New information on the Jurassic lepidosauromorph *Marmoretta oxoniensis*

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ABSTRACT

The earliest known crown-group lepidosaurs are known from the Middle Triassic; however, their stem group is poorly sampled, with only a few representative fossils found. This is partly due to the small size and delicate bones of early stem-lepidosaurs (= non-lepidosaurian lepidosauromorphs), which make both preservation in the fossil record and subsequent discovery less likely. The Middle Jurassic lepidosauromorph *Marmoretta oxoniensis* Evans is re-examined using high-resolution μCT scanning to reveal parts of the skull anatomy that were previously unknown. These include a squamosal, postorbital, more complete parietal, pterygoids, and an articulated posterior section of the mandible. Some differences between this and other *Marmoretta* specimens were identified as a result, such as the arrangement of palatal teeth and the shape of the parabasisphenoid. The status of *Marmoretta* as a stem lepidosaur or stem squamate has been debated. To evaluate this, we tested the phylogenetic position of *Marmoretta* by including our new data in an adapted phylogenetic character matrix. We recover *Marmoretta* as a stem-lepidosaur and sister to *Fraxinisaura rozynekae.* Our findings support the hypothesis that both taxa belonged to a clade of non-lepidosaurian lepidosauromorphs that co-existed with lepidosaurs into the Middle Jurassic.

KEY WORDS: reptiles, lepidosaurs, skull, Jurassic, phylogeny.

LEPIDOSAURS comprise more than 10,000 extant species (Evans & Jones 2010), including squamates (lizards, snakes and amphisbaenians) and *Sphenodon*, the only extant rhynchocephalian. The earliest fossils of crown-group lepidosaurs occur in the early Middle Triassic (~240 million years ago; Jones *et al*. 2013), and their stem-lineage must extend back at least into the Permian, as indicated by the earliest occurrences of their extant sister taxon, Archosauromorpha (e.g. Ezcurra *et al.* 2014). However, the anatomy of stem-group lepidosaurs (i.e. non-lepidosaurian lepidosauromorphs) is not well known. Early stem-group lepidosaurs are currently represented by a few taxa primarily of early-middle Triassic age (Evans & Jones 2010), including the Early Triassic taxa *Paliguana whitei* (Carroll 1975) and *Sophineta cracoviensis* (Evans & Borsuk-Białynicka 2009), the Middle Triassic *Fraxinisaura rozynekae* (Schoch & Sues 2018), and, less certainly, the kuehneosaurs (specialised gliding reptiles with uncertain phylogenetic affinities, from the Early-Late Triassic; Evans & Jones 2010).

Marmoretta oxoniensis is a fossil lepidosauromorph from the Bathonian (166.1–168.3; Middle Jurassic; Gradstein *et al*. 2012) of the UK known from several localities in southern England and the Isle of Skye, Scotland (Evans 1991; Waldman & Evans 1994). It is also known from the late Jurassic of Portugal (Evans 1991). Most studies have considered *Marmoretta* as a stem-group lepidosaur (Schoch & Sues 2018), in which case it might represent a relict lineage, being significantly younger than other stem-group lepidosaurs. However, a recent phylogenetic study found it as a stem-group squamate (Simões *et al*. 2018), raising questions about its phylogenetic position. Nevertheless, *Marmoretta* has the potential to provide important anatomical data on deep lepidosaurian and lepidosauromorph divergences.

Most specimens of *Marmoretta* are fragmentary and disarticulated bones collected from screenwashing of bulk sediments (e.g. Evans 1991). However, specimens from the Isle of Skye include a semi-articulated partial skeleton NMS G1992.47.1a–b; Waldman and Evans 1994). The original description of this specimen was carried out without removing the fossil material from the host matrix – a partially metamorphosed limestone, which was resistant to acid preparation. Only relatively superficial mechanical preparation was undertaken and only the bones revealed on the surface of the blocks were described. Substantial further remains are enclosed within matrix and have not been studied until now.

Here, we provide a re-description and virtual reconstruction of the skull of *Marmoretta* based on synchrotron tomography of NMS G1992.47.1a–b and micro-CT scans of the posterior portions of the mandibular rami from a different specimen, CAMSM X9991 (an incomplete specimen comprising the posterior portion of the right lower jaw; Waldman & Evans 1994). We use the new data from these scans in a phylogenetic analysis using Bayesian inference based on extensive revision of the matrix of Simões et al. (2018). We find that *Marmoretta* is a stem-group lepidosaur, and sister to *Fraxinisaura.*

