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Steneosaurus edwardsi (Thalattosuchia: Teleosauridae), the largest known crocodylomorph of the Middle Jurassic

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Teleosaurids were a clade of marine crocodylomorphs that were globally distributed during the Jurassic Period. They evolved a wide range of body sizes, from small (~2–3 m) to very large (> 9 m). Until now, the largest known Middle Jurassic teleosaurid was '*Steneosaurus*' *obtusidens*, from the Oxford Clay Formation of the UK. Here, we re-examine a very large Oxford Clay specimen (ilium, ischium, and femur) that had been tentatively attributed to '*S.*' *obtusidens*. Based on comparative anatomical study with the '*S.*' *obtusidens* holotype and referred specimens of *Steneosaurus edwardsi* and *Steneosaurus leedsi*, we conclude that this very large individual actually pertains to *S. edwardsi*. Based on comparisons with the *Machimosaurus mosae* neotype (which has a complete femur and skeleton), we estimate a total length in excess of 7 m for this large *S. edwardsi* individual, making it the largest known Middle Jurassic teleosaurid. Therefore, along with the closely related genus *Machimosaurus*, this clade of large-bodied Middle–Late Jurassic teleosaurids were the largest species during the first 100 million years of crocodylomorph evolution. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**, 911–918.

ADDITIONAL KEYWORDS: Callovian – crocodile – England – Oxford Clay Formation – Teleosaurid.

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INTRODUCTION

Teleosauridae, along with Metriorhynchidae, constitute the first radiation of marine crocodylomorphs – Thalattosuchia (Andrews, 1913; Buffetaut, 1982; Vignaud, 1995; Hua & Buffetaut, 1997; Young & Andrade, 2009). Teleosaurids were a clade of semi-aquatic Jurassic crocodylomorphs that frequented coastal, lagoonal, and brackish ecosystems, and are also known from freshwater environments (Buffetaut, 1982; Vignaud, 1995; Hua & Buffetaut, 1997; Young *et al.*, 2014). Teleosaurids are characterized by an elongate tubular rostrum, oval-shaped external nares, dorsally inclined orbits, a transversely expanded premaxilla and anterior dentary, and enlarged supratemporal fenestrae (Andrews, 1909; Andrews, 1913; Adams-Tresman, 1987; Vignaud, 1995; Hua & Buffetaut, 1997; Hua, 1999). Teleosaurids are relatively uncommon in the open-shelf environment of the Oxford Clay Formation of England, although some nearly complete skeletons are known (Andrews, 1913). '*Steneosaurus*' *obtusidens* Andrews, 1909 has been considered to be the largest known Oxford Clay teleosaurid (Andrews, 1913; In press-Young *et al.*, in press). Here, we show that one very large specimen that Andrews tentatively attributed to '*S.*' *obtusidens* (based on its large size) actually pertains to a different taxon.

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The specimen, NHMUK PV R3898, consists of a left femur, ilium, and ischium. All three bones are larger than those of most other teleosaurids (apart from very large *Machimosaurus* specimens), and have a distinct robustness and thickness not commonly seen in teleosaurids (except in large-bodied taxa such as '*S.*' *obtusidens* and *Machimosaurus mosae*; Andrews, 1913; Hua, 1999; Young *et al*., 2014). The muscle attachment surfaces are extremely rugose and well developed. The ilium and ischium articulate with one another and appear to derive from the same individual. We compared NHMUK PV R3898 with other teleosaurid specimens, in particular with the holotype of '*S.*' *obtusidens* (NHMUK PV R3168) and nearly complete referred specimens of *Steneosaurus edwardsi* Eudes-Deslongchamps, 1868a (NHMUK PV R3701) and *Steneosaurus leedsi* Andrews, 1909 (NHMUK PV R3806).

ABBREVIATIONS

Institutional

MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, UK; PETMG, Peterborough Museum and Art Gallery, Peterborough, UK.

