

ABSTRACT. Teleosaurids were a clade of crocodylomorphs that attained near-global distribution during the Jurassic Period. Within Teleosauridae, one particular sub-clade of durophagous/macrophagous taxa achieved large body sizes and were apex predators in shallow marine environments during the Late Jurassic and Early Cretaceous in Europe and around the coast of the Tethys Seaway. Unfortunately, the origins of this clade are still poorly understood. '*Steneosaurus*' *obtusidens* is a little-studied macrophagous species from the Oxford Clay Formation (Callovian, Middle Jurassic) of the United Kingdom and near Migné-les-Lourdines (middle Callovian) in France. Despite being considered a sister taxon of the Late Jurassic taxon *Machimosaurus*, the taxonomy of '*S.*' *obtusidens* remains unclear. Although three different synonymies have been proposed (variously a subjective synonym of other taxa), these taxonomic hypotheses have not been based on detailed anatomical comparisons and thus have not been tested. Here we re-describe of the holotype of '*S.*' *obtusidens*, demonstrate that it is indeed a valid taxon, restrict the referred specimens to a fragmentary skeleton, nearly complete skull, and partial rostrum, and establish a new monotypic genus, *Lemmysuchus*. Our re-description reveals five autapomorphies for *L. obtusidens*, and nine apomorphic characters that support the tribe Machimosaurini (*Lemmysuchus* + *Machimosaurus*).

Key words: Crocodylomorpha – *Machimosaurus* – *Steneosaurus* – *Lemmysuchus* – Teleosauridae – Thalattosuchia

## INTRODUCTION

Teleosaurid crocodylomorphs were a near-globally distributed clade that inhabited shallow marine and brackish ecosystems throughout the Jurassic (Buffetaut, 1982a, 1982b; Hua, 1999; Johnson *et al.*, 2015), and survived into the Early Cretaceous (Fanti *et al.*, 2016; Jouve *et al.*, 2016). These animals are often viewed as marine analogues of extant gavials because of their elongate and tubular snout, dorsally directed orbits, and high tooth count, all of which suggest a primarily piscivorous diet (Andrews, 1909, 1913; Buffetaut, 1982a, 1982b). However, within Teleosauridae, some taxa have been considered to be durophagous and/or macrophagous, because they had shorter snouts, proportionally enlarged supratemporal fenestrae (i.e. increased jaw adductor musculature), blunt tooth crown apices, serrated carinae, and extensive enamel ornamentation (Andrews, 1909, 1913; Buffetaut, 1982a; Hua *et al.*, 1994; Hua, 1999; Martin & Vincent, 2013; Young & Steel, 2014; Young *et al.*, 2014a, 2014b, 2015a, 2015b; Fanti *et al.*, 2016; Jouve *et al.*, 2016).

The Late Jurassic-Early Cretaceous (Oxfordian to Hauterivian) taxon *Machimosaurus* is the best-studied macrophagous teleosaurid, known from both cranial and post-cranial remains, and isolated teeth from numerous countries (Sauvage & Liénard, 1879; Krebs, 1968; see Young *et al.*, 2014a for an overview). Here we use the taxonomy of Young *et al.* (2014a), rather than that of Martin *et al.* (2015) following the rationale of Foffa *et al.* (2015) and because a new phylogenetic analysis of *Machimosaurus* supports the multi-taxic hypothesis (see Fanti *et al.*, 2016). The sister taxon to *Machimosaurus*, '*Steneosaurus*' *obtusidens* Andrews, 1909, is a controversial taxon from the Middle Jurassic of Europe. Over the past three decades its validity has been questioned, and three different subjective species (both *Machimosaurus* and *Steneosaurus*) synonymies have been proposed (see Adams-Tresman, 1987; Hua *et al.*, 1994;

Pierce *et al.*, 2009). Recent studies, however, have considered '*Steneosaurus*' *obtusidens* to be a distinct taxon (Martin & Vincent, 2013; Young *et al.* 2014a, 2015b). This taxonomic confusion hinders our understanding of the origins of the macrophagous teleosaurid sub-clade Machimosaurini.

Thus, the aim of this paper is to shed light on the early evolution of durophagous/macrophagous teleosaurids by re-investigating the validity of '*S.*' *obtusidens*. We re-describe the holotype of '*Steneosaurus*' *obtusidens* (which consists of a complete cranium and mandible, and the majority of the postcranial skeleton), demonstrate that it is a valid taxon and establish a new monotypic genus. We restrict the referred specimens of this species to a fragmentary skeleton, a nearly complete skull and a partial rostrum, and show that most of the cranial and post-cranial material previously referred to '*Steneosaurus*' *obtusidens* belongs to other taxa. In addition, we assign three isolated teeth (two from the Oxford Clay Formation and one from the Cornbrash Formation) to Machimosaurini indet. Finally, based on the holotype and referred specimens, we conclude that '*S.*' *obtusidens* was present in the Callovian Oxford Clay Formation of England, and the *Erymnoceras coronatum* ammonite Zone (thus being contemporaneous with the Peterborough Member of the Oxford Clay Formation) of Migné-les-Lourdines of France.

## *'STENEOSAURUS' OBTUSIDENS: HISTORICAL BACKGROUND*

### HISTORICAL SETTING

The holotype of '*Steneosaurus*' *obtusidens* (Natural History Museum, London, NHMUK PV R 3168) is part of the Leeds Fossil Collection (Peterborough Member, Oxford Clay Formation; Middle Callovian) held at the NHMUK. Charles Andrews established the name *Steneosaurus*

*obtusidens* for NHMUK PV R 3168 (Andrews, 1909) when he described the Leeds Collection teleosaurids. Later, Andrews (1913) tentatively referred two more Leeds Collection specimens to '*S.*' *obtusidens* (NHMUK PV R 3169 and NHMUK PV R 3898). Andrews (1913) listed no specific criteria for the referral of these two specimens to '*S.*' *obtusidens* and his decision may simply have been based on the large size and robusticity that both specimens share with the holotype. Andrews (1913) later noted similarities between '*S.*' *obtusidens* and *Steneosaurus durobrivensis* Andrews, 1909, stating that (1913: 131): "if it were not for the peculiarity of the teeth, [the former] might almost have been referred to that species [*S. durobrivensis*]". The possibility that the '*S.*' *obtusidens* morphotype is a late ontogenetic variant of *S. durobrivensis* has also been raised (Andrews, 1913; Steel, 1973) (Note that *S. durobrivensis* is now considered to be a subjective junior synonym of *Steneosaurus edwardsi* Eudes-Deslongchamps, 1868; see Johnson *et al.*, 2015).

The first worker to formally synonymise '*S.*' *obtusidens* with *S. durobrivensis* (= *S. edwardsi*) was Adams-Tresman (1987). As noted by Young *et al.* (2015b), the anatomical comparisons made between '*S.*' *obtusidens* and *S. edwardsi* (as *S. durobrivensis*) were not based on the '*S.*' *obtusidens* holotype (NHMUK PV R 3168), but on referred specimens (i.e. NHMUK PV R 3169, Peterborough Museum and Art Gallery, Peterborough, PETMG R39 and PETMG R178). We agree with Adams-Tresman (1987) that PETMG R39 matches the '*S.*' *obtusidens* holotype (see discussion). However, the other two specimens lack the apomorphies of the '*S.*' *obtusidens* holotype (see description below), and thus cannot be referred to this taxon (we argue that they instead should be referred to *S. edwardsi*, see discussion). This means that Adams-Tresman's (1987) discussion regarding tooth morphology and dorsal osteoderm ornamentation were correct and NHMUK PV R 3169 and PETMG R178 do indeed belong to *S. edwardsi*.

However, we show below that these characteristics are distinct from those in the '*S.* *obtusidens*' holotype, NHMUK PV R 3168. Young *et al.* (2015b) also noted that Adams-Tresman (1987) did not discuss the presence of three sacral vertebrae in the '*S.*' *obtusidens* holotype, while Andrews (1913: 132) considered it likely to be an "individual peculiarity" of the holotype. The neotype of *Machimosaurus mosae* Sauvage & Liénard, 1879, also has three sacral vertebrae (Hua, 1999; Young *et al.*, 2014a). Another set of characteristics not mentioned by Adams-Tresman (1987) are the pronounced socket-like reception pits along the maxilla and dentaries for the opposing tooth row. Again, this may have been due to Andrews (1913: 131) being unsure if they were a natural characteristic or a result of post-mortem deformation. However, this is another characteristic that the '*S.*' *obtusidens* holotype (NHMUK PV R 3168) shares with *Machimosaurus* (Buffetaut, 1982b; Lepage *et al.*, 2008; Young *et al.*, 2014a; note that Young *et al.*, 2014a considered vertically orientated, interlocking dentition, with pronounced reception pits at the premaxillary, maxillary and dentary interalveolar spaces to be a *Machimosaurus* apomorphy). It is unclear whether Adams-Tresman (1987) was being selective in what characteristics the '*S.*' *obtusidens* referred specimens and the *S. durobrivensis* holotype and referred specimens shared, or simply being cautious in regards to morphologies unique to the '*S.*' *obtusidens* holotype.

'*Steneosaurus*' *obtusidens* was also considered to be a subjective junior synonym of the Kimmeridgian species *Machimosaurus hugii* von Meyer, 1837 (Hua *et al.*, 1994; Hua 1996, 1999). However, these authors noted that the taxonomy of blunt-toothed teleosaurids still required further study. More recently Pierce *et al.* (2009) suggested that '*S.*' *obtusidens*, *Steneosaurus hulkei* Andrews, 1913, and *S. durobrivensis* (all Callovian taxa; the species *S. edwardsi* was not mentioned) were subjective junior synonyms of *M. hugii*. This synonymy and corresponding species diagnoses have been criticised and rejected (see Martin & Vincent, 2013;

Young *et al.*, 2014a; Johnson *et al.*, 2015) and, indeed, all phylogenetic analyses that include the relevant taxa do not support any of the two proposed synonymies (*S. durobrivensis* = *S. edwardsi* and *M. hugii*). In these analyses '*S.* *obtusidens*' is consistently found to be the sister taxon of *Machimosaurus*, whilst *S. durobrivensis* (= *S. edwardsi*) is the sister taxon to this sub-clade (Young *et al.*, 2012; Martin & Vincent, 2013; Young, 2014; Fanti *et al.*, 2016; Young *et al.*, 2016a). Recent papers have agreed that '*S.* *obtusidens*' is a distinct taxon (Martin & Vincent, 2013; Young *et al.* 2014a, 2015b). Finally, Jouve *et al.* (2016) established the tribe Machimosaurini for '*S.* *obtusidens*, *Machimosaurus* and indeterminate Bathonian specimens (based on shared craniodental morphologies; see introduction).

## GEOLOGICAL SETTING

The Oxford Clay Formation (OCF) is a Jurassic (Callovian - lower Oxfordian) lithostratigraphic unit that is well-known from extensive exposures that extend from the western Dorset coast to northern Yorkshire of England (Selden *et al.*, 2008). The entire OCF is composed of two main facies: the lowermost Peterborough Member, and an upper facies that comprises the Stewartby Member and Weymouth Member (Cox *et al.*, 1992; Martill *et al.*, 1994; Selden *et al.*, 2008).

The Peterborough Member, referred to in older literature as the Lower Oxford Clay, consists of compact olive-coloured shaly clays and black and organic-rich fissile shales (Hudson & Martill, 1994; Martill *et al.*, 1994). This member contains a diverse vertebrate fauna, including: bony fish and chondrichthyans, marine reptiles (ichthyosaurs, plesiosaurs, pliosaurs, and thalattosuchians), and rare dinosaur and pterosaur remains (Martill *et al.*, 1994). Oxygen isotope values (Kenig *et al.*, 1994) indicate that the OCF was deposited in a shallow marine, open-shelf environment.