MATERIAL AND METHODS

NMS G1992.47.1a–b consists of two blocks, one containing the skull and some postcranial material including 14 presacral vertebrae, partial ribs, an interclavicle and clavicles, and partial humerus, radius, ulna, femur and tibia (NMS G1992.47.1a) (Fig. 1), and the second, slightly smaller block, containing more postcranial material including a hand, seven presacral vertebrae with ribs, and the missing portions of humerus, radius, and ulna (split across both blocks) (NMS G1992.47.1b). We used high-resolution computed microtomography (μCT) scanning to make 3D visualisations of the specimen enclosed within the rock. Here we focus on the skull description and phylogenetic implications. Synchrotron computed tomography of the skull block (NMS G1992.47.1a) was carried out at The European Synchrotron Radiation Facility (ESRF) using propagation phase contrast microtomography on the ID17 biomedical beamline. The images generated had an isotropic pixel size of 6.35μm and were produced using a 90 keV monochromatic beam. Overall, 2499 images were produced from the combination of two radiographs with 0.1 second exposure times. The images were reconstructed with PyHST2 (Mirone *et al*. 2014) using the single distance phase retrieval approach (Paganin *et al*. 2002). The final images were then processed post production to change the bit depth from 32 to 16 bits, a weighted average was used for vertical and lateral stitching of the series of acquisition, a ring correction applied (Lyckegaard *et al*. 2011), and finally volume cropping (V Fernandez, pers. comm. 2019). The posterior portions of lower jaws (CAMSM X9991) were scanned at a resolution of 10.4 µm using a Nikon Metrology XT H 225 ST High Resolution CT Scanner at the University of Bristol, School of Earth Sciences. The specimen was scanned using X-ray settings of 175 kV and 103 µA, with 3141 projections each captured for an exposure time of 0.5 second.

Image volumes were segmented using Mimics Research (http://biomedical.materialise.com/mimics) resulting in 3D models that were exported as .ply files then imported to Blender (http://www.blender.org) for reconstruction and 2D rendering of the figures presented here. Our scan data and 3D models are available on Morphosource (www.morphosource.org/projects/000349957).

Institutional abbreviations. CAMSM, Sedgwick Museum of Earth Sciences, Cambridge, UK; NHMUK, Natural History Museum, London, UK; NMS, National Museums of Scotland, Edinburgh, UK.

SYSTEMATIC PALAEONTOLOGY

DIAPSIDA Osborn, 1903
LEPIDOSAUROMORPHA Gauthier et al., 1988
Marmoretta, Evans 1991

Type and only species. Marmoretta oxoniensis Evans, 1991

Type specimen. Natural History Museum, London (NHMUK) R12020, anterior portion of right maxilla from the Kirtlington Mammal Bed at the base of the Forest Marble, Old Cement Works Quarry, Kirtlington, Oxfordshire.

Referred specimens. NMS G1992.47.1a–b and CAMSM X9991 and other specimens (Panciroli *et al*. 2020) from Isle of Skye, Scotland, and many isolated additional bones from Kirtlington Old Cement Works, England (Evans 1991, Evans *et al*. 1998), Leigh Delamere, England (Evans & Milner 1994), and Guimarota, Portugal (Evans 1991).

Diagnosis revised from Evans (1991). Small lepidosauromorph; large upper and lower temporal fenestrae; premaxillae paired, each with deep posterolateral maxillary facet; small posteroventral process of the jugal; narrow fused frontals; palatine with small teeth that decrease in size medially from a larger row along the medial choana margin to smaller scattered teeth on the ventral surface; pterygoids bear three rows of teeth which radiate anteriorly; long and slender dentary with subpleurodont teeth; coronoid with prominent coronoid process which emerges dorsally through the lower temporal fenestra. The following features are autapomorphies: fused parietal forming a broad parietal table, parietal foramen absent, large midline crest; long anterior process of the maxilla, specialized maxillary/premaxillary overlap; dorsoventrally wide posterior (squamosal) process of the postorbital that overlaps on to a broad shallow facet on the squamosal.

SKULL DESCRIPTION

The skull is preserved and partially disarticulated in block NMS G 1992.47.1a (Fig. 1). It includes mostly complete fused parietals, fused frontals, left and right prefrontals, almost complete right maxilla, partial right premaxilla, right postfrontal, right postorbital, left and right jugals, right squamosal, right quadrate and quadratojugal, partial left and right ectopterygoids, mostly complete left and right pterygoids, partial left and right palatines, parabasisphenoid, basioccipital, mostly complete right dentary, less complete left dentary, left and right coronoids, broken right prearticular, and a right articular. Post-depositional crushing has resulted in fragmentation and disarticulation of the lower jaws and cranial elements. Waldman and Evans (1994) reconstructed the skull based on the bones observable in the prepared specimen, which did not include new elements revealed by the μCT data, such as the squamosal and the full extent of the parietal crest. We present a new reconstruction of the skull of *Marmoretta oxoniensis* using information from NMS G 1992.47.1a and CAMSM X9991 (Fig. 2), including the palatal region, which is poorly preserved.

