sachs and Kear 2017; Serratos et al. 2017; Otero et al. 2014). Additionally, CAMSM X50356 differs from the basal elasmosaurids such as the "Speeton Clay Plesiosaurian" from the Hauterivian of England, *Jucha squalea* Fischer et al., 2021, *Eromangasaurus australis* (Sachs, 2005b) Kear, 2007, and *Callawayasaurus colombiensis* Welles, 1962, by lacking the lateral keel on cervical centra (Welles 1962; Kear 2007; Benson and Druckenmiller 2014; Fischer et al. 2021). The lack of lateral keels on CAMSM X50356 is interpreted here as not related to the immature condition, as other immature elasmosaurids show well developed lateral keels (O'Gorman et al. 2018).

The cervical centra of CAMSM X50356 are relatively short compared to many elasmosaurids (Sato 2003; Sachs, 2005a; O'Keefe and Hiller 2006) , being only slightly longer than high, as long as high, or higher than long, depending on the location of the cervical region (Fig. 3). However the cervical centra of CAMSM X50356 are not markedly short along the neck as in *Zarafasaura oceanis*, the elasmosaurinae *Nakonanectes bradti* Serratos et al., 2017, and aristonectines (Lomax and Wahl 2013; Serratos et al. 2017; Otero et al. 2018; O'Gorman 2019). Additionally, because the specimen is not mature it is probable that the cervicals would have undergone at least a slight additional elongation during life. Therefore, it could be supposed that some cervicals of this specimen should become slightly more elongated in its adult form.

The minimum number of dorsal vertebrae of CAMSM X50356 is twenty, a dorsal vertebral count lower than those of *Callawayasaurus colombiensis* (23 dorsal vertebrae) and *Zarafasaura oceanis* (26 dorsal vertebrae). However, it is likely that there are some missing elements in CAMSM X50356, so the original number is not known but it was possibly more than 20. This is greater than the dorsal vertebral counts recorded for *Kawanectes lafquenianum* (Gasparini & Goñi, 1985) O'Gorman, 2016a (15 dorsal vertebrae), *Morenosaurus stocki* Welles, 1943 (17 dorsal vertebrae), *Vegasaurus molyi* O'Gorman et al., 2015 (17 dorsal vertebrae), and *Albertonectes vanderveldei* Kubo et al., 2012 (16 dorsal vertebrae) (Welles 1943; Kubo et al. 2012; O'Gorman et al. 2015; O'Gorman 2016a).

CAMSM X50356 shows 5 sacral centra differing from *Zarafasaura oceanis*, which has three sacral centra (Lomax and Wahl 2013) and more similar to the sacral vertebral count of the elasmosaurines *Elasmosaurus platyurus* Cope, 1869 (4); *Terminonatator ponteixensis* Sato, 2003 (4/+4); *Albertonectes vanderveldei* (5) and 5 sacral vertebrae in *Fluvionectes sloanae* Campbell et al., 2021 (Sato 2003; Sachs 2005a; Kubo et al. 2012; Campbell et al. 2021)

The caudal vertebrae of CAMSM X50356 bear a single ventral foramen, similar to many leptocleidians, and some elasmosaurids including *Hydrotherosaurus alexandrae* Welles, 1943, *Elasmosaurus platyurus*, *Kawanectes lafquenianum*, and *Vegasaurus molyi* (Welles 1943; O'Gorman et al. 2015; O'Gorman 2016a). This differs from the paired or multiple foramina present in many other plesiosaurians, including elasmosaurids such as *Aristonectes* spp. (Otero et al. 2018). Additionally it lacks a laterally projected parapophysis present in *Kawanectes lafquenianum* and *Nakonanectes bradti* (O'Gorman 2016a, b; Serratos et al. 2017; Otero et al. 2018).

Finally, CAMSM X50356 shows a glenoid facet of the scapula as long as the coracoid facet in dorsal view (Fig 9A), which differs from *Wapuskanectes betsynichollsae* Druckenmiller & Russell, 2006, in which the glenoid facet is shorter than the coracoid facet (Druckenmiller and Russell 2006: fig. 4).

Nomenclatural background.—Previously, material of the Cambridge Greensand with features similar to CAMSM X50356 has been referred to as "*Plesiosaurus planus*" (Owen, 1864), "*Plesiosaurus euryspondilus*" (Seeley, 1869), and "*Stereosaurus platyomus*" (Seeley, 1869), however, both are currently considered to be nomina dubia (Welles 1962). For details of collections numbers see of all the specimens mentioned see Seeley (1869).