Anatomical

A, acetabulum; ac in, acetabular incision; ant il art s, anterior iliac articulation surface; ant pr, anterior process of ilium; fem h, femoral head; isch bl, ischial blade; path, area of pathology (marks); post il art s, posterior iliac articulation surface; s, sacral attachment area; s1, first sacral rib attachment point; s2, second sacral rib attachment point; supraac cr, supraacetabular crest; tro, fourth trochanter.

SYSTEMATIC PALAEONTOLOGY

Crocodylomorpha Hay, 1930

Thalattosuchia Fraas, 1901

Teleosauridae Geoffroy Saint-Hilaire, 1831

Steneosaurus Geoffroy Saint-Hilaire, 1825

Steneosaurus edwardsi Eudes-Deslongchamps, 1868 (Figs 1–3)

Holotype

MNHN.F RJN 118, incomplete skull.

Type locality and horizon

Falaises des Vaches Noires, Département du Calvados, Basse-Normandie, France. Either from the

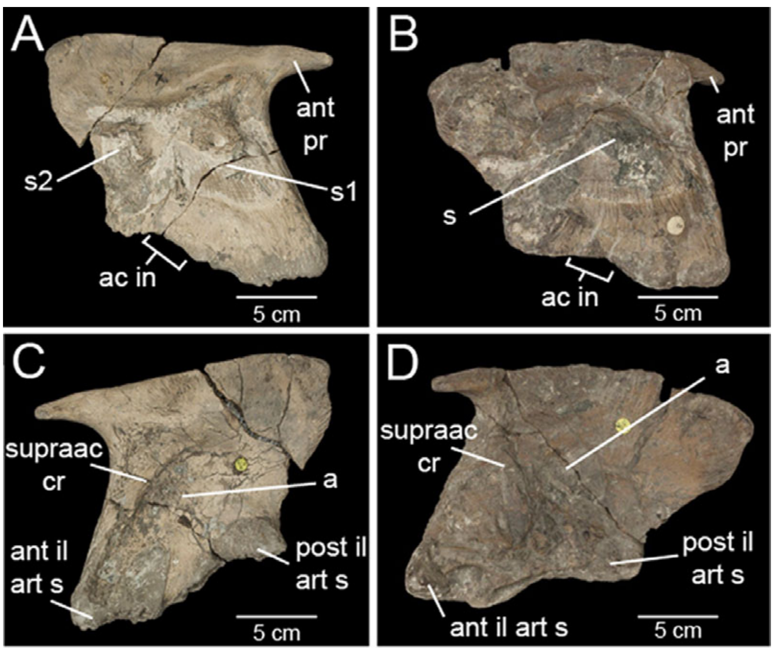

Figure 1. Ilium of NHMUK PV R3898 (referred to as *Steneosaurus edwardsi*) in medial (A) and lateral (C) views. Ilium of NHMUK PV R3168 (holotype of *'Steneosaurus' obtusidens*) in medial (B) and lateral (D) views.

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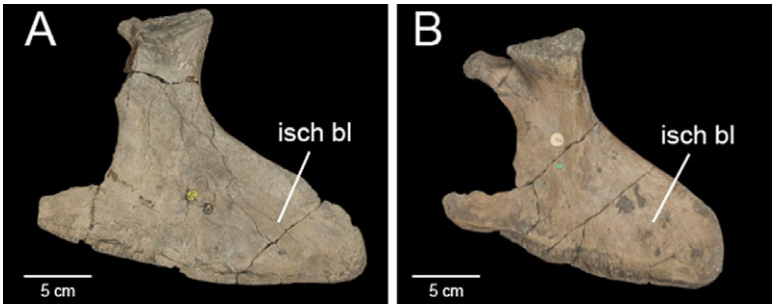

Figure 2. Ischium of NHMUK PV R3898 (referred to as *Steneosaurus edwardsi*) (A) and of NHMUK PV R3168 (holotype of '*Steneosaurus*' obtusidens) (B) in lateral view.