The dark grey portions of the articulated skull reconstruction are elements that have only been preserved on one side and have been duplicated and mirrored in figures 2A, C, and E. These include the right prefrontal (the right prefrontal is present although less complete than the left - therefore the left prefrontal has been mirrored in this reconstruction), and the entirety of the left mandibular ramus and skull except the jugal and prefrontal. The most notable of these are the anteroventral process of the postorbital, which is missing, revealing the postorbital facet of the jugal in dorsal view. The anterior process of the maxilla is also missing, leaving the maxillary facet of the premaxilla exposed in lateral and dorsal view. Proposed positions for the nasals and dorsal processes of the premaxilla are also marked by dashed lines in the figure 2B and 2D.

The lack of a preserved squamosal-parietal contact renders the squamosal position provisional and also creates uncertainty with respect to the squamosal-quadrate articulation.

CRANIUM

Premaxilla – A partial right premaxilla is preserved, missing the anterior and posterior portions. Its lateral surface is slightly convex. There are six alveoli, of which only one contains a tooth (Figure 3 E-G). It is likely that at least one more alveolus was present posteriorly, and another anteriorly, giving a minimum of eight marginal teeth in the premaxilla. A mediolaterally deep, ‘V’-shaped, maxillary facet is present on the posterolateral surface of the premaxilla. A subnarial ramus extends medially from the anteromedial surface. The ascending anterodorsal process is missing in NMS G 1992.4.7.1a. However, specimens from Kirtlington (NHMUK R12022; [Evans 1991]) show that this process is long and tapers dorsally to separate the external nares across the midline anteriorly, thus dividing the external nares unlike in *Kuehneosaurus* (Evans 2009).

Maxilla – Most of the right maxilla is preserved, but only a partial alveolar shelf of the left maxilla remains. The apex of the dorsal process of the right maxilla is broken, and the facets for the lacrimal and prefrontal are therefore not preserved (Fig.3). The anterior portion of the right maxilla is also incomplete, although the length of the missing section is unknown. The maxilla is elongate and gracile anteroposteriorly, and the dorsal process appears to curve medially, possibly due to deformation. The preserved portion of the anterior process is relatively long, comprising 0.28 of the total anteroposterior length of the maxilla (Fig 3). This is longer than in other stem-group lepidosaurs like *Sophineta*, and most extant squamates, in which the anterior process (AP) is shorter relative to the total maxilla length (ML), (e.g. *Sophineta* AP/ML= 0.13 (Evans & Borsuk-Białynicka 2009); *Iguana*, 0.19; *Japalura*, 0.15; *Hemidactylus*, 0.11; *Tropidophorus*, 0.16; *Cordylus*, 0.21 (Evans, 2008)). Rhynchocephalians also possess short anterior processes of the maxilla (*Sphenodon* (AP/ML = 0. 13 (Jones 2008)), or even lack them entirely e.g. *Palaeopleurosaurus posidoniae* and *Pleurosaurus goldfussi* (Jones 2008). The long anterior process of *Marmoretta* is similar to that of some squamates such as *Lanthanotus borneensis* (0.38) and varanids (e.g. *Varanus salvator*, 0.31 (Evans, 2008)), but shorter than that of the Triassic stem-lepidosaur, *Fraxinisaura* (AP/ML = 0.51, Schoch & Sues 2018) and the extinct mosasaurians, in which the rostral part of the maxilla can form most of the bone.

A long shallow facet for the jugal is present posterodorsally on the medial surface of the maxilla. Two entrances for the superior alveolar canal are also visible on the dorsal surface of the alveolar shelf; the larger of the two is dorsal to the 16th alveolus, and the smaller is just anterior to this. The palatine facet is a horizontal groove on the alveolar shelf just posterior to the base of the dorsal process. A row of three neurovascular foramina open on the lateral surface of the maxilla, ventral and posterior to the dorsal process, and similar to those seen in *Sophineta* (Evans & Borsuk-Białynicka 2009).

Twenty-three maxillary alveoli are present, 18 of which bear in situ teeth. This is slightly fewer than the estimated total of 25–30 maxillary teeth based on bulk-sample specimens from screenwashing at Kirtlington (Evans 1991). The difference is most likely due to incomplete preservation in NMS G 1992.47.1a. The teeth are conical with a slight apicolingual curvature. Tooth implantation is pleurodont (sensu Bertin *et al.* 2018). There is a substantial difference in height between the labial and lingual walls of the maxilla, with the labial surface of the tooth root attached to the medial side of the labial wall (Fig. 4). This asymmetry of implantation is less evident in the dentary. However, here a basal plate supports the teeth lingually, a condition associated with ‘labial pleurodonty’ (Lessman 1952, Zaher and Rieppel 1999, Bertin et al. 2018). With the exception of some smaller replacement teeth, the maxillary tooth row is approximately isodont, with tooth heights ranging from ~0.8-0.9 mm.