The Cornbrash Formation is a Bathonian - Callovian (Middle Jurassic) lithostratigraphic unit that underlies the OCF (Wright, 1977). This stratigraphic section consists of medium to fine-grained limestone that is bioturbated, yields many reptilian fossils, and stretches from the Weymouth area to the Scarborough area in the UK (Cox & Sumbler, 2002), similar to the OCF. The Cornbrash Formation is comprised of two main units, the Cornbrash Limestone and the Cornbrash Shales, which form a transgressional marine cycle (Wright, 1977). The Cornbrash Formation represents a section of the Great Oolite Group (Sellwood *et al.*, 1985).

Migné-les-Lourdines (the locality of specimen LPP.M.21) is a small town just North of Poitiers, France. The *Erymnoceras coronatum* ammonite Zone in France is Middle Callovian (Bruent, 1969; Vignaud, 1995), and is also represented within the Peterborough Member of the OCF in the UK. At Migné-les-Lourdines this ammonite zone is represented by a white calcareous limestone (Brunet, 1969).

## ABBREVIATIONS

### INSTITUTIONAL

CAMSM, Sedgewick Museum of Earth Sciences, University of Cambridge, Cambridge, UK; DORCM, Dorset County Museum, Dorchester, UK; GLAHM, The Hunterian Museum, Glasgow, UK; GPIT, Paläontologische Sammlung der Eberhard Karls Universität Tübingen, Tübingen, Germany; LPP, Institut de paléoprimateologie, paléontologie, humaine ; évolution et paléoenvironnements Université de Poitiers, Poitiers, France; MNHN, Muséum national d'histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, UK; NMS, Naturmuseum Solothurn, Solothurn, Switzerland; NOTNH, Nottingham Natural History Museum, Nottingham, UK; OUMNH, Oxford University Museum of Natural History, Oxford,

UK;. PETMG, Peterborough Museum and Art Gallery, Peterborough, UK; SMNS, Staatliches Museum für Naturkunde Stuttgart, Baden-Württemberg, Germany.

## ANATOMICAL

XII, cranial nerve 12; ac dep, acetabular depression ; ac in, acetabular incision (acetabular notch); an, angular; ant f, anterior flange of second sacral vertebra ; ant pr, anterior process of ilium; ar, articular; art f, articular facet; atl, atlas; ax, axis; bas, basisphenoid; cen, vertebral centrum; clp, lateral process of calcaneum; cmp, medial process of calcaneum; cor, coronoid; cor gr, coronoid groove; den, dentary; fm, foramen magnum; fo, foramina; fr, frontal; ft, “fourth trochanter” rugose area; fem h, femoral head; fib, fibula; gf, glenoid fossa; hc, humeral concavity; hs, humeral shaft; if, incisive foramina; isch bl, ischial blade; jug, jugal; k, keel of osteoderms; lac?, uncertain lacrimal area; le, lateral epicondyle (of humerus); m con, medial condyle of femur ; me, medial epicondyle (of humerus; mx, maxilla; mx gr, maxillary groove; na, nasal; ns, neural spine; oc, occipital condyle; od, odontoid; or, orbit; pal, palatine; par, parietal; pat, pathology; pit, ornamentation pit on dorsal surface of osteoderms; pmx, premaxilla; pmx1-2, first and second premaxillary tooth; pn, pubic neck; po, postorbital; poz, postzygapophyses; pp, pubic plate; prf, prefrontal; prz, prezygopophyses; pt, pterygoid; pub, pubis; q, quadrate; rib h, rib head; s1, first sacral vertebra; s2, second sacral veretebra; s3, third sacral (refers to first caudal) vertebra; spl, splenial; sq, squamosal; st h, sternal head; sub r, subhorizontal anterior ridge of ilium ; sup cr, supraacetabular crest of ilium ; sup occ, supraoccipital ; supr fen; supratemporal fenestra; san, surangular; tub, tuberculum; tp, transverse process; t tub, tibial tuberosity; vac?, vacuity.

## SYSTEMATIC PALAEOLOGY

CROCODYLOMORPHA Hay, 1930 (*sensu* Nesbitt, 2011)

THALATTOSUCHIA Fraas, 1901 (*sensu* Young & Andrade, 2009)

TELEOSAURIDAE Geoffroy Saint-Hilaire, 1831

MACHIMOSAURINI Jouve *et al.*, 2016

MACHIMOSAURINI INDETERMINATE.

- v 1905 *Machimosaurus rigauxi* Sauvage – Blake, p. 26, Plate 1 figure 5a-c
- v 2014a *Machimosaurus rigauxi* Sauvage – Young *et al.*, p. 3

We have identified isolated teeth that have characteristic Machimosaurini dental pattern (see *Lemmysuchus* description): GPIT/RE/301, CAMSM J64508, and OUMNH J.14464. The first tooth crown GPIT/RE/301 (Fig. 12E -I) is from the Oxford Clay Formation of Peterborough and was excavated before 1906. It was sold to the Eberhard Karls Universität in Tübingen, Germany, during the first decade of the twentieth century. A note in the collections by E. Buffetaut in 1981 suggested that it could be ‘*Steneosaurus*’ *obtusidens*, while another specimen note by B. Stürtz (a commercial fossil collector from Bonn) suggested that it might belong to *Machimosaurus* but was similar to the genus *Steneosaurus*. The tooth is conical, robust with a blunt apex, and posteriorly curved. The majority of the root is missing. The tooth is single cusped, and has no accessory cusps or cingula. The enamel ridges are well-defined and pronounced, and are close in parallel vertical rows. The enamel ornamentation is similar to the *L. obtusidens* holotype (NHMUK PV R 3168), with randomly arranged ridges near the apex that are straight, parallel, and closely packed together towards the root of the tooth.

Another isolated tooth, CAMSM J64508 (Fig. 12J-P), was collected in Fletton (Cambridgeshire) and is also possibly from the Leeds Collection. It has originally been regarded (by whom is unknown) as a pliosaurid of the genus *Simolestes*, most likely for its size. However, the curvature, blunt apex, presence of pronounced carinae and ornamentation patterns distinguish it from any late Middle Jurassic pliosaurids. The tooth is conical and has a circular cross-section which is maintained through the whole apicobasal length. As typical in *Machimosaurus* and *L. obtusidens* the tip of the crown is blunt (Young *et al.*, 2014a, 2014b). The considerable size of the crown (approximately 5cm apicobasal length) and the height to length ratio suggests CAMSM J64508 may be one of the large dentary or premaxillary pseudocaniniform teeth. The crown is clearly ornamented by long continuous and evenly-spaced apicobasal ridges that occur with the same density on the labial, mesial and lingual sides. As in *Machimosaurus* and *L. obtusidens*, the ornamental ridges on the apex become shorter until they form the characteristic anastomosed pattern (Young *et al.*, 2014a, 2015a, 2015b). Interestingly, this ornamentation pattern is convergent with the Late Jurassic metriorhynchid *Torvoneustes carpenteri* (Wilkinson *et al.*, 2009). In CAMSM J64508 the carinae are present although almost indistinguishable for most of the crown length (Fig. 14G). However, they can be observed in the apical “anastomosed region”. The carinal keel is considerably clearer on one side than the other. The ornamentation pattern of the apex contacts the carinae forming false serrations (Young *et al.*, 2015b).

Tooth OUMNH J.14464 (Fig. 12Q-T) is from the Cornbrash Formation and was figured by Blake as *Machimosaurus rigauxi* Sauvage, 1879 (Blake, 1905, p. 26, plate 1 figure 5a-c). The crown of this tooth is intact and the root is missing. The apex is slightly pointed and the entire tooth is conical and mediolaterally thickened. The mesial and distal carinae are faint, not as pronounced as in GPIT/RE/301, and when viewed with the naked eye terminate in the middle of

the tooth. The numerous enamel ridges run ventrally parallel and close together. At the apex the ridges are disoriented and extend in random patterns, much as how Andrews (1913) described the teeth of the *L. obtusidens holotype* (NHMUK PV R 3168).

The two tooth crowns from the Oxford Clay Formation (GPIT/RE/301 and CAMSM J64508) may be referable to *Lemmysuchus obtusidens*. However, as they are isolated crowns, we refrain from making that assignment. The *Machimosaurus rigauxi* tooth (OUMNH J.14464) is interesting as it is from the Cornbrash Formation, a lithostratigraphic unit that *L. obtusidens* is currently not known from.

*LEMMYSUCHUS* GEN. NOV.

Fig. 1-21

*ZooBank Life Science Identifier (LSID) for new genus*

urn:lsid:zoobank.org:act: [TO BE ADDED UPON ACCEPTANCE]

*Type species*

*Steneosaurus obtusidens* Andrews, 1909 [following recommendation 67B of the International Commission on Zoological Nomenclature (ICZN) code]. Now referred to as *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov.

*Etymology*

‘Lemmy’s crocodile’. *Lemmy* referring to Ian Fraser Kilmister, better known as ‘Lemmy’, the deceased founder, bassist and lead singer of Motörhead, and *suchus* is the Latinised form of the Greek *soukhos* (σοῦχος), meaning crocodile.

### *Diagnosis*

Same as the only known species (monotypic genus).

### *LEMMYSUCHUS OBTUSIDENS* (ANDREWS, 1909) COMB. NOV.

- v\* 1909 *Steneosaurus obtusidens* sp. nov. – Andrews, p. 306, Plate 9 figure 2
- v 1913 *Steneosaurus obtusidens* Andrews – Andrews, p. 130, Text-fig. 50, Plate 7 all figures (*partim*)
- v 1969 *Steneosaurus* cf *heberti* Morel de Glasville – Brunet, Plate 1 figure b-b' (LPP.M.21)
- v 1973 *Steneosaurus obtusidens* Andrews – Steel, p. 33, Figure 13.13
- v 1987 *Steneosaurus durobrivensis* Andrews – Adams-Tresman, p. 205 (*partim*)
- 1993 *Steneosaurus* cf *heberti* Morel de Glasville – Vignaud
- v 1994 *Machimosaurus hugii* von Meyer – Hua *et al.*, p. 15 (*partim*)
- v 1996 *Machimosaurus hugii* von Meyer – Hua, p. 1562 (*partim*)
- v 2009 *Machimosaurus hugii* von Meyer – Pierce *et al.*, p. 1085 (*partim*)
- v 2013 *Steneosaurus obtusidens* Andrews – Martin & Vincent, p. 192
- v 2014a '*Steneosaurus*' *obtusidens* Andrews – Young *et al.*, p. 3
- v 2014b '*Steneosaurus*' *obtusidens* Andrews – Young *et al.*, p. 2
- v 2016 '*Steneosaurus*' *obtusidens* Andrews – Jouve *et al.*, p. 4

### *Holotype*

NHMUK PV R 3168, complete cranium and mandible in articulation, atlas-axis complex, six post-axial cervical vertebrae, fourteen dorsal vertebrae, three sacral vertebrae, twenty-one caudal vertebrae, one complete cervical rib and twenty cervical rib fragments, forty-nine dorsal rib fragments (fewer than five complete ribs), two gastralia fragments, one right scapula, one distal fragment of a humerus, one ulna, one right ilium, both ischia, one pubis, both femora, one tibia, possible pieces of fibulae or carpals/tarsal elements, five ankle bones (including a calcaneum,

distal tarsal and astragalus), four phalanges, numerous dermal osteoderms (approximately fifty-six), thirty-three isolated teeth, and numerous bone fragments (Fig. 1-3, 12A-D, 13-21).

#### *Etymology*

‘Lemmy’s blunt-toothed crocodile’. From the Latin for blunt (*obtusus*) and tooth (*dens*). Named for the blunt apices of the teeth.

#### *Type locality*

Peterborough, England, UK. The exact age and area of collection of this specimen is not known, original Leeds Collection Number 6.

#### *Type horizon*

Peterborough Member, Oxford Clay Formation, Ancholme Group. Middle Callovian, Middle Jurassic.

#### *Referred specimens*

PETMG R39, largely incomplete rostrum, fragment of right mandibular ramus, partial dorsal osteoderm and five dorsal vertebral centra. PETMG R31, five vertebral centra (two dorsals and three sacrals), are associated with PETMG R39 and very likely belong to the same individual (see Discussion) (Peterborough Member, Oxford Clay Formation, Ancholme Group; Middle Callovian).