It is interesting that Seeley (1869: xv), stated: "These names are only intended for the convenience of students using the Museum, and not necessarily to take rank as names of described species". So, it is not clear if this were intended to be erected as formal species names.

Particularly interesting is that "*Stereosaurus platyomus*" is characterized by Seeley as having propodials without the trochanter developed (Seeley 1869); a feature that is now known to be usually present in juvenile specimens and that can be modified through ontogeny. (Brown 1981; Otero et al. 2014). We examined specimens at CAMSM that were historically labelled under these two names, specifically those stored at the holotype collection: CAMSM B56749, B56751, B56754, B56762, "*Plesiosaurus planus*" (Owen, 1864); CAMSM B56768–83, "*Plesiosaurus euryspondilus*" (Seeley, 1869); and CAMSM B57027–32, B57033–37, B27038–41, B57042–44, "*Stereosaurus platyomus*" (Seeley, 1869).

The morphology of these specimens is consistent with the general morphology of CAMSM X50356, including cervical vertebrae with centra as long as high or slightly longer, with flat ventral surfaces and absence of both the lateral ridge and ventral notch. However, we do not consider these specimens or CAMSM X50356 to have diagnostic features at the species level. Hence, the early-diverging elasmosaurid species represented by CAMSM X50356 and other specimens remains unnamed here.

Phylogeny and cervical features.—CAMSM X50356 is recovered as the basalmost elasmosaurid by our phylogenetic analysis. This position indicates that elongated cervical centra with absence of lateral ridge are the basal condition of elasmosaurids, consistent with the widespread occurrence of those states in other plesiosaurian groups. Previously the lateral ridge has been recorded in almost all other elasmosaurids (Sato 2003; Hiller et al. 2017; Serratos et al. 2017; O'Gorman 2019; Fischer et al. 2021) with the exception of taxa that have secondarily shortened the cervical centra such as *Aristonectes parvidens* Cabrera, 1941, *Wunyelfia maulensis* Otero & Soto Acuña, 2021, and *Nakonanectes bradti* Serratos et al., 2017 (O'Gorman 2016; Serratos et al. 2017; Otero and Soto-Acuña 2021). Therefore the lack of correlation between cervical elongation (present in CAMSM X50356) and the lateral ridge (absent in CAMSM X50356) is thus recorded here for the first time as CAMSM X50356 is the only elasmosaurid with cervical central longer than high but without lateral ridges, and its recovered phylogenetic position indicates this is the basal condition among elasmosaurids.

Acknowledgements

The authors thank to the curator Matt Riley (Sedgwick Museum, Cambridge, UK) for allowing the study of the specimens under their care. The authors thank Peggy Vincent (Muséum National d'Histoire Naturelle) and Lene Delsett (Natural history museum, University of Oslo). This contribution was supported by PICT (Proyecto de Investigación Científica y Tecnológica) 2015-0678 and PICT-2018-02443.

Editor: Daniel Barta

References

Araújo, R., Polcyn, M.J., Lindgren, J., Jacobs, L.L., Schulp, A.S., Mateus, O., Olimpio Gonçalves, A., and Morais, M.-L. 2015. New aristonectine elasmosaurid plesiosaur specimens from the Early Maastrichtian of Angola and comments on paedomorphism in plesiosaurs. *Netherlands Journal of Geosciences* 94: 1: 93–108.

Bardet, N. 1994. Extinction events among Mesozoic marine reptiles. *Historical Biology* 7: 313–324.

Bardet, N., Fischer, V., and Machalski, M. 2016. Large predatory marine reptiles from the Albian–Cenomanian of Annopol, Poland. *Geological Magazine* 153: 1–16.

Barrett, P.M. and Bonsor, J.A. 2021. A revision of the non-avian dinosaurs '*Eucercosaurus tanyspondylus*' and '*Syngonosaurus macrocercus*' from the Cambridge Greensand, UK. *Cretaceous Research* 118: 104638.

Benson, R.B.J. and Druckenmiller, P.S. 2014. Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. *Biological Reviews* 89: 1–23.

Benson, R.B.J., Evans, M., and Druckenmiller, P.S. 2012. High diversity, low disparity and small body size in plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic boundary. *PLoS ONE* 7 (3): e31838.