Prefrontal – The prefrontals are crescentic in lateral view, forming the anterior margin of the orbit. Each prefrontal consists of an anteroposteriorly expanded ventral portion, which has a concave medial surface and convex lateral surface (Fig. 5). From this arises a tapering, rod-like dorsal process that bears a double facet for the frontal on its medial surface, divided by a narrow longitudinal ridge. Anteroventrally, the prefrontal bifurcates into a short anteromedial process and a longer posterolateral process that curves laterally at an acute angle to form the orbital margin. Specimens from Kirtlington show a broad and shallow facet in between the two prongs – probably for the reception of the lacrimals (Evans 1991), although these are not preserved in NMS G 1992.47.1a.

Jugal – Both the left and right jugals are preserved. These are roughly triangular in lateral view, comprising an anteroposteriorly broad ventral portion that articulates with the maxilla, and a tapering posterodorsal process that contacts the postorbital forming the ventral part of the postorbital bar (Fig. 6). The jugal facet extends further ventrally than the reconstructed ventral tip of the postorbital, and it appears that the ventral process of the postorbital is missing its distal part. The medial surface of the jugal bears a facet anteriorly, which most likely articulated with the ectopterygoid. The anterodorsal surface of the jugal forms the posteroventral rim of the orbit and is mediolaterally thickened compared to its posterior surface. A small posteroventral process is present, entering the anteroventral region of the temporal emargination. Although small, this process is more pronounced than seen in *Sophineta* (Evans & Borsuk-Białynicka 2009), but smaller than that of *Fraxinisaura,* in which the posteroventral process of the jugal is dorsoventrally deep and extends further posteriorly (Schoch & Sues 2018). The absence of the lower temporal bar is a plesiomorphic feature in saurians, as well as being present in some non-saurian neodiapsids such as *Acerosodontosaurus* (Bickelmann *et al*. 2009) and *Lanthanolania* (Modesto & Reisz 2002).

Postorbital – Only the right postorbital is preserved. It comprises three processes (Fig. 7). The ventral process forms the dorsal part of the postorbital bar and bears a facet for the jugal on its posterior surface. The dorsomedial process forms the anterior margin of the upper temporal fenestra and bears a facet for the postfrontal on its anterior surface. It forms the lateral margin of the upper temporal fenestra and bears a facet for the squamosal on its medial surface. The posterior process is broken and displaced dorsally and has been re-articulated to the anterior region of the postorbital in our reconstructions (Fig. 2A–B). The concave anterior surface of the dorsal and ventral processes forms a large part of the posterior orbital margin (Fig. 7). The posterior process is dorsoventrally broad and mediolaterally thin, extending posteriorly to the posterior margin of the temporal region, where it articulates with the lateral surface of the squamosal in an overlapping contact (Fig. 7A). It is rhomboidal with a curved ventral border. The morphology of the posterior process differs from that seen in Kirtlington specimens (Evans 1991) in which the posterior process is narrower dorsoventrally than seen in NMS G 1992.47.1a. The ventral process of the postorbital as reconstructed by Evans (1991) is also longer and more slender than in NMS G 1992.47.1a. although this apparent difference is probably an artefact caused by the loss of the distal end of the ventral process in the Skye specimen, as indicated by the unoccupied lower half of the postorbital facet on the jugal.

Frontal – The frontals are fused into a median plate with a slightly raised area extending anteroposteriorly along the midline (Fig. 8A). The anteromedial and posterior portions of the bone are damaged and missing. The overall shape of the median frontal is approximately rectangular, transversely broader posteriorly than anteriorly, and narrowest at mid-orbit (around 66% of the posterior transverse width). The ventral margins of the frontal bear distinct cristae cranii that follow the curve of the orbit and are somewhat shallower than in the early rhynchocephalian *Diphydontosaurus* (Whiteside 1986). The dorsal surface of the frontal is anteroposteriorly convex, as is most clearly evident in anterodorsal view (Fig. 8D). The lateral surface is embayed by the dorsal margin of the orbit, suggesting a juvenile or sub-adult ontogenetic stage (see Evans 1991). Well-defined triangular facets for the postfrontals are evident in the posterolateral corners of the bone, tapering anteriorly. Shallow facets for the nasals are present on the preserved anterolateral surface of the frontal, with long prefrontal facets evident along the anterolateral margins.

Postfrontal – Only the right postfrontal is present in NMS G 1992.47.1a (Fig. 9). The overall shape of the bone is triradiate, with a dorsal frontal process, posteromedial parietal process, and ventral postorbital process. The dorsal surface bears a facet for the frontal and the medial surface of the ventral process bears an elongate, triangular facet for the postorbital. This facet extends only for around one-third of the mediolateral width of the postfrontal, leaving a large posteromedial portion that participated in the anterior margin of the upper temporal opening. The posteromedial process is relatively short with a weak parietal facet on its medial surface.

The postfrontal of *Marmoretta* is similar to that of *Sophineta* ((Evans & Borsuk-Białynicka 2009), although in the latter taxon the anteromedial and dorsal processes are somewhat longer.