LPP.M.21, nearly complete skull (left lateral portion not preserved from the orbit to the squamosal) and mandible (anterior region is preserved) (*Erymnoceras coronatum* ammonite Zone, Middle Callovian).

NOTNH FS3361, partial rostrum, including the premaxillae and part of the maxillae (horizon and locality unknown, thought to be Oxford Clay Formation because of the state of preservation).

#### *Emended diagnosis*

Teleosaurid crocodylomorph with the following unique combination of characters (proposed autapomorphic characters are indicated by an asterisk \*): the rostrum external surface is strongly convex, in particular the nasals\*; partial or complete fusion of the internasal suture\*; axis lacks diapophyses (shared with *Steneosaurus bollensis*; see Westphal, 1962); the ilium anterior process is small and anteroposteriorly shortened\*; on the ilium the acetabulum is shallow and poorly developed\*; shallow supraacetabular crest on the ilium\*; the dorsal osteoderm ornamentation is composed of small-to-large, irregularly shaped pits that radiate from the centre of the keel and are arranged in a starburst pattern (to a certain extent similar to *Machimosaurus mosae*; Hua, 1999; Young *et al.*, 2014a)\*.

#### *Characteristics shared with Machimosaurus*

*Lemmysuchus obtusidens* shares the following nine synapomorphies with *Machimosaurus* (*sensu* Young *et al.*, 2014a): (1) conical teeth with blunt/rounded apices; (2) tooth enamel ornamentation varies along the crown, i.e. in the basal region enamel ornamentation is composed of numerous apicobasally aligned ridges of high relief, which transition into an anastomosed

pattern in the apical region; (3) teeth have true and false denticles on the carinae; (4) ratio of crown apicobasal height to basal transverse width can be as low as 1.8 in the posterior teeth; (5) pronounced socket-like reception pits along the maxilla and dentaries for the opposing tooth row; (6) the supratemporal fossae are parallelogram-shaped in dorsal view; (7) three sacral vertebrae; (8) ischial blade posterior margin is blunt and sub-square in shape; and (9) proximal tibia strongly deflects anteriorly.

However, *L. obtusidens* lacks the following eight *Machimosaurus* autapomorphies (*sensu* Young *et al.*, 2014a; note that the two axis neural spine autapomorphies cannot be determined in *L. obtusidens* due to preservation):

1. Three alveoli per premaxilla (*L. obtusidens* has four alveoli per premaxilla).
2. The first premaxillary alveoli are orientated strongly anteroventrally (*L. obtusidens* lacks this condition).
3. Eighteen–twenty-two alveoli per maxilla (*L. obtusidens* has at least 29 alveoli per maxilla).
4. Nineteen–twenty-five alveoli per dentary (*L. obtusidens* has approximately 29 alveoli per dentary).
5. Presence of carinae is variable in *Machimosaurus* spp. (in *L. obtusidens* all teeth have carinae).
6. The rostrum is broad and mesorostrine, constituting fewer than 60% of the basicranial length (in *L. obtusidens* the rostrum is 61.2% of basicranial length and is less broad, thus falling slightly outside the condition seen in *Machimosaurus*).
7. Ratio of maximum supratemporal fossa length to basicranial length is greater than 27% (in *L. obtusidens* this ratio is 25.8%).

8. Medial quadrate hemicondyle is considerably smaller than the lateral hemicondyle (in *L. obtusidens* both condyles are large and similar in size).

*Lemmysuchus obtusidens* (NHMUK PV R3168), *Machimosaurus*, , *Steneosaurus heberti* Morel de Glasville, 1876 (MNHN.F 1890-13) and *Steneosaurus edwardsi* (NHMUK PV R3701) share three characteristics: (1) anterior processes of the jugals are very elongate and slender, so that they largely restrict a lacrimal-maxilla contact on the external surface, except for the anterolateral margins of the lacrimals which do contact the maxillae (Fig. 6); (2) the Meckelian canal is not deeply excavated on the dorsal surface of the splenials (Fig. 9) in contrast to other thalattosuchians such as *Steneosaurus leedsi* (NHMUK PV R3320); and (3) the closure of the antorbital fenestrae (Fig. 22) (see description below on how we conclude that '*L. obtusidens*' lacks these fenestrae). Note that Young *et al.* (2014a) listed the absence of antorbital fenestrae was shared by *Machimosaurus* (SMNS 91415) and *S. heberti*. *Lemmysuchus obtusidens* also shares one characteristic with *S. heberti* (MNHN.F 1890-13); dorsoposterior curvature of the posterior mandibular rami (Fig. 23).

#### *Character note*

*Lemmysuchus obtusidens* has two characteristics that are well-developed in the holotype but not clear in other OCF teleosaurid specimens (because of the typically poor preservation of skulls, through dorsoventral crushing and/or shearing). These are: 1) a large nuchal crest on the supraoccipital, and 2) large and pronounced paired occipital tuberosities (somewhat similar to those seen in dyrosaurid crocodyliforms, which are developed to a much greater extent; e.g. MNHN.F ALG 1). These characteristics, albeit in a reduced form, are also seen in *Teleosaurus cadomensis* Lamouroux, 1820 (MNHN cast of an adult skull, MNHN.F AC 8746; Jouve, 2009),

*Steneosaurus heberti* (MNHN.F 1890-13) and *Machimosaurus buffetauti* Young *et al.*, 2015 (SMNS 91415; Martin & Vincent, 2013; Young *et al.*, 2014a).

## DESCRIPTION

The holotype of *Lemmingsuchus obtusidens*, NHMUK PV R 3168, comprises a nearly complete skeleton (Figs. 1-3, 12A-D, 13-21) (Andrews, 1909, 1913). The cranium and mandible adhere together so tightly that the cranium palatal view and mandible dorsal view is inaccessible; LPP.M.21, however, preserves the palatal view, which is easily accessible (Fig. 8C-D), and NOTNH FS3361 preserves part of the rostrum, including the premaxillae (Fig. 10-11). The cranium has experienced dorsoventral compression and has numerous fractures making it difficult to discern sutures from breaks. However, PETMG R39 is well preserved (Fig. 4-6), and the preorbital area, cranium palatal surface and part of the mandibular dorsal surface can be described from this specimen.

## CRANIUM

The cranium of *Lemmingsuchus obtusidens* (NHMUK PV R 3168) (Figs. 1-3) is approximately 1.4 m long (Andrews, 1909, 1913). It is similar to *Machimosaurus* in terms of overall anatomy and robusticity. The rostrum is more robust and proportionally shorter than those of other Middle Jurassic teleosaurids (e.g. *Steneosaurus leedsi*, *S. heberti*, *Mycterosuchus nasutus*) (Andrews 1913), and comprises 61.2% of the total skull length (the 51% ratio given in Andrews, 1913 was a typographical error). The anterior premaxilla and dentaries are laterally expanded as in other teleosaurids (e.g. Andrews, 1909, 1913; Hua, 1999; Martin & Vincent, 2013; Young *et al.*,

2014a). In NHMUK PV R 3168 (Fig. 1), the preorbital region is deformed, possibly due to an infection of the bone caused by a bite (there is a large tooth deeply embedded in this region of the cranium). Conversely, PETMG R39 (Fig. 4-5) and LPP.M.21 (Fig. 8A-B) are well preserved in this area. Based on NHMUK PV R 3168 (Fig. 1-3), LPP.M.21 (Fig. 8) and PETMG R39 (Fig. 4-5) the orbits would have been large, oval in shape, and oriented more anteroposteriorly than in most other teleosaurids (such as *Steneosaurus leedsi* NHMUK PV R 3806). In dorsal view, the supratemporal fenestrae (Fig. 1) are considerably longer than wide and are considerably longer than the orbits. The cranial description refers to the holotype (NHMUK PV R 3168) unless otherwise specified. **Due to the fragility and heaviness of the NHMUK PV R 3168 cranium, the authors were unable to flip it over to observe the palates.** Therefore, all information pertaining to the palatal surface comes from LPP.M.21.

*Premaxillae.* The premaxillae (Fig. 1, 2, 3A, 3C) are large and robust, surround the external narial opening, and face anterodorsally. The external nares are laterally expanded and their posterior margins do not reach beyond the third premaxillary alveolar pair. The anterior two-thirds of the premaxilla is laterally expanded and the anterior margin is ventrally deflected, giving the snout a scoop-like appearance. In LPP.M.21 (Fig. 8A-B) and NOTNH FS3361 (Fig 10-11) the incisive foramen (= naso-oral fenestra) is very small and is situated in the middle of the suture of the premaxillae. In dorsal view the premaxilla-maxilla suture is well-developed and W-shaped. The left premaxilla-maxilla suture is directed proximodistally parallel towards the middle of the rostrum with two small, pointed, posterior-oriented processes edges in dorsal view. The premaxilla contains four teeth, with the fourth (posterior-most) being the largest. The first two premaxillary alveoli are nearly confluent, with a thin interalveolar lamina separating them. The interalveolar lamina is missing in NOTNH FS3361 and LPP.M.21, making it appear as

though there were only three premaxillary teeth present (this feature is noted in Vignaud, 1997). There is a diastema between the last premaxillary tooth and the first maxillary tooth. In life, large dentary caniniform teeth would have been present (as in *Machimosaurus* and other large teleosaurids, Andrews, 1909, 1913; Martin & Vincent, 2013).

*Maxillae.* The maxillae (Fig. 1, 2, 3A, 3C) form a substantial part of the rostrum. Their lateral margins are sub-parallel in dorsal view. The maxilla separates the nasals from the premaxillae. The precise maxillary tooth count is difficult to determine but there are approximately **twenty-nine** alveolar pairs (Andrews, 1913). The specimen LPP.M.21 has **twenty-nine** alveolar pairs (Fig. 8C-D) and NOTNH FS3361 preserves approximately twenty-six alveolar pairs (the posterior portion of the maxilla is missing) (Fig. 10E-F). The lateral surface of the maxilla is ornamented by well-spaced, deep foramina that are visible in dorsal, lateral and anterior views (Fig. 1-2, 3A-B). The maxillary tooth row ends anterior to the anterior-most border of the suborbital fenestra. Numerous deep reception pits for dentary teeth are along the middle and anterior regions of the ventral-lateral margin of the maxillae (Fig. 2). The posterolateral regions of both maxillae in PETMG R39 have a groove which follows approximately parallel with the long anterior process of the jugal (Fig. 4-6). This feature is shared with *Machimosaurus*, *S. heberti* (MNHN.F 1890-13) and *S. edwardsi* (Martin & Vincent, 2013; Young *et al.*, 2014a). There is a small pathology on the ventral right maxilla in NOTNH FS3361 (Fig. 10).

*Jugals.* The jugals are triradiate and form the lateral border of the orbit (Fig. 1-2, 4-6, 8A-B) as in other teleosaurids (Andrews, 1909, 1913). The jugal is dorsally compressed by the postorbital-squamosal, and is ventrally compressed by the dentary due to poor preservation. The anterior margin of the jugal runs between the lacrimal and posterior regions of the maxilla (Fig.

2, 3A, 3C). This feature is shared among *S. edwardsi* (PETMG R175), *S. heberti* (MNHN.F 1890-13), *L. obtusidens* (PETMG R39) (Fig. 4-6), *Machimosaurus hugii* (NMS 7012), and possibly also *M. buffetauti* (the holotype SMNS 91415 is poorly preserved in this region). However, it is only in *Lemmingsuchus* and *Machimosaurus* that the jugal is extremely elongate, it anteriorly extends and reaches the anterior end of the lacrimal. The postorbital-jugal or quadratojugal-jugal contacts cannot be seen clearly in NHMUK PV R 3168, as the specimen is crushed in those areas. In LPP.M.21, the postorbital-jugal contact is anteroposteriorly straight (Fig. 8A-B). The quadratojugal-jugal contact is not clear in either NHMUK PV R 3168 or LPP.M.21.