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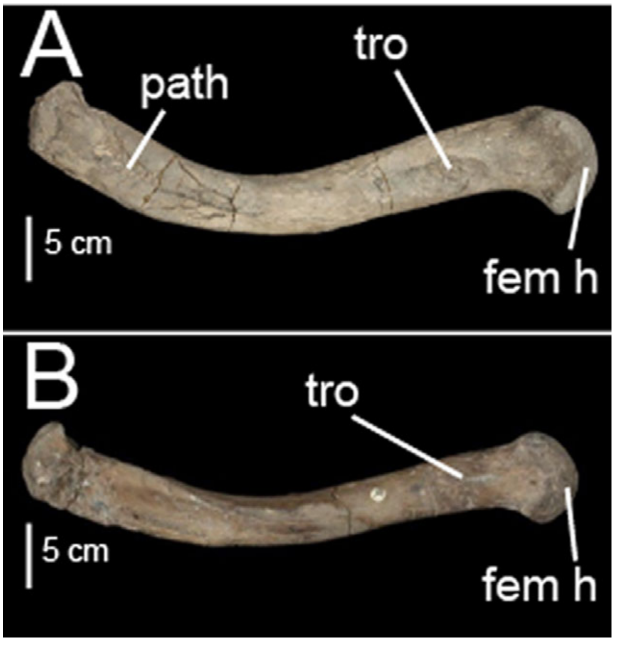

Figure 3. Femur of NHMUK PV R3898 (referred to as *Steneosaurus edwardsi*) (A) and of NHMUK PV R3168 (holotype of '*Steneosaurus' obtusidens*) (B) in medial view.

Marnes de Dives Formation or the Marnes de Villers Formation. Late Callovian or lowermost Oxfordian.

Discussed material
NHMUK PV R3898, left ilium, ischium, and femur.

Discussed material locality and horizon
Peterborough, UK. Peterborough Member, Oxford Clay Formation, Ancholme Group. Middle Callovian.

Taxonomic note
Adams-Tresman (1987) made *Steneosaurus durobrivensis* the senior subjective synonym of all 'short'-snouted teleosaurids (*Steneosaurus hulkei*, '*S.*' *obtusidens*, and *Steneosaurus depressus*) from the Oxford Clay Formation based principally on linear measurement morphometrics. This was because *S. durobrivensis* was the oldest available name of those four taxa; however, more recent papers have refuted the synonymy of '*S.*' *obtusidens* with *S. durobrivensis* based on comparative morphological studies and phylogenetic analyses (e.g. Vignaud, 1995; Martin & Vincent, 2013; Young *et al*., 2014, In pressin press). The '*S.*' *obtusidens* holotype is currently being redescribed, which will clarify its anatomy and evolutionary relationships. However, one paper (Pierce, Angielczyk & Rayfield, 2009) posited an unusual synonymy, in which the Oxford Clay species *S. durobrivensis*, *S. hulkei*, and '*S.*' *obtusidens* were referred to the Late Jurassic taxon *Machimosaurus hugii*. The resulting species diagnosis that is largely undiagnostic and has characteristics not found in all specimens, the approximate 15-million-year-long geological range, and exceptional morphological diversity within this 'species' have all been robustly criticized (Martin & Vincent, 2013; Young *et al*., 2014).

Curiously, Adams-Tresman (1987) also stated that the type specimen of *S. edwardsi* (from Callovian-Oxfordian deposits of Normandy, France) had been destroyed during the Second World War and thus could not be compared with the Oxford Clay specimens. She noted that as *S. edwardsi* had been named over 50 years before *S. durobrivensis*, it would be the senior subjective synonym of the 'short'-snouted teleosaurids. However, the *S. edwardsi* holotype was not destroyed during the Battle of Caen in 1944, as the specimen was housed in the Muséum national d'Histoire naturelle, Paris (MNHN). After comparing the *S. edwardsi* holotype with the Oxford Clay specimens, Vignaud (1995) proposed that *S. edwardsi* was the senior subjective synonym of the 'short'-snouted teleosaurids *S. durobrivensis* and *S. hulkei*. Vignaud (1995) considered '*S.*' *obtusidens* to be a distinct taxon and *S. depressus* to be a junior subjective synonym of *Steneosaurus heberti*. Based on our own examinations

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of the specimens, we agree with the taxonomy set out by Vignaud (1995), and we use the binomial *S. edwardsi* for the 'short'-snouted Oxford Clay teleosaurids.