Benson, R.B.J., Evans, M., Smith, A.S., Sassoon, J., Moore-Faye, S., Ketchum, H.F., and Forrest, R. 2013. A giant pliosaurid skull from the Late Jurassic of England. *PLOS ONE* 8: e65989.

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 British Museum of Natural History (Geology)* 35: 253–347.

Cabrera, A. 1941. Un plesiosaurio nuevo del Cretaceo del Chubut. *Revista del Museode La Plata* 2: 113–130.

Campbell, J.A., Mitchell, M.T., Ryan, M.J., and Anderson, J.S. 2021. A new elasmosaurid (Sauropterygia: Plesiosauria) from the non-marine to paralic Dinosaur Park Formation of southern Alberta, Canada. *PeerJ* 9: e10720.

Codrington, T. 1908. Note on the fossil remains of a Plesiosaurus from Savernake. *Magazine of the Wiltshire Archaeological and Natural History Society* 35: 114–114.

Codrington T. 1864. Geology of the Berks and Hants extension, any Marlborough railtops. *Magazine of the Wiltshire Archaeological and Natural History Society* 9: 167–193.

Cope, E.D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society (new series)* 14: 1–252.

Cruickshank, A.R.I. and Fordyce, R.E. 2002. A new marine reptile (Sauropterygia) from New Zealand: further evidence for a Late Cretaceous Austral radiations of cryptoclidid plesiosaur. *Palaeontology* 45: 557–575.

de Blainville, H.D. 1835. Description de quelques espèces de reptiles de la Californie, precédée de l'analyse d'un système général d'herpetologie et d'amphibiologie. *Nouvelles Archives du Museumd'Histoire Naturelle* 4: 233–296.

Druckenmiller, P.S. and Russell, A.P. 2006. A new elasmosaurid plesiosaur (Reptilia: Sauropterygia) from the Lower Cretaceous Clearwater Formation, northeastern Alberta, Canada. *Paludicola* 5: 184–199.

Evers, S.W., Barrett, P.M., and Benson, R.B.J. 2019. Anatomy of *Rhinochelys pulchriceps* (Protostegidae) and marine adaptation during the early evolution of chelonioids. *PeerJ* 7: e6811.

Fischer, V., Bardet, N., Guiomar, M., and Godefroit, P. 2014. High diversity in Cretaceous ichthyosaurs from Europe prior to their extinction. *PLOS ONE* 9: e84709.

Fischer, V., Benson, R.B.J., Druckenmiller, P.S., Ketchum, H.F., and Bardet, N. 2018. The evolutionary history of polycotylid plesiosaurians. Royal Society Open Science 5 (3): 172177.

Fischer, V., Maisch, M.W., Naish, D., Liston, J., Kosma, R., Joger, U., Krüger, F.J., Pardo-Pérez, J., Tainsh, J., and Appleby, R.M. 2012. New ophthalmosaurids from the Early Cretaceous of Europe demonstrate extensive ichthyosaur survival across the Jurassic–Cretaceous boundary. *PLOS ONE* 7: e29234.

Fischer, V., Zverkov, N. G., Arkhangelsky, M.S., Stenshin, I.M., Blagovetshensky, I.V., and Uspensky, G.N. 2021. A new elasmosaurid plesiosaurian from the Early Cretaceous of Russia marks an early attempt at neck elongation. *Zoological Journal of the Linnean Society* 192: 1167–1194.

Gasparini, Z. and Goñi, R. 1985. Los plesiosaurios cretácicos de América del Sur y del continente antártico. *Congresso Brasileirode Paleontología* 8: 55–63.

Gasparini, Z., Martin, J.E., and Fernandez, M. 2003. The elasmosaurid plesiosaur Aristonectes Cabrera from the Latest Cretaceous of South America and Antarctica. *Journal of Vertebrate Paleontology* 23: 104–115.

Gallois, R., Morter, A.A., and Owen, H.G. 2016. The stratigraphy of the Gault Formation (Early Cretaceous, Albian) in East Anglia and south-east England. *Proceedings of the Geologists' Association* 127: 606–628.

Goloboff, P.A. and Catalano, S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221–238.

Grove, R. 1976. *The Cambridgeshire Coprolite Mining Rush*. 51 pp. Oleander Press, Cambridge.

Gutarra, S., Stubbs, T.L., Moon, B.C., Palmer, C., and Benton, M.J. 2022. Large size in aquatic tetrapods compensates for high drag caused by extreme body proportions. *Communications Biology* 5: 380.