*Nasals.* The nasals (Fig. 1, 2, 3A, 3C) are large triangular bones exposed on the dorsal surface of the posterior rostrum and orbital area. Both nasals (in NHMUK PV R 3168) are missing their anterior and posterior regions. The nasal anterior processes extend past the third maxillary tooth. Deformation, due to an embedded tooth from another animal (which is circular in cross-section and has left a striated impression behind), obscures the view of the anterior region of the nasal anterior processes. The nasals have a little ornamentation, consisting of faint ridges. There is a faint internasal midline suture on the anterior rostrum; further posteriorly there is no internasal suture, suggesting the nasals are partially or completely fused. This is seen in NHMUK PV R 3168 as well as LPP.M.21 (Fig. 8A-B), NOTNH FS3361 (Fig. 10A-B) and PETMG 39 (Fig. 4A-B). Both nasals form the beginning of a dorsally-directed “dome” towards the medial contact with the frontal. PETMG 39 (Fig. 4-5) and NOTNH FS3361 (Fig. 10) show the beginning of the “dome” in the anterior nasals (as the posterior nasals are not preserved in NOTNH FS3361). In LPP.M.21 (Fig. 8A-B), it is not clear if the nasals are convex (due to dorsoventral crushing, although this could be an ontogenetic feature), and the nasal anterior

processes are approximately one-third of the posterior rostrum and have well-developed near-parallel suture contacts with the maxillae.

*Prefrontals.* The prefrontals (Fig. 1-2) are slightly sub-circular in dorsal view and form the anteromedial border of the orbits. The prefrontal contacts the nasal medially and the lacrimal laterally. The frontal-prefrontal contact cannot be clearly seen even in the better preserved PETMG R39 due to breaks in this area (Fig. 4-6). In LPP.M.21 (and to some extent on the right side in NOTNH FS3361). However, in LPP.M.21, the prefrontal contacts the frontal posteromedially at a straight angle (Fig. 8A-B). The prefrontals are well-developed and tear-shaped (Fig. 8A-B, 10).

*Lacrimals.* The lacrimals are better preserved in PETMG R39 (Fig. 4-6) and LPP.M.21 (Fig. 8A-B) than in NHMUK PV R 3168 (Fig. 1-2) even though the medial and posterior margins are not preserved well. The lacrimals are large and triangular as in other teleosaurid taxa (Andrews, 1909, 1913), and constitute most of the anterior-lateral border of the orbits. Andrews (1913) reported paired openings approximately 5 to 7 cm anterior to the lacrimal in NHMUK PV R 3168 that he considered to be antorbital fenestrae, describing them as no more than 5 cm in length and longer than wide (Andrews, 1913). PETMG R39 (Fig. 4-6), NOTNH FS3361 (Fig. 10) and LPP.M.21 (Fig. 8A-B) show that *Lemmysuchus obtusidens* did not have antorbital fenestrae. As such, we interpret these “openings” in NHMUK PV R 3168 to be cracks caused by compression.

*Frontal.* The frontal (Fig. 1, 2, 3A, 3C) is a large and deep (dorsoventrally thickened) bone with no evidence of a midline suture. The anterior region slightly slopes anteriorly in conjunction with the posterior nasal and descends posteriorly, giving it a “domed” appearance (Fig. 2, 3A, 3C). The anterior process is not preserved; however, it is well-preserved in

LPP.M.21 (Fig. 8A-B), showing that it is as short as in most other teleosaurids (e.g. *S. leedsi*, see Andrews, 1913). The frontal contributes to the posteromedial border of the orbits (Fig. 1-2) and is well seen in LPP.M.21 (Fig. 8A-B). The frontal forms a straight vertical contact with the postorbital in dorsal view and forms the anterior medial borders of the supratemporal fenestrae. The ornamentation on the frontal does not differ from other OCF teleosaurids and consists of pronounced irregular ridges radiating from the centre of the bone.

*Postorbitals.* The large, robust postorbitals (Fig. 1, 3A, 3C) form the lateral and part of the posteroventral border of the orbits. In lateral view the dorsoventral suture of the postorbital contacts the squamosal and the left postorbital strongly contacts the frontal and forms the posterior margin of the orbit. Because both postorbitals are broken, the postorbital bars are not preserved in NHMUK PV R 3168. In LPP.M.21, the postorbital bar is similar to other OCF teleosaurids (Fig. 8A-B). It forms the posterior margin of the orbit, is slightly anteroposteriorly thickened and of standard mediolateral length.

*Parietal.* The unornamented parietal (Fig. 1, 2, 3A, 3C) is a single bone with no trace of a midline suture that contributes to the medial and posterior borders of the supratemporal fenestrae. Dorsally the parietal does not overhang the occipital condyle. The parietal bar is relatively thin and anteroposteriorly elongated. The posterior region of the parietal is anteriorly concave. In LPP.M.21 there is little to no ornamentation on the parietal (Fig. 8A-B).

*Squamosals.* The squamosals (Fig. 2, 3B, 3D) are large, anteroposteriorly elongate, L-shaped bones, and are well-preserved in LPP.M.21 (Fig. 8A-B). The squamosal forms the posterolateral border of the supratemporal fenestrae and its posterolateral surface is concave. It contacts the quadrate posteroventrally in lateral view. The squamosal bar is robust and anteriorly

contacts the postorbital bar (together forming the supratemporal arch). In NHMUK PV R 3168 the left squamosal is distorted and flattened due to poor preservation.

*Quadrates.* The quadrates (Fig. 1, 3B, 3D) are large, robust, and are strongly sutured to the squamosals and quadratojugals. The anterodorsal region of the quadrate contacts the squamosal and quadratojugal while the posteroventral margin articulates with the angular (= jaw joint) and medially contacts the exoccipital. The posteroventral lateral and medial hemicondyles are approximately the same size and length. They are both elongated mediolaterally, are oval in shape, and have rounded posterior edges. In occipital view the hemicondyles posteriorly extend further than the exoccipitals. The right quadrate is well-preserved while the left quadrate is not. In LPP.M.21, the quadrates large and mediolaterally expanded in ventral view (Fig. 8C-D).

*Quadratojugals.* The quadratojugals are dorsally and ventrally compressed and are not visible in dorsal view. The posterior region of the quadratojugal is expanded mediolaterally to accommodate the quadrate and extends slightly further than the outermost tip of the quadrate.

*Ectopterygoids.* Only the right ectopterygoid is preserved in NHMUK PV R 3168. Anteriorly it contacts with the maxilla. The contact with the pterygoids and palatines cannot clearly be seen. The dorsal surface of the ectopterygoid is slightly concave. The right ectopterygoid is preserved in LPP.M.21, and curves ventromedially (Fig. 8A-B).

*Supraoccipital.* The supraoccipital is positioned ventral to the parietal and is only visible in occipital view (Fig. 3B, 3D). The ventral edge is not triangular but curved so it appears as two 'lobes' (Fig. 3). A large nuchal crest (Fig. 3B, 3D) is situated directly in the middle of the supraoccipital.

*Exoccipital.* The exoccipital makes up the majority of the occipital surface of the cranium. The right side has been medially compressed and the dorsal rim curves medially, while

the left side tilts dorsally and flares mediolaterally. The **exoccipital** is dorsally expanded above the foramen magnum, as in *Machimosaurus buffetauti* and *M. mosae* (Hua, 1999; Martin & Vincent, 2013). Laterally the **exoccipital** descends rapidly, so in occipital view it appears almost box-like. The exoccipitals contribute to the occipital condyle. The **paraoccipital** processes are small and the lateral wings are elongate and robust. The foramen for cranial nerve **XII** is small and parallel to the foramen magnum (Fig. 3B, D).

*Basioccipital.* The basioccipital contributes to the ventral region of the foramen magnum and is slightly wider than tall. The occipital condyle is larger and more circular than the foramen magnum. In ventral view (LPP.M.21), two well-developed and slightly anteroposteriorly elongated basioccipital tuberosities are visible, with the left one being larger due to variable preservation (Fig. 8C-D).

*Pterygoid.* **The right pterygoid wing is present, but** it is poorly preserved; it is unclear how complete the pterygoid wing is in this specimen without access to the palatal view. The left pterygoid is similarly broken but the lateral pterygoid wing is accessible laterodorsally. It is large and elongated craniocaudally and lateromedially. The dorsal surface of the wing is concave and the posterior region curves anteromedially, possibly due to breakage. In ventral view (LPP.M.21), the pterygoid is thin and elongated, and contributes to the medial and posterior borders of the suborbital fenestrae, which are tear-shaped (thin anteriorly, wide and slightly rounded posteriorly) (Fig. 8). In LPP.M.21, the anterior process of the pterygoid articulates with the palatines (Fig. 8C-D).

*Palatines.* All information from the palatines comes from LPP.M.21 and PETMG R39. The palatines (Fig. 8C-D) are dorsoventrally thin, elongate bones and are similar in form to other teleosaurids, such as *S. leedsi* (NHMUK PV R 3806) (Andrews, 1913). In LPP.M.21 the anterior

regions of both palatines are not preserved and both posterior regions are slightly deformed; however, PETMG R39 preserves the anterior palatines that are slightly rounded, have small anterior processes, and articulate with the posterior processes of the maxillae (Fig. 4C-D). The palatines contact one another along the skull midline until posteriorly they are separated by the anterior process of the pterygoid. The anterior extensions of the palatine are nearly parallel to the maxillary tooth row, similar to *Machimosaurus buffetauti* (Martin & Vincent, 2013).

*Basisphenoid.* The anterior surface of the basisphenoid (LPP.M.21) is deformed (Fig. 8C-D). This structure has two elongated posterolaterally-directed processes and comes into posterior contact with the quadrate.

*Other elements.* The proötic and laterosphenoid are not visible in dorsal or ventral views, and as a result we could not properly describe these bones.

## MANDIBLE

The mandible of NHMUK PV R 3168 is diagenetically deformed and attached to the cranium so that the dorsal surface is not visible. The mandibular symphysis measures ~58 cm, contributing ~42.3% of the entire length (Young *et al.*, 2015b). Among other specimens only a short segment of the right mandibular ramus in PETMG R39 is preserved and it clearly shows the contact amongst the dentary, angular and splenials to be posterior to the mandibular symphysis on the ventral side. The majority of the mandible is also preserved in LPP.M.21, as the posterior-most areas are missing. Our mandibular description refers to the holotype (NHMUK PV R 3168) unless otherwise specified.

*Dentary.* The dentary (Fig. 1, 2, 3A, 3C) is a long major element of the lateral surface of the lower jaw, as in the majority of crocodylomorphs. The anterior end of the dentary is spatulate

and laterally enlarged as in *Machimosaurus* (Young *et al.*, 2014a). There are approximately **twenty-nine** (possibly one or two more alveoli) alveoli per dentary (at least **twenty-five** alveoli per dentary in LPP.M.21) of which approximately **twenty-two to twenty-four** are adjacent to the mandibular symphysis (Andrews, 1913; Young *et al.*, 2015b). Many of the teeth are missing but those still *in situ* are well-preserved and complete. The four anterior-most teeth are elevated dorsally when compared to the rest of the tooth row, as normally seen in teleosaurids such as *S. leedsi* (Andrews, 1913). The dentition is strongly heterodont compared to other teleosaurids; the teeth in the anterior region are large and have a higher crown base to length ratio, whereas the posterior crowns are characterised by a lower ratio. The interalveolar distance is generally smaller than half the alveolar length but always longer than a quarter of the alveolar length.

*Surangular and angular.* The surangular (Fig. 2) is thin and posteriorly elongated in lateral view. The surangular, in conjunction with the angular and articular bones, is anteroposteriorly elongated, and forms a distinctive ‘V’ shape. The anterior region of each surangular gradually terminates near the last alveolus of the dentary. The posterior margin of the surangular is rounded and it bounds a small mandibular fenestra. The angular (Fig. 2) is elongate and occupies a more extensive area than the surangular in lateral view. The angular is more robust than the surangular with a strong dorsal curvature (Fig. 2) which articulates with the retroarticular process of the articular. The dorsal and the ventral surfaces of the angular are not viewable in NHMUK PV R 3168. The prearticulars, which are supposed to be present (Andrews, 1913), **are not seen and therefore can only be seen in palatal view.**

*Articular.* The anterior region of the articular of NHMUK PV R 3168 is hidden by the quadrate and surrounding bones. The retroarticular process is, however, extremely elongate and triangular-shaped in dorsal view and it bears a strongly pronounced anteroposterior keel, which

separates the medial and lateral grooves. Both grooves are concave, in particular the lateral ones. The posterior end of the retroarticular process is slightly rounded, concave, and curves dorsolaterally. The glenoid fossa is large and faces mediodorsally.