Correct nominal authority of S. edwardsi

The correct nominal authority for *S. edwardsi* is Eudes-Deslongchamps, 1868. This is the first paper in which the species was described and diagnosed. The older paper referring to *Teleosaurus edwardsi* (Eudes-Deslongchamps, 1867) is a *nomen nudum* under Article 12 of the ICZN Code, but importantly it does not qualify under Article 8 of the ICZN Code. In mentioning a partial mandible, Eudes-Deslongchamps (1867) made the following statement: 'Il appartient à une espèce nouvelle, que je décrirai prochainement dans mon *Prodrome* sous le nom de *Tel. Edwardsi*'('It belongs to a new species, which will be described shortly in my prodrome as *Tel. edwardsi*'); thus, he clearly did not consider the name to have been formally described.

Note that the text of Eudes-Deslongchamps (1867) and Eudes-Deslongchamps (1868b) are exceptionally similar, with the sentence on '*Tel. Edwardsi*' being identical. The confusion comes from there being two different authors for these papers: Jacques-Armand Eudes-Deslongchamps and his son, Eugène Eudes-Deslongchamps. The paper Eudes-Deslongchamps (1868b) was written by Jacques-Armand and it was published in the first volume of the second series of Bulletin de la Société Linnéenne de Normandie along with the other papers presented at the 1866 meetings of the Société linnéenne de Normandie. However, the papers Eudes-Deslongchamps (1867, 1868a) were published by Eugène, after the death of his father, Jacques-Armand, in January 1867. Eudes-Deslongchamps (1867) was published separately by le Blanc-Hardel; therefore, it circulated before the similar text (i.e. Eudes-Deslongchamps, 1868b), which was published in Bulletin de la Société Linnéenne de Normandie.

The paper Eudes-Deslongchamps (1868a), published by Eugène, described *Teleosaurus cadomensis* and the various *Teleosaurus* species that his father coined, but within the subgenus *Steneosaurus*. This text appears in the widely cited book 'Notes paléontologiques' (Eugène Eudes-Deslongchamps, 1863–1869), which is an updated volume including previously published work together in one book.

Eudes-Deslongchamps (1868a) established the species as: 'STENEOSAURUS EDWARDSI (*Eud. Desl.*), 1866'; thus, he considered it to have already been named (as noted above, *Steneosaurus* was treated as a subgenus of *Teleosaurus*). Article 11.6 of the ICZN Code, publication as synonymy, states: 'A name which when first published in an available work was treated as a junior synonym of a name then used as valid is not thereby made available'. Article 11.6.1 states: 'However, if such a name published as a junior synonym had been treated before 1961 as an available name and either adopted as the name of a taxon or treated as a senior homonym, it is made available thereby but dates from its first publication as a synonym'. Clearly, Eudes-Deslongchamps (1868a) treated *T. edwardsi* as an available name and he adopted the specific name for his validly described taxon. Consequently, under Article 11.6.1, *Teleosaurus* (*Steneosaurus*) *edwardsi* is an available name. However, the authorship is Eudes-Deslongchamps, 1868a, not Eudes-Deslongchamps, 1867 or 1868b (or 1866, based on when the name was first presented at a conference). This is based on Article 50.7 of the ICZN Code, which states: 'If a scientific name (taken, for example, from a label or manuscript) was first published in the synonymy of an available name and became available before 1961 through the provisions of Article 11.6, its author is the person who published it as a synonym, even if some other originator is cited, and is not the person who subsequently adopted it as a valid name'.

DESCRIPTION

Ilium

The ilium (Fig. 1) is elongated, expanded, and robust. The attachment sites for both sacral ribs are clearly visible, with two large and distinct depressions (Fig. 1A). The acetabulum (Fig. 1B) is deeply concave, with the anterior-most part of the supraacetabular crest projecting laterally. The anterior process is long and slender, and with no medial or lateral curvature along its length. The tip is slightly pointed. The acetabular incision is extremely large and covers approximately half of the medial surface of the ilium. It is an inverse 'U'-shape and shallow, yet anteroposteriorly elongated. Along the ventral margin the anterior and posterior ischium articulation surfaces are well separated. The anterior ischium articulation surface point is much larger than the posterior one, being elongated ventrally. The posterior ischium articulation surface is small with a straight ventral surface and does not show any dorsoventral elongation.