Hart, M.R. 1973. Foraminiferal inference for the age of the Cambridge Greensand. *Proceedings of the Geologists' Association* 84: 65–82.

Hart, M.B. and Lyndsey, R.F. 2020. Micropalaeontology and stratigraphical setting of the Cambridge Greensand. *Geological Society, London, Special Publications* 498: 147–163.

Hiller, N., O'Gorman, J.P., Otero, R.A., and Mannering, A.A. 2017. A reappraisal of the Late Cretaceous Weddellian plesiosaur genus *Mauisaurus* Hector, 1874. *New Zealand Journal of Geology and Geophysics* 60 (2): 112–128.

Joyce, W.G. 2025. A review of helochelydrid shell material from late Albian to early Cenomanian greensands of Southern England, United Kingdom. *The Anatomical Record* 308: 1633–1645.

Kear, B.P. 2007. Taxonomic clarification of the Australian elasmosaurid *Eromangasaurus*, with reference to other austral elasmosaur taxa. *Journal of Vertebrate Paleontology* 27: 241–246.

Ketchum, H.F. and 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.

Kubo, T., Mitchell, M.T., and Henderson, D.M. 2012. *Albertonectes vanderveldei,* a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. *Journal of Vertebrate Paleontology* 32: 557–572.

Latil, J.L., Jaillard, E., Bardet, N., Raisossadat, N., and Vincent, P. 2021. The Albian–Cenomanian transition in a shelf-basin transect: Biostratigraphy, sedimentology and paleontology of Jebel Mghila, Central Tunisia. *Cretaceous Research* 124: 104809.

Lomax, D.R. and Wahl, W.R. 2013. A new specimen of the elasmosaurid plesiosaur *Zarafasaura oceanis* from the Upper Cretaceous (Maastrichtian) of Morocco. *Paludicola* 9: 97–109.

Machalski, M. 2018. The Cenomanian ammonite *Schloenbachia varians* (J. Sowerby, 1817) from the Cambridge Greensand of eastern England: Possible sedimentological and taphonomic implications. *Cretaceous Research* 87: 120–125.

Maddison W.P. and Maddison D.R. 2011. *Mesquite: A Modular System for Evolutionary Analysis. Version 2.75* [available from: http://mesquiteproject.org, last accessed December 1, 2023].

Madzia, D. and Cau, A. 2020. Estimating the evolutionary rates in mosasauroids and plesiosaurs: discussion of niche occupation in Late Cretaceous seas. *PeerJ* 8: e8941.

McGowan, C. 1972. The systematics of Cretaceous ichthyosaurs with particular reference to the material from North America. *Rocky Mountain Geology* 11: 9–29.

O'Gorman, J.P. 2016a. A small body sized Non-Aristonectine Elasmosaurid (Sauropterygia, Plesiosauria) from the late Cretaceous of Patagonia with comments on the relationships of the Patagonian and Antarctic Elasmosaurids. *Ameghiniana* 53: 245–268.

O'Gorman, J.P. 2016b. New insights on the *Aristonectes parvidens* (Plesiosauria, Elasmosauridae) holotype: news on an old specimen. *Ameghiniana* 53: 397–417.

O'Gorman, J.P. 2019. Elasmosaurid phylogeny and paleobiogeography, with a reappraisal of *Aphrosaurus furlongi* from the Maastrichtian of the Moreno Formation. *Journal of Vertebrate Paleontology* 39: e1692025.

O'Gorman, J.P. 2021. The most complete specimen of *Kawanectes lafquenianum* (Sauropterygia, Plesiosauria): New data on basicranial anatomy and possible sexual dimorphism in elasmosaurids. *Cretaceous Research* 125: 104836.

O'Gorman, J.P., Carignano, A.P., Calvo-Marcilese, L., and Panera, J.P.P. 2023. A new elasmosaurid (Sauropterygia, Plesiosauria) from the upper levels of the La Colonia Formation (upper Maastrichtian), Chubut Province, Argentina. *Cretaceous Research* 152: 105674.

O'Gorman, J.P., Coria, R.A., Reguero, M., Santillana, S., Mörs, T., and Cárdenas, M. 2018. The first non-aristonectine elasmosaurid (Sauropterygia; Plesiosauria) cranial material from Antarctica: New data on the evolution of the elasmosaurid basicranium and palate. *Cretaceous Research* 89: 248–263.