*Splénial.* All of the information on the splénial comes from LPP.M.21. Only the anterior regions of these bones are preserved. The splénial (Fig. 9) is situated medially and is mediolaterally thinner in width than the dentaries. Both splénials begin at approximately the fifteenth mandibular alveoli in the dentaries. While the coronoids are not preserved, the sulci where they are hosted are. They participate with the mandibular symphysis, and the anterior extension begins at approximately the **twenty-first** alveoli of the dentaries and continue parallel, and eventually past, the tooth row.

## DENTITION

As discussed above, the dentition of NHMUK PV R 3168 is both heterodont and serrated (with both true and false denticles; Young *et al.*, 2015b). The holotype has **thirty-three** isolated teeth, as well as *in situ* teeth: approximately **twenty-nine** in each dentary, four per premaxilla, and approximately **twenty-nine** (possibly more) per maxilla (verified by LPP.M.21). The teeth (Fig. 12A-D) are conical, robust, single-cusped and bicarinate, as in *Machimosaurus* (**Martin & Vincent**, 2013; Young *et al.*, 2015a, 2015b; Foffa *et al.*, 2015; Fanti *et al.*, 2016). They have a blunt apex in comparison to other *Steneosaurus* species (Andrews, 1913). The enamel is thinner towards the base of the crown and becomes progressively thicker towards the apex (Fig. 12A-D), much like in *Machimosaurus* (Young & Steel, 2014).

There are many protruding apicobasal enamel ridges on these teeth, giving them a “wrinkled” texture. These apicobasal ridges are close to one another and run parallel from the

base of the crown to approximately three quarters of the entire tooth. At the apex the ridges are considerably shorter and are organised in the typical anastomosed pattern that has been described for other members of Machimosaurini (Young *et al.*, 2014a, 2015b; Jouve *et al.*, 2016). Teeth with blunter apices are situated in the middle and posterior regions of the tooth-row and those with sharper apices are near the anterior. The teeth have true denticles and false denticles (Young *et al.*, 2015b), although the latter cannot be seen clearly with the naked eye. True denticles are situated on the carina and false denticles are formed via interactions between the carina and enamel ridges (Young *et al.*, 2015b).

## POSTCRANIAL SKELETON

*Vertebral column and ribs.* Most of the vertebral column of NHMUK PV R 3168 is preserved, so our description of vertebrae is based on this specimen unless otherwise specified.

The first (atlas) and second (axis) vertebrae are fused together, forming the well-developed “complex” (Fig. 13A) that is common in teleosaurids (Andrews, 1913; Martin & Vincent, 2013). The axis neural arch is not present and the odontoid and intercentrum are not distinct from one another due to the degree of atlas-axis fusion. The lateral surfaces of the axis are concave and have large protruding regions for the parapophyses. There are no diapophyses present behind the odontoid process on the axis, which is slightly larger than the atlas.

The centra of the remaining six cervical vertebrae are amphicoelous, slightly longer in width than height, and have sub-circular anterior and posterior articular surfaces. There is a small notch in the middle of the dorsal margin of the centrum that is visible in anterior view. In lateral view the centra are slightly spool-shaped with concave ventral margins similar to *Machimosaurus* (Martin & Vincent, 2013). The **prezygapophyses** are slightly anterior to the

centrum edge, with the anterior articular facets facing ventrally and curving inwards. The **postzygapophyses** extend laterally just above the base of the neural spine. The posterior articular facets face dorsally and the transverse processes are laterally wide. The neural spine is rectangular and nearly as tall as the centrum.

Only one complete cervical rib is preserved. It is T-shaped in dorsal view and has a distinct dorsomedial curvature (Fig. 13B). Both the tubercular and capitular processes of this rib are rounded, and its tubercular is larger than the capitular. The distal area behind the processes is short and does not extend posteriorly while the area in front is considerably more elongated.

**Fourteen** robust thoracic vertebrae are preserved in NHMUK PV R 3168 although only one is complete. The centra (Fig. 14) are massive and appear spool-shaped in ventral view. The articular surfaces are amphicoelous and oval (slightly taller in length than wide). The neural spine is short and broad, and not as tall as the centrum. The transverse processes are long and wide, and are positioned approximately at the centre of the neural arch. They are broadened anteroposteriorly, with rounded proximal ends (Fig. 14). There is a second projection on the transverse process, separated from the vertebral body by a small concavity. This projection is small, circular, and laterally faced.

The dorsal ribs (Fig. 13C) are dichoccephalous and have robust heads and bodies. The capitulum of these ribs is proximodistally lengthened and dorsally rounded (Fig. 13C) and each neck is elongated, separating the capitulum from the tuberculum. The articular facets are flat and separated from the top of the tuberculum. The tuberculum is a small nodule located in the middle of the rib body. The articular facet and tuberculum are both laterally shifted so that they are nearly situated on the lateral edge of the body. The costal groove is deep and runs from the

ventral tuberculum to near the end of the rib body, disrupting an otherwise sub-circular cross-section. The sternal end of the rib is anteroposteriorly flat, straight and thin in width.

There are three sacral vertebrae (Fig. 15) (Andrews, 1913). The first two are true sacral vertebrae and the first caudal vertebra acts as a pseudo-sacral, as it looks and functions as a third sacral. This 'third' sacral has large, mediolaterally expanding transverse processes and an expanded lateral iliac attachment area, much like the two true sacrals. The neural spines are short and robust and the sacral ribs curve and contact one another (Andrews, 1913). The anterior margin of the posterior area of the second sacral vertebra (Fig. 15B, D) has a large, expanded projecting flange. The presence of a "third" sacral vertebra is an autapomorphy shared by *L. obtusidens* and *Machimosaurus* spp. within Thalattosuchia (Young *et al.*, 2014a).

Only **twenty-one** caudal vertebrae are preserved. However, it is likely that the total caudal vertebral count is similar to that of *S. leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701), of around thirty-six to thirty-eight (Andrews, 1913) or even higher (as in *S. edwardsi* PETMG R275). The caudal vertebrae become increasingly thinner and smaller from anterior to posterior. The typical posterior caudal vertebral centrum is thin, taller than wide, and strongly hourglass-shaped. The neural spines are thin, tall, and higher than the centrum.

*Shoulder girdle and fore-limb.* No coracoids are preserved. The scapulae (16A-B) are of the typical thalattosuchian type similar to *S. leedsi* (NHMUK PV R 3806) (Andrews, 1909, 1913), being elongate bones with a slender body. The proximal and distal regions extend mediolaterally, with the distal end being slightly larger. The scapular glenoid fossa (16B) is half-moon shaped. The proximal region of the humerus (16C-D) is not preserved, so the deltopectoral crest and proximal head cannot be described. The shaft of the humerus is straight and the distal end is rounded. There is a concave, oval (Andrews, 1913) depression in the middle of the distal

end of the humerus in lateral view (16D). The ulna is similar in shape to other Callovian teleosaurids such as *S. leedsi* (Andrews, 1913). The proximal region is slightly deformed and fractured. The radius is a squat, straight bone, and is unornamented.

*Pelvic girdle and hind-limb.* The ischium (Fig. 17A-B) is squat and robust and only preserved in NHMUK PV R 3168. The two proximal articulation processes are divided by a small yet deep oval notch. The smaller process has a circular proximal head while the larger process is posterolaterally curved. A large protruding ridge runs proximodistally in line with the second proximal process. Two small, sub-circular “bumps”, presumably for muscle attachment, are present approximately 10 cm from the posterior edge. These are not as prominent in other teleosaurids, such as *S. leedsi*. The ischial blade (Fig. 17A-B) is large, expanded, and thick, with the posteroventral, sub-square border. The anterior flange is thin and broken.

Both NHMUK PV R 3168 and PETMG R39 preserve an ilium. However, in the latter specimen it is still articulated with the sacrum and femoral head, is missing the anterior side, and is still partially covered in matrix. Conversely, the NHMUK PV R 3168 ilia (Fig. 17C-D) are well-preserved, square-shaped and compact. The anterior-facing vertical outer rim has a slight sub-horizontal curvature (Fig. 17C-D). The medial attachment points of the sacral ribs are faint (Fig. 17C) so that it is difficult to tell the anterior iliac facet and posterior iliac facet apart from one another (Fig. 17C). The acetabular depression (or acetabular notch) is a smooth U-shaped arch in lateral view (Fig. 17C) and is halfway through the ventral articulating points with the pubis and ischium. The anterior articulation facet in front of the incision is larger than that of the posterior articulation facet, and extends ventrally. The supraacetabular crest (Fig. 17D) is poorly developed, as is the shallow acetabulum (Fig. 17D). The preacetabular (= anterior process) (Fig. 17D) is shortened (with respect to other thalattosuchians) and well rounded, and curves laterally.

The majority of one pubis is preserved in NHMUK PV R 3168 (Fig. 17E-F) but the pubic boot is missing. Conversely, the ventral part of the pubis is possibly preserved in matrix in PETMG 39 (PETMG R31) (Fig. 24D). The body and distal region of the neck of the NHMUK PV R 3168 pubis are deformed into curving medially. The anterodistal pubic plate is expanded and rounded along the ventral rim (Fig. 17E-F).

All the information on the hind-limb comes from NHMK PV R 3168. The femur (Fig. 18) is slender and long, with a weak sigmoidal curvature throughout the shaft, which is typical of many teleosaurids (Andrews, 1909, 1913). The proximal head (Fig. 18) extends medially into the acetabulum while the anterior region of the femoral head is ventrally curved. There is a large concavity on the posterolateral surface of the head. The posterior margin of the head is rugose, and this rugosity continues down through the neck of the femur. In dorsal view, the head is circular to sub-circular, with an expanded posteromedial tuber. The “fourth trochanter” (i.e. no true process, just the rugose area mentioned before) is small compared to other Callovian teleosaurids and is situated on the medial neck of the femur (Fig. 18). The two posterodistal condyles - medial (greater) and lateral (lesser) - are clearly visible with the medial condyle being slightly larger (Fig. 18).

The tibia (Fig. 19) is a robust bone with the proximal end being larger than the distal end. In dorsal view the proximal end is heart-shaped. The tibial tuberosity (Fig. 19A, 19C) is large and projects posterodistally. In lateral view it is directed ventrally at a sharply obtuse angle (Fig. 19C). The medial side of the tibial neck is slightly concave, while the lateral side is flat (Andrews, 1913). The distal end is rounded, although it is obstructed by the distal area of the fibula. The fibula (Fig. 19) is an elongate, slender, and straight bone, with only the distal half preserved. It is slightly smaller in width (Fig. 19A) than the tibia.

There are three ankle bones (Fig. 20): the calcaneum (Fig. 20A-D), astragalus (Fig. 20E-G), and cuboid (Fig. 20H-I). They are all robust and large, with well-developed articulation surfaces. Excluding the clear difference in the large size, the three ankle bones resemble those of other teleosaurids (Andrews, 1913). All metacarpal and metatarsal fragments are slender, as are four complete phalanges (all relatively the same length).

*Osteoderms.* Fifty-six dorsal, mostly unarticulated osteoderms are present in NHMUK PV R 3168. Smaller osteoderms are box-shaped, whereas larger ones are elongate and oval. A prominent anteroposteriorly-directed keel is present (Fig. 21), being more pronounced in larger osteoderms. The pits on the dorsal surface of larger osteoderms (Fig. 21) are oval, elongate, deep, and spaced apart. They radiate outwards from the centre of the keel in a “starburst” pattern. The pits generally become larger further from the center of the osteoderms. Some pits merge with one another along the outermost lateral margins of the osteoderms. The ventral surfaces of all osteoderms are smooth and unaltered.