Parietal – The parietal of *Marmoretta* is a single, fused element. The anterior portion of the parietal is broken on the right side, but well-preserved on the left. This area is not embayed along the midline, and it is likely that a parietal foramen was absent, as noted by Evans (1991). Laterally, the parietal provides the dorsomedial margin of the upper temporal opening. This is best preserved on the left side, where the margin is slightly convex, rather than embayed. The dorsal surface of the parietal bears a prominent, mediolaterally narrow median (sagittal) crest. Either side of the crest, the dorsal surface is transversely convex. Two low, transversely orientated dome-like ridges form distinctive structures on the dorsal surface (Fig. 10). The first dome rises gradually from the fronto-parietal suture, before diminishing sharply to form a transverse fossa approximately half way along the length of the parietal. The second extends posteriorly from this fossa to form a slightly lower dome and shallow fossa. The posterior part of the parietal is inclined posterodorsally from this fossa, forming a short ascending flange at approximately 45°, converging posteriorly to the level of the median crest (Fig. 10). Paired, anteroposteriorly oriented tubercles are present laterally at the base of the short ascending flange (Fig. 10). These tubercles have a hemispherical morphology and merge with the dorsal surface of the parietal anteriorly. The tubercles, and the posterior region of the parietal in general, are broken, but may have continued as lateral processes of the parietal, as in *Huehuecuetzpalli* (Reynoso 1998) and *Dalinghosaurus* (Evans & Wang 2005), or the short ascending flange may have extended posterodorsally, in a similar fashion to that seen in the Permian weigeltisaurid *Coelurosauravus elivensis* (Evans & Haubold 1987; Bulanov & Sennikov 2015).

The large parietal sagittal crest of *Marmoretta* is an unusual feature compared to other early lepidosauromorphs. Some Jurassic and Cretaceous rhynchocephalians (e.g. *Palaeopleurosaurus; Kallimodon; Priosphenodon* (Klein & Scheyer 2017) possess a short crest on a narrow parietal table, with distinctly ventrally orientated lateral flanges (Rieppel 1994). A midline crest on the parietal is also known in several early archosauromorphs (e.g. *Protorosaurus, Macrocnemus, Trilophosaurus* and the rhynchosaurs *Mesosaurus* and *Howesia* (Gottmann-Quesada & Sander 2009; Li, *et al*. 2007; Heckert, *et al*. 2006; Pineiro, *et al*. 2012; Dilkes 1995)). Simões *et al*. (2018 Supp. Info.) suggested that the sagittal crest only occurs in taxa with ventrally directed lateral margins of the parietal, i.e. with a narrow parietal table. *Marmoretta* in an exception in this case in that the skull table is broad and the lateral margins are only moderately ventrolaterally inclined.

Squamosal – The right squamosal is preserved in NMS G 1992.47.1a. and is enclosed in matrix such that it was not described in previous studies (Evans 1991, Waldman and Evans 1994). As preserved, the squamosal is a large, triangular element. The lateral surface curves posteromedially to form a narrow contribution to the occipital region of the cranium (Fig. 11). It is a broadly plate-like bone, lacking clearly defined rami, unlike the tetraradiate squamosal in *Sophineta* or the triradiate squamosals of *Pamelina, Huehuecuetzpalli* and *Megachirella* (Evans 2009; Reynoso 1998; Evans & Borsuk-Białynicka 2009). There is a small posteroventral process, where the bone thickens, which bears a deep, wedge-shaped facet on the posteromedial surface for articulation with the dorsal (cephalic) condyle of the quadrate. The anteroventral process is broken distally, and most likely extended further ventrally, as implied by the presence of a facet on the anterolateral surface of the quadrate dorsal process. The morphology of that facet (Fig. 12) suggests that the ventral process of the squamosal terminated close to or in contact with the dorsal part of the quadratojugal (see Evans 1991). The squamosal lacks an emargination between the postorbital process and the anteroventral process. The lateral surface of the squamosal bears a broad, shallow facet anteroventrally for articulation with the postorbital (Fig. 11). This differs from the tongue and groove articulation of the postorbital/squamosal in *Megachirella* (Simões *et al*. 2018), but is somewhat similar to the same facet in the Lower Jurassic rhynchocephalian *Gephyrosaurus bridensis* (Evans 1980) and the overlapping contact of *Sophineta* where a shallow postorbital facet is also present on the lateral face of the squamosal (Evans & Borsuk-Białynicka 2009). The squamosal tapers dorsally towards its contact with the parietal, although the contact itself is not preserved and cannot be determined. The posterior surface of the squamosal is distinctly concave in lateral view, and this may have supported the tympanic membrane, since a tympanic crest or conch is absent from the quadrate and the retroarticular process is much reduced or absent (Fig, 11).