Ischium

The ischium (Fig. 2) has a robust proximal region, with the ischial blade being mediolaterally narrower and more gracile. Only the basal region of the anterior process is preserved, but it is robust. From where the area of breakage is observed, it is likely that the ischial notch (gap between the anterior and posterior processes) was large, oval, and deep. The posterior

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process is expanded and is faintly concave (contributing to the acetabulum). It is weakly triangular-shaped in dorsal view (the lateral margin being triangular).

The ischial 'neck' narrows and then expands into a large ventral ischial blade. The ischial blade is thin in width and somewhat anteroposteriorly expanded. The posterior margin of the ischial blade is subtriangular in shape. The anterior flange of the ischial blade is very thin and has a straight, vertical, 90° outer margin (although most of the anterior flange is broken and missing). There are numerous large, pronounced striations on both the medial and lateral surfaces, indicative of muscle attachment.

Femur

The femur (Fig. 3) is particularly massive. The general shape, particularly the distal area, displays a more sigmoidal curvature than the femur of '*S.*' *obtusidens* (NHMUK PV R3168). The neck and shaft are robust. In dorsal view, the head has a distinctive 'kidney-bean' shape. The distal condyles are more elongated anteroposteriorly than mediolaterally. The greater (medial) condyle is much larger compared with that of the lesser (lateral) condyle, especially when viewed in ventral view. The fourth trochanter is large, slightly raised, and expands proximodistally. There is an area consisting of a series of approximately eight to ten elongate, closely spaced, marks on the ventral and lateral surfaces on the femur (Fig. 3). These marks are currently considered to be bite marks.

DISCUSSION

The ilium, ischium, and femur of NHMUK PV R3898 differ from those seen in the '*S.*' *obtusidens* holotype (NHMUK PV R3168), and are instead more similar to those of *S. edwardsi*. The following characters differ between NHMUK PV R3898 and the '*S.*' *obtusidens* holotype: (1) the anterior process of the ilium is long and slender, whereas in '*S.*' *obtusidens* the process is shortened and proportionally more robust; (2) the sacral rib articulation points on the medial surface of the ilium are very large, well developed, and easily differentiated from one another, whereas in '*S.*' *obtusidens* they are shallow and quite difficult to differentiate (although this could be preservational); (3) the acetabular depression is deep and well developed, and the supraacetabular crest is pronounced, whereas in '*S.*' *obtusidens* the acetabular depression is shallow and the supraacetabular crest is nearly non-existent; (4) the posterodistal margin of the ischial blade is subtriangular in shape, whereas in '*S.*' *obtusidens* the posterodistal margin is subsquare; (5) the distal condyles of the femur are similar in size, whereas in '*S.*' *obtusidens* there is a significant difference in the size of the condyles; and (6) the femur is less sigmoidal than that of '*S.*' *obtusidens*.

Comparing NHMUK PV R3898 with *S. edwardsi* and *S. leedsi*, the specimen shares the following characteristics: (1) the ilium anterior process of NHMUK PV R3898 is long, similarly to that in *S. edwardsi* (NHMUK PV R3701) and *S. leedsi* (NHMUK PV R3806); however, the anterior process in *S. leedsi* (NHMUK PV R3806) is more robust than the quite slender processes of NHMUK PV R3898 and *S. edwardsi* (NHMUK PV R3701); (2) both of the distal femoral condyles of '*S.*' *obtusidens* (NHMUK PV R3168) and *S. leedsi* (NHMUK PV R3806) are similar in size, whereas in NHMUK PV R3898 and *S. edwardsi* (NHMUK PV R3701) the greater condyle is noticeably larger than the lesser condyle; (3) in dorsal view, the femoral head of *S. edwardsi* (NHMUK PV R3701) is 'kidney bean' shaped, whilst '*S.*' *obtusidens* (NHMUK PV R3168) has a more subcircular femoral head and *S. leedsi* (NHMUK PV R3806) has a subcircular to slightly triangular femoral head; and (4) the posterodistal margin of the ischial blade has a subtriangular shape in NHMUK PV R3898 and in both *S. edwardsi* (NHMUK PV R3701) and *S. leedsi* (NHMUK PV R3806); however, in *S. leedsi* the blade is noticeably dorsoventrally less deep than in both NHMUK PV R3898 and *S. edwardsi* (NHMUK PV R3701).