## DISCUSSION

### SPECIMENS PREVIOUSLY REFERRED TO ‘*STENEOSAURUS*’ *OBTUSIDENS*

Andrews (1913) referred two large, but very incomplete, specimens to ‘*Steneosaurus*’ *obtusidens*: NHMUK PV R 3169 and NHMUK PV R 3898. The former comprises one scapula, right coracoid, left ulna, one radius, right ilium, femora, pubes, tibiae, a fibula, five carpal/tarsal bones, one hyoid, three tracheal rings, five osteoderms, and numerous teeth and fragmentary elements. Nine characteristics differentiate NHMUK PV R 3169 from *Lemmysuchus obtusidens*:

(1) the tibial tuberosity is not angled as in *L. obtusidens* (NHMUK PV R 3168). Instead it is directed almost 180 degrees horizontally, similar to *Steneosaurus leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701 and PETMG R178) (Fig. 24A-C).

(2) While the femur of NHMUK PV R 3169 is long and gracile, somewhat similar to *L. obtusidens* (NHMUK PV R 3168), it is slightly smaller in length and width (possibly from a smaller individual; Fig. 25A-C).

(3) In dorsal view, the femoral head is larger and more triangular than that of *L. obtusidens* (NHMUK PV R 3168), due to an enlarged posteromedial tuber (Fig. 25A-C). This is somewhat similar to the condition seen in the metriorhynchid *Tyrannoneustes lythrodectikos* (GLAHM V1145; Young *et al.*, 2013).

(4) The greater femoral condyle of the NHMUK PV R 3169 is much larger than the lesser condyle (Fig. 25A-C), as opposed to *L. obtusidens* (NHMUK PV R 3168) in which the greater condyle is only slightly larger than the lesser condyle.

(5) The ilium has a slender, elongate anterior process, as opposed to the short, stubby anterior process of *L. obtusidens* (NHMUK PV R 3168) (Fig. 25D-F).

(6) The ilium has only two sacral rib articulation surfaces, and these are large and well developed. In *L. obtusidens* (NHMUK PV R 3168) the ilia have three poorly developed sacral rib articulation surfaces (Fig. 25D-F).

(7) The acetabulum is deep, and the anterior-most ridge of the ilium is vertical, whereas in *L. obtusidens* (NHMUK PV R 3168) the acetabulum is poorly concave (see Fig. 17D).

(8) The anterodistal rim of the pubic plate is straighter and sub-square, whereas in *L. obtusidens* (NHMUK PV R 3168) the pubic plate rim is rounded and circular.

(9) The osteoderms of NHMUK PV R 3169 are an enigma. Out of the five osteoderms preserved, two have a dorsal pitting pattern similar to that of *L. obtusidens* (NHMUK PV R 3168). These pits are elongated, and radiate out from the centre of the keel. The other three are similar with those seen in *S. edwardsi* (NHMUK PV R 3701 and PETMG R178). The pits are not elongated and occur in a random arrangement (Fig. 24D-F). Thus we can conclude that NHMUK PV R 3169 is not *L. obtusidens*, and is morphologically more similar to *S. edwardsi* (NHMUK PV R 3701) or *S. leedsi* (NHMUK PV R 3806).

Andrews' (1913) second *L. obtusidens* referred specimen, NHMUK PV R 3898, consists of an ilium, ischium and femur. All three bones are very large and robust. However, the features in these bones differ vastly from those seen in the *L. obtusidens* holotype (NHMUK PV R 3168). The ilium of NHMUK PV R 3898 has: (1) an elongate and slender anterior process; (2) a pronounced supraacetabular crest; and (3) a strongly concave acetabulum (Fig. 23E; see Johnson *et al.*, 2015). This differs from the *L. obtusidens* (NHMUK PV R 3168) ilium, which has a short anterior process, a greatly reduced supraacetabular crest, and a shallow acetabulum (Fig. 25D). The ischium of NHMUK PV R 3898 has a sub-triangular posteroventral margin of the ischial blade (Johnson *et al.*, 2015), as opposed to the broad, sub-square posteroventral margin in *L. obtusidens* (NHMUK PV R 3168). As Johnson *et al.* (2015) showed, these morphologies exclude NHMUK PV R 3898 from *L. obtusidens*, and demonstrate that it in fact pertains to *S. edwardsi*.

Two additional specimens from the Peterborough Member of the OCF are here referred to *Lemmysuchus obtusidens*: PETMG R39 and PETMG R178. The first specimen, PETMG R39, is a partial skull (Fig. 4-6) and partial mandible (only preserving the anterior end of the mandibular symphyseal region) (Fig. 7), four articulated dorsal vertebrae (Fig. 26A-B), an osteoderm fragment, sacrum, and some isolated bone fragments (Fig. 26C-D). Parts of this

specimen have been referred to PETMG R31, another specimen that it has been constantly mixed and stored with. However, a specimen registration entry mentions that PETMG R31 “fits with R39”. Nevertheless, the preservation and texture of the bones and the matrix are identical in both specimens, which importantly also share autapomorphies of *L. obtusidens*. Based on these lines of evidence we consider PETMG R39 and PETMG R31 belonging to the same individual and both pertain to *L. obtusidens*. The skull of PETMG R39 (Fig. 4-6) includes the nasals, posterior maxillae, jugal and anterior orbit. Several alveoli are visible on both lateral sides of the maxillae. The alveoli are separated by variable interalveolar spaces (always fewer than one alveolus length but longer than half) and most teeth are still *in situ*. Two erupting teeth show the typical Machimosaurini crown ornamentation. This specimen is referable to *L. obtusidens* due to the following features: 1) closure of the antorbital fenestrae; 2) there is a slight beginning of a “dome” near the posterior section of the nasals; 3) the teeth have blunt apices, denticles, and the characteristic Machimosaurini enamel ornamentation pattern; 4) an extreme anteroposterior elongation of the jugal.

PETMG R31 consists of five articulated vertebrae (two complete dorsal, two complete and one incomplete sacral), incomplete ilium, femur and pubis (or ischium?) (Fig. 26C-D). The sacral vertebrae largely resemble the *L. obtusidens* holotype (NHMUK PV R 3168). Although the posterior-most vertebra is incomplete, one of its ribs is partially preserved, and there is little doubt that it is a sacral rib due to its shape and dimension, with an expanded flange. The fragmentary status of the specimen and abundant matrix around the bones does not allow direct comparison of other elements. Thus, PETMG R31 pertains to *Lemmysuchus* based on the presence of three sacral vertebrae, and the fact that it likely belongs with PETMG R39.

The second specimen, PETMG R178, represents a nearly complete skeleton. However, it lacks characteristics seen in the *L. obtusidens* holotype (NHMUK PV R 3168). The dorsal rim of larger cervical ribs does not curve dorsomedially. The shape and position of the tuberculum in the dorsal ribs is similar to *S. edwardsi* (NHMUK PV R 3701) whereas *L. obtusidens* (NHMUK PV R 3168) displays a more medial position of the tuberculum. The ilium has a deep well-developed acetabulum and an elongate, slender anterior process (differing from the shallow acetabulum and the proportionally shorter anterior process seen in *L. obtusidens* (NHMUK PV R 3168) (Fig. 25D-E). The ischium is gracile and the posteroventral margin of the ischial blade is sub-triangular in shape, which differs from the robust ischium with a square-shaped posteroventral ischial blade of *L. obtusidens* (NHMUK PV R 3168). The proximal tibia is not strongly deflected anteriorly as in *L. obtusidens* (NHMUK PV R 3168) and *Machimosaurus* (Hua, 1999). The skull of PETMG R178 lacks the strongly convex (“domed”) nasals seen in *L. obtusidens* (NHMUK PV R 3168 and PETMG R39), although this may be due to preservation. The dorsal osteoderm ornamentation differs from that seen in *L. obtusidens* (NHMUK PV R 3168). The pitting pattern is random, as seen in *S. edwardsi* (NHMUK PV R 3701). Thus, PETMG R178 is not referable to *L. obtusidens*, and is more morphologically similar to *S. edwardsi*.

Hua *et al.* (1994) described a fragmentary skeleton from the upper Callovian of Villers-sur-Mer, Calvados, France, and referred it to ‘*S.* *obtusidens*. It was the first non-English specimen referred to *L. obtusidens*. However, comparing the figures from Hua *et al.* (1994) with the *L. obtusidens* holotype (NHMUK PV R 3168) shows that the ischium, ilium, and dorsal osteoderms do not match. In the French specimen, the ilium anterior process is much more elongated and slender than that seen in the *Lemmysuchus* holotype (NHMUK PV R 3168). The

supraacetabular crest is pronounced, the acetabular depression is strongly concave, and the posterior margin of the ischial blade is sub-triangular. The osteoderm (Hua *et al.*, 1994; Figure 1a) lacks the ‘starburst’ pattern of pits. As with PETMG R178, this specimen more closely resembles *S. edwardsi* than *L. obtusidens*.

Foffa *et al.* (2015) described an incomplete mandible (DORCM G3939), which preserves the symphyseal region up to approximately the nineteenth alveoli (alveoli one and two are missing). Due to the incompleteness of its preservation, the lower jaw could not be confidently assigned to a taxon, but was referred to '*S.* cf. *obtusidens*'. It is difficult to determine for certainty whether DORCM G3939 is *L. obtusidens*, as so little of it is preserved; however, the high symphyseal tooth count, the Meckelian canal not being exposed on the dorsal surface of the splenials, the blunt tooth apices, the anastomosed apical enamel ornamentation, presence of denticles, and deep reception pits place it within Machimosaurini. If this specimen does belong to *L. obtusidens*, it expands the stratigraphic range of this taxon into the early Oxfordian.

#### COMPARISON WITH OTHER OCF TELEOSAURIDS

*Lemmingsuchus obtusidens* (NHMUK PV R 3168, PETMG R39) has numerous teleosaurid apomorphies including: a laterally expanded premaxilla and anterior dentary, and a relatively small frontal (Andrews, 1913). However, *L. obtusidens* has a number of autapomorphies, particularly in the postcranial skeleton (Tables 1 and 2).

Andrews (1913) recognised some of these autapomorphies: (1) three sacral vertebrae; (2) blunt, heavily ornamented teeth; and (3) a unique osteoderm pattern (however, points 1 and 2 are now recognised as characters shared with *Machimosaurus*, see diagnosis and discussion; Young *et al.*, 2014a, 2015b; Jouve *et al.*, 2016). While Andrews (1913) gave a generally good

description of the skull, we disagree with some of his observations regarding the antorbital fenestrae, lacrimal, and sacral vertebrae. These autapomorphies readily distinguish it from two common OCF teleosaurids, *S. leedsi* and *S. edwardsi*.