Quadrate– The right quadrate is preserved in NMS G 1992.47.1a and is similar to the juvenile quadrate of *Marmoretta* (NHMUK R12040) described by Evans (1991) from Kirtlington Quarry. The quadrate consists of a mediolaterally expanded ventral portion that bears the articular condyles for the mandibles, a sheet-like anteromedial process, which extends to contact the quadrate ramus of the pterygoid, and a rod-like dorsal shaft that articulates with the squamosal dorsally via a convex condylar surface. The dorsal shaft also bears a large facet for articulation with the ventral process of the squamosal along its anterolateral surface. The medial surface of the quadrate shaft bears a low, horizontal ridge and may have received the columella of the stapes at the level of the dorsal margin of the quadratojugal.

In ventral view the anteromedial process of the quadrate forms a right angle with the axis of the lateral mandibular condyle~~s~~. The medial condyle is mediolaterally narrow and anteroposteriorly longer than the lateral condyle, which is mediolaterally wide. The anteromedial process bears a broad, shallow facet for articulation with the pterygoid on its posteromedial surface, and is broken anteriorly (Fig. 12).

The quadrate conch is absent, as noted previously (Evans 1991). The presence of the quadrate conch was considered to be a synapomorphy of Lepidosauriformes (=total-group lepidosaurs excluding kuehneosaurs; equivalent to Lepidosauromorpha here) by Gauthier *et al*. (1988), who considered the conch to be present in *Paliguana*. The lack of a conch in *Sphenodon* represents a secondary loss (Gauthier *et al*. 1988), because the conch is present in basal rhynchocephalians like *Gephyrosaurus and Diphydontosaurus* (Evans 1981; Whiteside 1986). Among early lepidosauromorphs, *Sophineta* also possesses a lateral conch, as does *Megachirella* (Evans & Borsuk-Białynicka 2009; Simões, *et al*. 2018). In general, the quadrate morphology is similar to that of *Sophineta*, although *Sophineta* exhibits a larger depression between the lateral and medial condyles and a straighter dorsal process (Evans & Borsuk-Białynicka 2009).

Quadratojugal — The quadrate of NMS G 1992.47.1a is articulated with a small, lenticular quadratojugal (Fig. 12). The quadratojugal lies ventral to the squamosal facet and may have contacted the squamosal. It articulates with the ventrolateral surface of the quadrate, enclosing a small quadrate-quadratojugal foramen laterally (Fig. 12).

Palatine – Both palatines are both partially preserved in NMS G 1992.47.1a. The thickened maxillary processes are present, but the medial and posterior portions that contact the pterygoids are missing, as are the anterior margins which would contact the vomer. The palatines are thin, dorsally concave plates of bone that have roughly triangular outlines. A field of small teeth is present on the convex palatal surface (Fig. 13). The palatine thickens laterally as it approaches the maxillary process, but the margins of the choana and suborbital fenestra are not preserved. Palatine teeth are widespread among tetrapods, including stem tetrapods (e.g. *Ichthyostega*), early amniotes (e.g. *Petrolacosaurus*), and many lepidosauromorphs (e.g. *Sophineta*, *Sphenodon*), but have been lost in many squamates (Matsumoto & Evans 2017). In *Marmoretta* the lateral row of palatal teeth is slightly enlarged (Fig. 13), differing from other early lepidosauromorphs except from rhynchocephalians such as *Diphydontosaurus* (Whiteside 1986). The condition in *Marmoretta* is weakly developed in comparison to rhynchocephalians, and we do not consider this to be a directly homologous character. The palatal teeth in NMS G 1992.47.1a are less organised than those in the Kirtlington specimen where distinct tooth rows are apparent. This may be a case of interspecific difference or due to preservation of the Skye specimen, which has resulted in the teeth being disturbed and not preserved in their life position.

Pterygoid – The pterygoids are anteroposteriorly long, each comprising a large, sheet-like palatal process and a narrow quadrate process that extends posterolaterally from the posteromedial part of the palatal process. Both pterygoids are missing their anterior and lateral portions. The broad palatal process has a gently concave ventral surface, and is thickened on the medial edge, which forms the lateral margin of the interpterygoid vacuity (Fig. 14). The palatal surface bears three rows of teeth that radiate anterolaterally from a position just adjacent to the basal articulation. The transverse processes (pterygoid flanges) of both pterygoids are damaged, with only a remnant of the left process remaining. It consists of a roughly triangular extension that thickens along the posterior margin where it joins the main body of the pterygoid lateral to the basal articulation. Overall, the pterygoid is very similar to that of *Fraxinisaura* (Schoch & Sues 2018). There are no teeth present on the transverse process. The quadrate process of the pterygoid curves posterolaterally to meet the medial wing of the quadrate. There is no development of the pit (fossa columellae) on the dorsal surface of the pterygoid quadrate ramus that forms a mobile articulation with the base of the epipterygoid in squamates.