In addition to the specific characters outlined above, one of the most intriguing features of these bones is their massive size. When comparing NHMUK PV R3898 with the '*S.*' *obtusidens* holotype, NHMUK PV R3898 is substantially larger (Table 1). The only measurements larger in the '*S.*' *obtusidens* holotype (NHMUK PV R3168) than in NHMUK PV R3898 are femoral head width and dorsoventral ischial blade length (although the ischial blade is broken and incomplete in NHMUK PV R3898; Table 1). However, this is expected; when viewed dorsally, the '*S.*' *obtusidens* holotype has a more subcircular femoral head than NHMUK PV R3898, which is elongated anteroposteriorly. The ischial blade of the '*S.*' *obtusidens* holotype is very deep dorsoventrally, giving it a characteristic subsquare shape, whereas, in NHMUK PV R3898, the ischial blade is less deep and has a subtriangular shape.

Interestingly, the femoral length of the *M. mosae* neotype is 44.2 cm (Hua, 1999), which is comparable with that of the '*S.*' *obtusidens* holotype (45.6 cm) but shorter than that of NHMUK PV R3898 (53 cm) (Andrews, 1913). At approximately 6 m in total body length, the shorter femur of the *M. mosae* neotype suggests that NHMUK PV R3898 was from a larger individual. This assumes that the scaling ratio of femoral length-to-total body length is comparable between

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Table 1. Biometric comparison of ilium, ischium, and femur measurements between NHMUK PV R3168 ('*Steneosaurus*' *obtusidens* holotype) and NHMUK PV R3898

Bone	Measurement	NHMUK PV R3168	NHMUK PV R3898
Ilium	Anterior ridge to posterior ridge (greatest length)	113.5	121.5
	Length of anterior articulation surface	60.0	63.5
	Width (thickness) of anterior process	9.0	12.5
	Width of anterior articulation surface	33.5	45.5
	Greatest dorsoventral height	188.0	231.0
Ischium	Greatest anteroposterior length	206.0	255.0
	Total height	181.0	207.0
	Dorsoventral length of the ischial blade	67.5	59.0
Femur	Femoral head proximodistal length	76.0	106.5
	Femoral head lateromedial width	56.5	51.5
	Femoral 'neck' proximodistal length	47.0	67.5
	Middle shalf anteroposterior width	44.5	59.5
	Greater condylar proximodistal length	62.5	74.0
	Lesser condylar proximodistal length	56.5	70.5
	Total femoral length	456.0	530.0

Measurements are given in mm, and are rounded up to the nearest 0.5 mm.

Table 2. Femur-to-basicranial length ratios of selected teleosaurids

Species	Age	Specimen/Reference	Femoral length	Basicranial length	Femur-to-basicranial ratio
Mycterosuchus nasutus	Middle Callovian	Andrews, 1913 (holotype)	40	100	0.4
Steneosaurus edwardsi	Middle Callovian	Andrews, 1913 (NHMUK PV R2074)	24.8	60	0.4133
Steneosaurus edwardsi	Middle Callovian	Andrews, 1913 (NHMUK PV R2865)	38.5	93.5	0.4118
Steneosaurus edwardsi	Middle Callovian	Andrews, 1913 (NHMUK PV R3701)	31.4	74	0.4243
Steneosaurus leedsi	Middle Callovian	NHMUK PV R3806	29.8	88	0.3386
Steneosaurus obtusidens	Middle Callovian	Andrews, 1913 (holotype)	45.6	116	0.3931
Machimosaurus mosae	Late Kimmeridgian-Early Tithonian	Hua, 1999 (neotype)	44.2	96.6	0.4576

Measurements are given in cm.

these two individuals; if so, then NHMUK PV R3898 would have been approximately 7.2 m long.