The skull of *L. obtusidens* (NHMUK PV R 3168) is marked similar to *Machimosaurus* (Table 1; see Krebs, 1967; Buffetaut, 1982a; Martin & Vincent, 2013; Young *et al.*, 2014a; Fanti *et al.*, 2016) in being large and robust. This is opposite of *S. leedsi* (NHMUK PV R 3806), which has a slender skull. *Steneosaurus edwardsi* (NHMUK PV R 3701, PETMG R178) has a large skull similar to *L. obtusidens* (NHMUK PV R 3168), with some specimens of *S. edwardsi* being even larger than the *L. obtusidens* holotype. Both *S. leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701) lack the dorsoventrally deep “domed” nasals-frontal as seen in *L. obtusidens* (NHMUK PV R 3168). The supratemporal fossae in *L. obtusidens* (NHMUK PV R 3168) extend further anteriorly along the frontal than those of *S. leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701). The articular, surangular, and angular bones of *L. obtusidens* (NHMUK PV R 3168) are more elongated anteroposteriorly than lateromedially, giving them a combined ‘V’ shape. This differs in comparison to *S. edwardsi* (NHMUK PV R 3701), in which the three bones are not elongated anteroposteriorly. *S. leedsi* (NHMUK PV R 3806) displays the same shape and anteroposterior elongation as *L. obtusidens* (NHMUK PV R 3168), although it is smaller and slenderer. The Meckelian canal is not excavated on the dorsal surface of the symphyseal splenial in *L. obtusidens* (NHMUK PV R 3168) (Fig. 27E), which it shares with *Machimosaurus mosae* neotype (Fig. 27F), *Steneosaurus edwardsi* (NHMUK PV R 3701) (Fig. 27C), and *Steneosaurus hulkei* (NHMUK PV R 2074) (Fig. 27D). Other thalattosuchians, such as *Steneosaurus leedsi* (NHM UK PV R 3806, NHMUK PV R 3320) (Fig. 27A-B), have the Meckelian canal deeply excavated on the dorsal surface of the splenial. As

mentioned before, *L. obtusidens* (PETMG R39) lacks any evidence of antorbital fenestrae (*contra* Andrews, 1913), the condition shared with *S. edwardsi* (PETMG R178), *Machimosaurus*, and *Steneosaurus heberti* (MNHN.F 1890-13). Small, slit-like fenestrae are present in *S. leedsi* (NHMUKPV R 3806). The teeth of *S. edwardsi* (NHMUK PV R 3701) and *S. leedsi* (NHMUK PV R 3806) are more elongate and slender than those of *L. obtusidens* (NHMUK PV R 3168), and have pointed apices continuously throughout the maxillae and dentaries, as well as lacking an anastomised apical pattern.

Aside from the osteoderms and sacral vertebrae, Andrews (1913) largely neglected to describe the postcranial skeleton. Herein, we have shown the postcrania of *L. obtusidens* to be distinctive (Table 2). One striking difference found in *L. obtusidens* (NHMUK PV R 3168) is the absence of axial diapophyses. These processes are present in *S. leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701). *Steneosaurus bollensis* however also lacks the axial diapophyses (see Westphal, 1962).

The two primordial sacrals in *L. obtusidens* (NHMUK PV R 3168) are similar in form to *S. leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701) (Andrews, 1913). The anterior projecting flange on the second sacral vertebra is seen in *S. leedsi* (NHMUK PV R 3806), although it is much smaller and does not extend anteriorly (Fig. 28B) as in *L. obtusidens* (NHMUK PV R 3168) (Fig. 28A). The cervical rib of *L. obtusidens* (NHMUK PV R 3168) (Fig. 29A) has a distinct medial curvature in the dorsal rim. The cervical ribs of *S. edwardsi* (NHMUK PV R 3701) and *S. leedsi* (NHMUK PV R 3806) both have straight, T-shaped dorsal rims (Fig. 29B-D). The area posterior to the tubercular and capitular processes of the cervical rib is also shorter than the anterior area in *L. obtusidens* (NHMUK PV R 3168), whereas in *S. edwardsi*

(NHMUK PV R 3701) and *S. leedsi* (NHMUK PV R 3806) they are more elongated (Fig. 28) and are approximately the same length.

There are three features seen in the dorsal ribs of *L. obtusidens* (NHMUK PV R 3168) in conjunction with *S. edwardsi* (NHMUK PV R 3701) and *S. leedsi* (NHMUK PV R 3806) (Fig. 30):

(1) Both the tuberculum and articular facet are shifted onto the medial edge of the rib in *L. obtusidens* (NHMUK PV R 3168), as described before. The position of these articular surfaces in *L. obtusidens* (NHMUK PV R 3168) could be due to either the massive size of the ribs causing the tuberculum to shift medially or are solely due to deformation. In *S. leedsi* (NHMUK PV R 3806) the tuberculum and articular surface are situated directly in the middle of the rib, and are small. In *S. edwardsi* (NHMUK PV R 3701) the tuberculum is also situated medially, but closer to the lateromedial edge of the rib.

(2) The proximal head of the ribs in *L. obtusidens* (NHMUK PV R 3168) and *S. edwardsi* (NHMUK PV R 3701) are elongated proximodistally and are rectangular in dorsal view. In medial view, the dorsal edges of the two specimens appear curved. In *S. leedsi* (NHMUK PV R 3806), the rib head is as long as it is wide. It is flat and circular in dorsal view and straight in medial view.

(3) The sternal rib end is flat in *L. obtusidens* (NHMUK PV R 3168) and *S. edwardsi* (NHMUK PV R 3701), while in *S. leedsi* (NHMUK PV R 3806) it is more rounded, similar to metriorhynchids (Wilkinson *et al.*, 2008).

There is also a combination of six pelvic and hind-limb characteristics that readily distinguishes *L. obtusidens* from *S. leedsi* and *S. edwardsi* (Table 2). These characteristics were not noted by Andrews (1909, 1913), and are here listed for the first time:

(1) The iliac anterior process in *L. obtusidens* is short and squat, as opposed to the elongate, slightly thinner processes *S. leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701) (Andrews, 1913).

(2) The poorly developed sacral rib attachment areas and acetabulum of *L. obtusidens* (NHMUK PV R 3168) differs from *S. edwardsi* (NHMUK PV R 3701) and *S. leedsi* (NHMUK PV R 3806) in that in *L. obtusidens* they are both poorly developed (possibly due to preservation).

(3) The posteroventral margin of the ischial plate in *L. obtusidens* (NHMUK PV R 3168) is sub-square in shape, and is not as blunt or widened as seen in metriorhynchids (e.g. Wilkinson *et al.*, 2008), but is broader than the sub-triangular posterior margin seen in *S. leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701) (Andrews, 1913).

(4) The anterodistal rim of the pubic plate is curved in a circular fashion, much like that seen in *S. leedsi* (NHMUK PV R 3806). This differs from *S. edwardsi* (NHMUK PV R 3701), in that the anterodistal pubic plate rim is straight and square-like with a sharp anterodistal edge.

(5) The sigmoidal curvature of the *L. obtusidens* (NHMUK PV R 3168) femur is most similar to *S. leedsi* (NHMUK PV R 3806) in being weak. In *S. edwardsi* (NHMUK PV R 3701, NHMUK PV R 3898) the curvature throughout the femur is strongly pronounced (Johnson *et al.*, 2015).

(6) In *L. obtusidens* (NHMUK PV R 3168) there is a distinctive sharply angled tibial tuberosity that is shared with *Machimosaurus* (Hua, 1999). In *S. leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701) the tibial tuberosity is horizontal and shows no angle.

The dorsal-surface “starburst” osteoderm ornamentation of *L. obtusidens* (NHMUK PV R 3168) differs from the ornamentations seen in *S. edwardsi* (NHMUK PV R 3701) and *S. leedsi*

(NHMUK PV R 3806) (Fig. 19D-F). In *S. edwardsi* (NHMUK PV R 3701 and PETMG R178), the majority of pits are circular in shape and are not as deep as *L. obtusidens* (NHMUK PV R 3168). The pits are closely packed together and are distributed in a random pattern, as opposed to the ‘starburst’ pattern in *L. obtusidens* (NHMUK PV R 3168). In *S. leedsi* (NHMUK PV R 3806), the majority of the pits are circular, with some being oval in shape. The pits radiate outwards in a sub-circular fashion and are closely packed together, which differs from *L. obtusidens* (NHMUK PV R 3168).

Andrews (1909, 1913) described the postcranial material (not including the dorsal osteoderms) of *L. obtusidens* as so similar “to that of *S. durobrivensis* [that] special description is unnecessary.” However, here we have shown that not only is the postcrania of *L. obtusidens* distinct, but there were at least two different postcranial morphotypes among OCF teleosaurids. A robust, stockier morphotype was represented by *Lemmysuchus* (i.e. stout ilia and tibiae, broad ischial blade, large centra, and three sacral vertebrae), and a slenderer morphotype was represented by *S. leedsi* and *S. edwardsi* (with gracile ilia, tibiae, and ischial blade, smaller centra, and two sacral vertebrae). These differences may reflect habitat partitioning among sympatric teleosaurids, with *L. obtusidens* suggested as being more terrestrial, and/or living in higher energy environments.

## BODY LENGTH

The basicranial length of the *L. obtusidens* holotype (NHMUK PV R 3168) is approximately 1.16 m. The vertebral column is not completely preserved. There is one dorsal and one cervical vertebrae missing, and the majority of the caudal region is missing. Using the Young *et al.* (2016b) basicranial length vs body length equations yields a total body length estimate of

between 556.995 cm and 558.173 cm. Using the femoral length vs body length equations yields a total body length estimate of between 575.742 cm and 582.3 cm. Young *et al.* (2016b) found femoral-based estimates to be the more reliable than cranial-based estimates, thus a body length of ~5.8m seems likely for *L. obtusidens*.

*Lemmysuchus obtusidens* has long been considered to be the largest teleosaurid in the Oxford Clay Formation (see Andrews, 1913; Young *et al.*, 2015b). However, as noted above, the largest specimen previously referred to *L. obtusidens* (NHMUK PV R 3898) has recently been re-assigned to *Steneosaurus edwardsi* (Johnson *et al.*, 2015). Young *et al.* (2016b) found NHMUK PV R 3898 to be between 659.51 cm and 666.66 cm using the femoral-based equations. Thus, *S. edwardsi* is the largest known crocodylomorph of the Middle Jurassic.

## CONCLUSIONS

Here we re-describe the holotype of '*Steneosaurus*' *obtusidens* (NHMUK PV R 3168), demonstrate that it is indeed a valid species, and establish a new monotypic genus, *Lemmysuchus*, for the taxon. It has five autapomorphies, and shares nine synapomorphies with *Machimosaurus*, thus supporting Machimosaurini (*Lemmysuchus* + *Machimosaurus*) (Young *et al.*, 2015a; Jouve *et al.*, 2016). This suite of characteristics falsifies the hypothesis that *Lemmysuchus obtusidens* is a subjective junior synonym of *Steneosaurus edwardsi*. Additionally, *L. obtusidens* lacks eight of the *Machimosaurus* autapomorphies (including three premaxillary alveoli, a considerably smaller medial hemicondyle, and variable presence of carinae) listed by Young *et al.* (2014a), thus falsifying the hypothesis that *L. obtusidens* is a subjective junior synonym of *M. hugii*. Moreover, most specimens previously referred to *Lemmysuchus obtusidens* are herein considered to pertain to other taxa. We conclude that only three specimens can reliably

be referred to *L. obtusidens*: a nearly complete skull (LPP.M.21) from the *Erymnoceras coronatum* ammonite Zone of Migné-les-Lourdines, France; an incomplete skull with associated postcranial elements from the Oxford Clay Formation of England (PETMG R39), and a partial rostrum though to be from the Oxford Clay Formation (NOTNH FS3361). As such, *L. obtusidens* was a somewhat rare taxon in the Callovian of Europe, currently known only from England and France. This contrasts with its sister taxon *Machimosaurus*, which was widespread and common in European and Tethys shallow marine and brackish ecosystems during the Late Jurassic.

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## FIGURE CAPTIONS

Figure 1. (A) Photograph and (B) line drawing of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype. Skull in dorsal view with additional details of the premaxillary dentition. Refer to the main text for the abbreviations list. Scale bar: 20 cm.

Figure 2. (A, C) Photograph and (B, D) line drawing of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype. Skull in left (A-B) and right (C-D) lateral views. Refer to the main text for the abbreviations list. Scale bar: 20 cm.

Figure 3. (A, C) Photograph and (B, D) line drawings of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype. Skull in anterior (A, C) and occipital (B, D) views. Refer to the main text for the abbreviations list. Scale bar: 10 cm.

Figure 4. (A, C) Photograph and (B, D) line drawing of PETMG R39, referred to as *Lemmysuchus obtusidens* (Andrews, 1909) comb, nov. Skull in dorsal (A-B) and palatal (C-D) views. Refer to the main text for the abbreviations list. Scale bar: 10 cm.

Figure 5. (A, C) Photograph and (B, D) line drawing of PETMG R39, referred to *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov. Skull in left (A-B) and right (C-D) lateral views. Refer to the main text for the abbreviations list. Scale bar: 10 cm.