Ectopterygoid – Both ectopterygoids are preserved, although the right bone is more complete than the left, and both are missing their medial portions, including the facet for articulation with the pterygoid. The ectopterygoids are small and comprise an expanded lateral plate for articulation with the maxilla and jugal (Fig, 15) from which a slender stem extends medially into the palate. The lateral articular surface is flat and dorsomedially deep, with a long, shallow ventral facet for the maxilla and a smaller posterodorsal facet for the jugal. The lateral flange of the ectopterygoid of *Marmoretta* is anteroposteriorly longer than that of *Sophineta* (Evans and Borsuk-Białynicka 2009) and *Diphydontosaurus* (Whiteside 1986). In *Fraxinisaura* the stem is thicker and not smoothly cylindrical (Schoch & Sues 2018).

Parabasisphenoid – The parabasisphenoid is a midline bone that tapers anteriorly, resulting in an approximately triangular outline. It is embayed posteriorly between paired, posterolateral parasphenoid wings. The parasphenoid rostrum (cultriform process) extends anteriorly, but only its base is preserved. The basipterygoid processes extend anteroventrally, the right being broken and the left only partially preserved, (Fig. 16). The posteroventral surface of the parabasisphenoid is concave, and the dorsal surface is also transversely concave and lacks the midline ridge seen in specimens referred to *Marmoretta* from Kirtlington Quarry NHMUK R12055 and NHMUK R12057 (Evans 1991). The internal carotid foramina perforate the ventral surface of the bone and enter the posterolateral part of the hypophysial fossa so that they are not visible in dorsal view. This also differs from the Kirtlington specimens NHMUK R12055 and NHMUK R12057 (Evans 1991) in which the foramina are located anteriorly within the fossa. It also differs from the parabasisphenoid in *Fraxinisaura*, which bears a patch of denticles on its ventral surface close to the base of the parabasisphenoid (Schoch and Sues 2018).

Basioccipital – The basioccipital forms an ovoid posteroventral occipital condyle (Fig. 17). The ventral surface of the bone bears a low transverse ridge, anterior to the occipital condyle. This becomes more prominent laterally on either side, forming two paired, ventrolaterally-projecting basal tubera. These are relatively large and appear similar to inferred adult specimens referred to *Marmoretta* from Kirtlington (NHMUK R12058 [adult] compared to those of NHMUK R12059 [juvenile] [Evans 1991]). Facets for the exoccipitals are present dorsolaterally on the occipital condyle. The dorsal surface of the basioccipital bears a longitudinal median ridge which spans the posterior two thirds of the bone; on either side of the ridge the bone is concave.

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Dentary – Both dentaries are incomplete, but the right is the better preserved, although it misses its anterior, posterior, and posteroventral sections. The dentary is long and slender with the medial surface divided into dorsal and ventral parts by the Meckelian groove, which has been narrowed dorsoventrally by post-mortem crushing (Fig. 18). As with the maxillary tooth row, the dentary teeth are implanted in the alveolar shelf, the labial wall of which is higher than the lingual wall, exposing most of the tooth bases lingually. The posterior portion of the right dentary had broken away from the main section of bone and has been repositioned accordingly for the reconstruction. This detached piece contains the posterior-most tooth and facets for the coronoid and surangular on its dorsomedial surface. The Meckelian groove is open medially in the anterior portion of the dentary, similar to NHMUK R12062 (Evans 1991).

Coronoid – Both left and right coronoids are present in NMS G 1992.47.1a and the left is present in CAMSM X9991. They are robust bones, comprising a dorsoventrally broad, sheet-like anteromedial process, a narrow, tapering posterolateral process, and a prominent coronoid process (Fig. 19). The ventral surface of the coronoid bears a groove-like horizontal facet for articulation with the dorsal surface of the dentary. The anteromedial process extends ventral to this, covering a portion of the medial surface of the dentary. The lateral surface of the anteromedial flange bears a small posterior facet for the prearticular. The coronoid process curves medially to produce a smooth concave posterior surface which serves as the insertion site for the mandibular adductor (Evans 1991).

Splenial – The splenial is not preserved in NMS G 1992.47.1a. However, it is present in articulation with the other bones of the posterior part of the mandible in CAMSM X9991. The splenial in CAMSM X9991 is incomplete, comprising only the posteroventral and posterodorsal parts of the bone, which are broken and appear as separate fragments. These articulate with the dentary, coronoid and prearticular.

Prearticular – The right prearticular is present in both associated specimens of *Marmoretta*. In NMSG1992.47.1a it is broken in half dorsoventrally and is missing the anterior and posterior ends. In CAMSM X9991 the prearticular is preserved in articulation with the rest of the lower jaw bones, aiding the analysis of NMSG1992.47.1a (Fig. 19). On the medial surface of the bone there is a shallow impression bordered dorsally by a low ridge that runs anterodorsally-posteroventrally, ending about three-quarters of the way along the bone. This marks the dorsal extent of the splenial facet. On the lateral surface there is a long v-shaped facet for the dentary positioned anteriorly on the thickened dorsal margin. Posteriorly the prearticular tapers to a point at which the ventral surface is contacted by the angular, and the dorsal surface by the articular.