O'Gorman, J.P., Gasparini, Z., and Salgado, L. 2014. Reappraisal of *Tuarangisaurus*? *cabazai* (Elasmosauridae, Plesiosauria) from the upper Maastrichtian of northern Patagonia, Argentina. *Cretaceous Research* 47: 39–47.

O'Gorman, J.P., Salgado, L., Olivero, E.B., and Marenssi, S.A. 2015. *Vegasaurus molyi*, gen. et sp. nov. (Plesiosauria, Elasmosauridae), from the Cape Lamb Member (lower Maastrichtian) of the Snow Hill Island Formation, Vega Island, Antarctica, and remarks on Wedellian Elasmosauridae. *Journal of Vertebrate Paleontology* 35: e931285.

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. and Hiller, N. 2006. Morphologic and ontogenetic patterns in elasmosaur neck length, with comments on the taxonomic utility of neck length variables. *Paludicola* 5: 206–229.

O'Keefe, F.R., Armour Smith, E., Clark, R.O., Otero, R.A., Perella, A., and Trask, P. 2025. A name for the Provincial Fossil of British Columbia: a strange new elasmosaur taxon from the Santonian of Vancouver Island. *Journal of Systematic Palaeontology* 23: 2489938.

Otero, R.A. and Soto-Acuña, S. 2021. *Wunyelfia maulensis* gen. et sp. nov., a new basal aristonectine (Plesiosauria, Elasmosauridae) from the Upper Cretaceous of central Chile. *Cretaceous Research* 118: 104651.

Otero, R.A., Soto-Acuña, S., and O'Keefe, F.R. 2018. Osteology of *Aristonectes quiriquinensis* (Elasmosauridae, Aristonectinae) from the upper Maastrichtian of central Chile. *Journal of Vertebrate Paleontology* 38: e1408638.

Otero, R.A., Soto-Acuña, S., O'Keefe, F.R., O'Gorman, J.P., Stinnesbeck, W., Suárez, M.E., Rubilar-Rogers, D., Salazar, C., and Quinzio-Sinn, L.A. 2014. *Aristonectes quiriquinensis*, sp. nov., a new highly derived elasmosaurid from the upper Maastrichtian of central Chile. *Journal of Vertebrate Paleontology* 34: 100–125.

Owen, R. 1860. On the orders of fossil and recent Reptilia, and their distribution in time. *Reports of the British Association for the Advancement of Science* 29: 153–166.

Owen, R. 1864. *A Monograph on the Fossil Reptilia of the Cretaceous Formations, Supplement No. IV Sauropterygia (*Plesiosaurus*)*. 18 pp. Palaeontographical Society, London.

Polcyn, M.J., Jacobs L.L., Araújo, R., Schulp, A.S., and Mateus, O. 2014. Physical drivers of mosasaur evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 400: 17–27.

Reed, F.R.C. 1897. *A Handbook to the Geology of Cambridgeshire*. x+276 pp. Cambridge University Press, Cambridge.

Sachs, S. 2005a. Redescription of *Elasmosaurus platyurus* Cope 1868 (Plesiosauria: Elasmosauridae) from the Upper Cretaceous (lower Campanian) of Kansas, USA. *Paludicola* 5: 92–106.

Sachs, S. 2005b. *Tuarangisaurus australis* sp. nov. (Plesiosauria: Elasmosauridae) from the Lower Cretaceous of northeastern Queensland, with additional notes on the phylogeny of the Elasmosauridae. *Memoirs of the Queensland Museum* 50: 425–440.

Sachs, S. and Kear, B.P. 2017. Redescription of the elasmosaurid plesiosaurian *Libonectes atlasense* from the Upper Cretaceous of Morocco. *Cretaceous Research* 74: 205–222.

Sachs, S., Lindgren, J., and Kear, B.P. 2018. Reassessment of the *Styxosaurus snowii* (Williston, 1890) holotype specimen and its implications for elasmosaurid plesiosaurian interrelationships. *Alcheringa* 42: 560–574.

Sachs, S., Lindgren, J., Madzia, D., and Kear, B.P. 2021. Cranial osteology of the mid-Cretaceous elasmosaurid *Thalassomedon haningtoni* from the Western Interior Seaway of North America. *Cretaceous Research* 123: 104769.