Figure 6. Close up of right lateral view of PETMG R39, referred to *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov, showing in detail the maxilla, jugal, nasal, and lacrimal bones. Outlines the jugal-maxilla and lacrimal-jugal contacts. Note the absence of antorbital fenestrae. Refer to the main text for the abbreviations list. Scale bar: 5 cm.

Figure 7. Partial mandible section of PETMG R39, referred to *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov. Refer to the main text for the abbreviations list. Scale bar: 10 cm.

Figure 8. (A, C) Photograph and (B, D) line drawing of LPP.M.21, referred to *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov. Skull in dorsal (A-B) and palatal (C-D) views. Refer to the main text for the abbreviations list. Scale bar: 10 cm.

Figure 9. (A) Photograph and (B) line drawing in dorsal view of the mandibular interior of LPP.M.21, referred to *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov. Refer to the main text for the abbreviations list. Scale bar: 10 cm.

Figure 10. (A-B) Dorsal, (C-D) left lateral, (E-F) ventral, and right lateral (G-H) photographs and line drawings of NOTNH FS3361, referred to *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov. Refer to the main text for the abbreviations list. Note the small incisive foramina and the number of alveoli in the premaxillae and maxilla. Scale bar: 10 cm.

Figure 11. Ventral close-up of (A) photo and (B) line drawing of NOTNH FS3361, referred to *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov. Refer to the main text for the abbreviations list. Scale bar: 10 cm.

Figure 12. Isolated tooth crowns of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov. A, NHMUK PV R 3168 (holotype) in (A) mesial view and (B) lingual close-up view and PETMG R39 (C-D) close-up detailed view of erupting tooth. Isolated tooth crowns referred to Machimosaurini indet.: GPIT/RE/301 (in E [posterior], F [labial], G [anterior], H [lingual], and I [dorsal] views); CAMSM J64508 (in J [posterior], K [labial], L [anterior], M [lingual], N [dorsal] views, O [ventral], and P [apex close-up] views); OUMNH J.14464 (in Q [posterior], R [labial], S [anterior], and T [lingual] views). Scale bar: (A) 2 cm; (B-T) 1 cm.

Figure 13. (A) Atlas-axis complex, (B) cervical rib, and (C) proximal thoracic rib of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype. Note there are no axial diapophyses and that the odontoid and intercentrum cannot clearly be distinguished. Atlas-axis complex is in lateral view, cervical rib is in ventral view, thoracic rib is in medial view. Refer to main text for the abbreviations list. Scale bar: 5 cm.

Figure 14. Dorsal vertebra of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype, in (A) anterior, (B) left lateral, (C) posterior, (D) right lateral, (E) dorsal, and (F) ventral views. Refer to the main text for the abbreviations list. Scale bar: 5 cm.

Figure 15. Sacral vertebrae of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype, in correct anatomical order. (A) Anterior, (B) dorsal, (C) posterior, (D) left lateral, and (E) right lateral views. Refer to the main text for the abbreviations list. Scale bar: 5 cm.

Figure 16. Scapula (A-B) and humerus (C-D) of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype. Scapula in (A) lateral and (B) medial views; humerus in medial (C) and lateral (D) views. Refer to the main text for the abbreviations list. Scale bar: 5 cm.

Figure 17. Pelvis of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype. Ischium in (A) medial and (B) lateral views, ilium in (C) medial and (D) lateral views, and pubis in (E) ventral and (F) dorsal views. Note that the acetabulum (D) is weakly concave and that the supraacetabular crest (D) is greatly reduced, and the pubic boot (E-F) is missing. Also, the medial and lateral sides of the ilium are not completely prepared. Refer to the main text for the abbreviations list. Scale bar: 5 cm.

Figure 18. Femur of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype in (A) medial and (B) lateral views. Refer to the main text for the abbreviations list. Scale bar: 10 cm.

Figure 19. Tibia of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype in (A) posterior, (B) anterior, and (C) lateral views. Note the anterior deflection of the

proximal region. Refer to the main text for the abbreviations list. Note the distal area of the fibula attached to the tibia. Scale bar: 5 cm.

Figure 20. Ankle of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype, including the calcaneum (A-D), astragalus (E-G), and cuboid (H-I). Calcaneum in (A) right dorsolateral, (B) anterior, (C) left dorsolateral, and (D) posterior views; astragalus in (E) dorsal, (F) ventral, and (G) posterior views; cuboid in (H) dorsal and (I) ventral views. Scale bar: 5 cm.

Figure 21. Dorsal osteoderm of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype in dorsal view. Note the characteristic ornamentation pattern, with elongated pits radiating from the centre of the keel. Refer to the main text for the abbreviations list. Scale bar: 5 cm.

Figure 22. Comparative photographs of *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype, *Machimosaurus*, *Steneosaurus heberti* (MNHN.F 1890-13) and *Steneosaurus edwardsi* (NHMUK PV R 2865) showing the absence of antorbital fenestrae. Scale bar:

Figure 23. Comparative photographs of (A) *Lemmysuchus obtusidens* (Andrews, 1909) comb. nov., NHMUK PV R 3168, holotype, and (B) *Steneosaurus heberti* (MNHN.F 1890-13), showing the distinct dorsoposterior curvature of the posterior mandibular rami. Scale bar:

Figure 24. Comparative line drawings of the tibiae in medial (left) and lateral (right) views of (A) *Lemmysuchus obtusidens* holotype (NHMUK PV R 3168), (B) NHMUK PV R 3169, and (C) *Steneosaurus edwardsi* (PETMG R178); comparative line drawings of the dorsal osteoderms in dorsal view of (D) *Lemmysuchus obtusidens* holotype (NHMUK PV R 3168), (E) NHMUK PV R 3169, and (F) *Steneosaurus edwardsi* (PETMG R178). Refer to the main text for the abbreviations list. Scale bar: 5 cm.

Figure 25. Comparative line drawings of the femora in medial view of (A) *Lemmysuchus obtusidens* holotype (NHMUK PV R 3168), (B) *Steneosaurus edwardsi* (NHMUK PV R 3898), and (C) *Steneosaurus edwardsi* (PETMG R178); comparative line drawings of the ilia in medial view of (D) *Lemmysuchus obtusidens* holotype (NHMUK PV R 3168), (E) *Steneosaurus edwardsi* (NHMUK PV R 3898), and (F) *Steneosaurus edwardsi* (PETMG R178). Refer to the main text for the abbreviations list. Scale bar: 5 cm.

Figure 26. Four articulated vertebrae of PETMG R39, referred to *Lemmysuchus obtusidens* (Andrews (1909) comb. nov., in (A) left and (B) right lateral views. Five articulated vertebrae (two dorsal, three sacral), incomplete ilium, femur and pubis (ischium?) of PETMG R31, which is thought to correspond to PETMG R39, in (C) left and (D) right lateral views. Scale bar: 10 cm.

Figure 27. Comparative photographs of *Steneosaurus leedsi* (A) NHMUK PV R 3806; (B) NHMUK PV R 3220, (C) *Steneosaurus edwardsi* (NHMUK PV R 3701), (D) *Steneosaurus hulkei* (NHMUK PV R 2074), (E) *Lemmysuchus obtusidens* (Andrews (1909) comb. nov., NHMUK PV R 3168) and (F) *Machimosaurus mosae* (taken from Young et al. 2014a, Fig. 19),

showing the shallow vs. deep excavation of the Meckelian **canal**. Note that (A-C) are much more deeply excavated and exposed than (D-F). Scale bar: 10 cm.

Figure 28. Comparative line drawings of (A) *Lemmysuchus obtusidens* holotype (NHMUK PV R 3168) and (B) *Steneosaurus leedsi* (NHMUK PV R 3806) articulated sacral vertebrae. Note that the anterior projecting flange on the second sacral vertebra in *S. leedsi* (B) does not extend anteriorly and is small. Refer to the main text for the abbreviations list. Scale bar: 5 cm.

Figure 29. Comparative line drawings of (A) *Lemmysuchus obtusidens* holotype (NHMUK PV R 3168), (B) *Steneosaurus leedsi* (NHMUK PV R 3806), and (C) *Steneosaurus edwardsi* (NHMUK PV R 3701); (D) PETMG R178, cervical ribs. Scale bar: 5 cm.

Figure 30. Comparative line drawings of (A) *Lemmysuchus obtusidens* holotype (NHMUK PV R 3168), (B) *Steneosaurus leedsi* (NHMUK PV R 3806), and (C) *Steneosaurus edwardsi* (NHMUK PV R 3701) dorsal ribs. Refer to the main text for the abbreviations list. Scale bar: 5 cm.

## TABLES

Table 1. Comparison of cranial characters between *Lemmysuchus obtusidens* and selected specimens of other teleosaurids.

Characteristics	<i>Lemmysuchus obtusidens</i> NHMUK PV R 3168 PETMG R39 (+ PETMG R31) LPP.M.21	<i>Machimosaurus buffetauti</i> SMNS 91415, Martin & Vincent (2013), Young <i>et al.</i> (2014a)	<i>Steneosaurus heberti</i> MNHN.F 1890-13	<i>Steneosaurus edwardsi</i> MNHN.F RJN 118, NHMUK PV R 3701, PETMG R178	<i>Steneosaurus leedsi</i> NHMUK PV R 3806
Antorbital fenestrae	Absent	Absent	Absent	Absent	Present
Nasal dorsal surface	Strongly convex	Slightly convex	Slightly convex	Slightly convex	Slightly convex
Frontal ornamentation	Yes: large circular pits	Yes: well-developed pits/ridges	Yes: ridges	Yes: circular pits	Yes: ridges
Supratemporal fenestra shape	Rectangular (anteroposteriorly elongated)	Rectangular (anteroposteriorly elongated)	Parallelogram (slightly anteroposteriorly elongated)	Parallelogram (slightly anteroposteriorly elongated)	Parallelogram (slightly anteroposteriorly elongated)
Occipital tuberosities	Yes: pronounced	Yes: pronounced	Yes: pronounced	No	No
Nuchal crest	Pronounced	Reduced	Reduced	Small	Small

Table 2. Comparison of post-cranial characters between *Lemmysuchus obtusidens* and selected specimens of other teleosaurids.

Characteristics	<i>Lemmysuchus obtusidens</i> NHMUK PV R 3168 PETMG R39 (PETMG R31)	<i>Machimosaurus buffetauti</i> and <i>M. mosae</i> Young <i>et al.</i> (2014a)	<i>Steneosaurus heberti</i> MNHN.F 1890-13	<i>Steneosaurus edwardsi</i> NHMUK PV R 3701 PETMG R178	<i>Steneosaurus leedsi</i> NHMUK PV R 3806
Ilium	Short anterior process; shallow acetabulum; faint supraacetabular crest	Long anterior process; deep acetabulum; well-developed supraacetabular crest	Long anterior process; deep acetabulum; well-developed supraacetabular crest	Long slender process, deep acetabulum; well-developed supraacetabular crest	Long anterior process; deep acetabulum; well-developed supraacetabular crest
Ischium	Broad ischial blade; sub-square posteroventral margin	Somewhat broad ischial blade; sub-square posteroventral margin	Slender ischial blade; sub-triangular posteroventral margin	Slender ischial blade; sub-triangular posteroventral margin	Slender ischial blade; sub-triangular posteroventral margin
Number of sacral vertebrae	3 (2 true, 1 pseudo)	3	2	2	2
Femur	Subtriangular head (dorsal view); medial condyle slightly larger than lateral condyle;	Triangular head (dorsal view); medial condyle larger than lateral condyle; sigmoidal	Triangular head (dorsal view); medial condyle larger than lateral condyle;	Triangular to ‘kidney-bean’ shaped head (dorsal view); medial condyle much larger than	Triangular head (dorsal view); medial condyle much larger than lateral condyle;

	sigmoidal		slightly sigmoidal	lateral condyle; slightly sigmoidal	sigmoidal
Tibial tuberosity	Sharply angled	Sharply angled	Horizontal	Horizontal	Horizontal