There is reasonable evidence to suggest that the Oxford Clay Formation species did not have a similar femoral length-to-total body length scaling ratio. Specimens from the Callovian have proportionally shorter femora in relation to basiocranial length compared with *M. mosae* (Table 2). The total body length of a nearly complete specimen of *S. leedsi* measures 428 cm (although the terminal caudal vertebrae are missing, which may explain the short body length) (Table 3) with the left femur measuring 29.8 cm (Table 2). Use of a femoral-body length ratio of *S. leedsi* results in a much larger estimated body length of 761.21 cm (Table 4). Therefore, as NHMUK PV R3898 has a femoral-to-basicranial length ratio intermediate between those of *M. mosae* and *S. leedsi*, the specimen probably had a body length between 7.2 and 7.6 m. The variation in femoral proportions makes it difficult to establish a reliable regression equation for estimating teleosaurid body length. Future studies will be needed to explore skeletal variation in this clade and to determine whether a useful proxy for estimating body lengths can be created.

Whilst it may appear curious that NHMUK PV R3898 is much larger than other Oxford Clay Formation and Marnes de Dives Formation (Normandy, France) teleosaurids, there are numerous skulls that have reached 1 m or more in length (e.g. Andrews, 1913; Adams-Tresman, 1987; Vignaud, 1995). Whilst

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Table 3. Skull and postcranial lengths for *Steneosaurus leedsi* (NHMUK PV R3806)

Measurement	NHMUK PV R3806
Basicranial length	880
Total preserved postcranial length	3400
Cervical and anterior dorsal vertebrae length (11 vertebrae)	800
Middle-late dorsal and sacral vertebrae (11 vertebrae)	820
Anterior caudal vertebrae (18 vertebrae)	935
Posterior caudal vertebrae (19 vertebrae)	845

Measurements are given in mm, and are rounded up to the nearest 0.5 mm.

Table 4. Body length estimates for NHMUK PV R3898, based on femur-to-total body length ratio of two teleosaurid species with differently proportioned femora

Femur-to-total body length ratio	NHMUK PV R3898
Steneosaurus leedsi ratio (428/29.8)	761.21
Machimosaurus mosae ratio (600/44.2)	719.45

Measurements are given in cm.

the largest skull from these formations is the '*S.*' *obtusidens* holotype (at 1160 mm), there is one Oxford Clay Formation *S. edwardsi* skull that is 1112 mm long (PETMG R175), and two more are longer than 900 mm (NHMUK PV R2865 and PETMG R178). Therefore, large *S. edwardsi* specimens may be uncommon, but they are far from being rare. It is possible that these large and robust individuals are older males, assuming a similar ontogeny to extant crocodylians (e.g. Tucker, 1997).

CONCLUSIONS

Herein, we show that the largest known teleosaurid specimen from the Oxford Clay Formation of England (a femur, ischium, and ilium) is not referable to '*S.*' *obtusidens*, but to *S. edwardsi*. Numerous morphological characteristics support this taxonomic change. In addition, based on biometric measurements of NHMUK PV R3898 and the '*S.*' *obtusidens* holotype, it is clear that the former is a much larger individual. Our body length estimate for NHMUK PV R3898 suggests that it exceeded 7 m. Therefore, *S. edwardsi* is the largest known Middle Jurassic teleosaurid. The only known Jurassic crocodylomorphs that are larger than *S. edwardsi* are the Late Jurassic taxa *M. mosae* (6–8 m in length) and *M. hugii* (9.26 m in length) (Young *et al.*, 2014). Therefore, *S. edwardsi*, '*S.*' *obtusidens*, and *Machimosaurus* were the largest crocodylomorphs in the teleosaurid subclade during their first 100 milion years of evolution.

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