Sachs, S., Madzia, D., Thuy, B., and Kear, B.P. 2023. The rise of macropredatory pliosaurids near the Early–Middle Jurassic transition. *Scientific Reports* 13: 17558.

Sato, T. 2003. *Terminonatator ponteixensis*, a new elasmosaur (Reptilia; Sauropterygia) from the Upper Cretaceous of Saskatchewan. *Journal of Vertebrate Paleontology* 23: 89–103.

Sato, T., Hasegawa, Y., and Manakoto, M. 2006. A new elasmosaurid plesiosaur from the Upper Cretaceous of Fukushima. Japan. *Paleontology* 49: 467–484.

Sedgwick, A. 1846. On the geology of the neighbourhood of Cambridge. including the formations between the Chalk escarpment and the Great Bedford Ievel. *Transactions of the British Association for the Advancement of Science* 1845: 40–47.

Seeley, H.G. 1866. The rock of the Cambridge Greensand. *Geolopical Magazine* 3: 302–307.

Seeley, H.G. 1869. *Index of the Fossil Remains of Aves, Ornithosauria and Reptilia, from the Secondary System of Strata Aranged in the Woodward Museum of the University of Cambridge*. xxiii + 143 pp. Deighton, Bell, and Co. Press, Cambridge.

Seeley, H.G. 1879. On the Dinosauria of the Cambridge Greensand. *Quarterly Journal of the Geological Society of London* 35: 591–635.

Seilacher, A. 1970. Begriff und Bedeutung der Fossil-Lagerstatten. *Neues Jahrbuch fur Geologie und Palontologie Monatshefte* 1970: 34–39.

Serratos, D.J., Druckenmiller, P., and Benson, R.B.J. 2017. A new elasmosaurid (Sauropterygia, Plesiosauria) from the Bearpaw Shale (Late Cretaceous, Maastrichtian) of Montana demonstrates multiple evolutionary reductions of neck length within Elasmosauridae. *Journal of Vertebrate Paleontology* 37: e1278608.

Soul, L.C. and Benson, R.B.J. 2017. Developmental mechanisms of macroevolutionary change in the tetrapod axis: a case study of Sauropterygia. *Evolution* 71: 1164–1177.

Unwin, D.M. 2001. An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of Eastern England. *Fossil Record* 4: 189–221.

Vincent, P., Bardet, N., Suberbiola, X.P., Bouya, B., Amaghzaz, M., and

Meslouh, S. 2011. *Zarafasaura oceanis*, a new elasmosaurid (Reptilia: Sauropterygia) from the Maastrichtian phosphates of Morocco and the palaeobiogeography of latest Cretaceous plesiosaurs. *Gondwana Research* 9: 1062–1073.

Vincent, P., Grosjean, A.S., Bert, D., Ferreira, J., Suchéras-Marx, B., Suan, G., Guinot, G., Perrier, V., Janneau, K., Brazier, J.M., and Sarroca, E. 2020. Paleoenvironmental context and significance of a partial elasmosaurid skeleton from the Albian of Haute-Provence, France. *Cretaceous Research* 108: 104293.

Welles, S.P. 1943. Elasmosaurid plesiosaurs with description of newmaterial from California and Colorado. *Memoirs of the University of California* 13: 125–254.

Welles, S.P. 1952. A review of the North American Cretaceous elasmosaurs. *University of California Publications in Geological Sciences* 29: 46–144.

Welles, S.P. 1962. A new species of elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. *University of California Publications in the Geological Sciences* 44: 1–96.

Wintrich, T., Hayashi, S., Houssaye, A., Nakajima, Y., and Sander, P.M. 2017. A Triassic plesiosaurian skeleton and bone histology inform on evolution of a unique body plan. *Science Advances* 3: e1701144.

White, H.J.O. 1932. *The Geology of the Country near Saffron Walden. Memoirs of the Geological Survey England and Wales. Explanation of Sheet 205*. xii+125 pp. Her Majesty's Stationer Office, London.

Worssam B.C. and Taylor, J.H. 1969. *Geology of the Country around Cambridge. Explanation of Sheet 188. Memoirs of the Geological Survey of Great Britain, England and Wales*. 159 pp. Her Majesty's Stationer Office, London.

Zverkov, N.G., Alexander O. Averianov, and Evgeny V.P. 2017. Basicranium of an elasmosaurid plesiosaur from the Campanian of European Russia. *Alcheringa: An Australasian Journal of Palaeontology* 42: 528–542.