Surangular – The right surangular is present in both NMSG1992.47.1a and CAMSM X9991, although it is more complete in the latter. The bone is long, extending from the posteroventral surface of the dentary, adjacent to about the 6th from last tooth, to the ventral surface of the articular. On the anterolateral surface there is a long, broad and shallow facet for the posterior region of the dentary and, just ventral to the tip of the dentary, there is an anterior surangular foramen. Posteriorly the surangular expands into a broad cup-like facet for the articular. Ventrally the surangular contacts the prearticular anteroventrally and the angular posteroventrally (Figs. 19 B and C).

Angular – The angular is not preserved in NMSG1992.47.1a, but the right bone is evident in CAMSM X9991. It is a small slender element that tapers at its anterior and posterior ends. The angular is positioned on the ventral surface of the lower jaw and contacts the surangular dorsolaterally, the prearticular and the articular dorsomedially (anterior – posterior), and the splenial ventrally.

Articular – The right articular is present in both associated specimens. It is a robust bone that makes up the posterior end of the lower jaw, with its dorsal surface articulating with the condyles of the quadrate. The ventral surface of the articular has a narrow but relatively deep medial facet for the prearticular. The medial surface of the bone continues dorsally from this facet and is mostly flat, expanding slightly at the dorsal surface. On the lateral side the articular is broad posteromedially and the ventrolateral surface narrows medially to form the lateral surface of the prearticular facet. The broad posteromedial portion of the bone is sheathed from below by the large surangular facet. Dorsally the articular slopes anteroposteriorly at an angle of~45°. The dorsal surface is divided by a central groove that is bordered by a tall projection medially, and a shorter, broader projection on the lateral side.

There is no development of a retroarticular process.

DISCUSSION

Our high-resolution synchrotron tomography of referred specimens of *Marmoretta oxoniensis* (NMS G 1992.47.1, CAMSM X9991) provides important new anatomical data. In particular it has clarified our understanding of the suspensorium and posterior region of the mandible, demonstrated the extent of the parietal sagittal crest and the pleurodont nature of the marginal tooth implantation. Our reconstruction of the skull of *Marmoretta* retains much of the general form of previous studies (Evans 1991, Waldman and Evans 1994). However, the dorsoventral height of the postorbital region of the cranium and the posterior portion of the mandible suggest a distinctive, anteriorly tapering skull-shape, augmented by the prominent sagittal crest.

The sagittal crest of *Marmoretta* differs from that of other reptiles in that it is combined with a transversely broad parietal table. The crest provides an attachment site for the external adductor muscle, which descends to attach to the medial surface of the coronoid eminence in the mandible. The coronoid eminence of *Marmoretta* bears a large concavity on the posteromedial surface for this adductor attachment, suggesting a strong closing force (King 1996). Although comparatively powerful bite-force is postulated in small (>2.5cm skull length) early Mesozoic diapsids, it is correlated with transversely narrow parietal tables and broad upper temporal openings in relation to the transverse width of the postorbital region (Pritchard *et al.* 2018). *Marmoretta* does not possess either of these features, although the adductor musculature in *Marmoretta* would have benefitted from extended dorsoventral length and may represent an ecomorphologically diverse approach to substantial bite-force in small diapsids.

The arrangement of the palatal teeth in NMS G 1992.47.1a differs from that recorded by Evans (1991) based on specimens from Kirtlington Old Cement Quarry (NHMUK R12045, R12046, R12047). NMS G 1992.47.1a possesses lateral palatine teeth that are slightly enlarged and are not positioned into distinct rows, unlike in the Kirtlington specimens. Also, the pterygoid of NMS G 1992.47.1a bears three tooth rows as opposed to the two described in the Kirtlington specimens (Evans, 1991; NHMUK R12052, R12054).

However, this is likely due to the more complete preservation of the pterygoids in NMS G 1992.47.1a compared to NHMUK R12052 and R12054.

Palatal teeth are considered an ancestral condition in amniotes, and appear in one form or another in most major clades although there is a general pattern of reduction in many lineages (Matsumoto & Evans 2017). Nevertheless, the morphology and inferred function of palatal teeth varies among taxa. The longitudinal rows of palatal teeth seen in *Marmoretta* suggest that they may have assisted with moving food towards the back of the mouth (Matsumoto & Evans 2015). In many extant lepidosaurs this function is carried out by a muscular tongue in conjunction with varying amounts of palatal dentition (Matsumoto & Evans 2017). The presence of anterior palatal teeth in *Marmoretta* (palatine and pterygoid, possibly vomer although this is unknown) and lack of posterior palatal teeth (parabasisphenoid and transverse process) suggest their main function was intraoral transport and that they were likely accompanied by a mobile tongue.

There are a few other differences between specimen NMS G 1992.47.1a and the Kirtlington specimens NHMUK R12037 (a juvenile postorbital) and NHMUK R12055 and NHMUK R12057 (parabasisphenoids) described by Evans (1991). These include the shape of the posterior process of the postorbital which is dorsoventrally taller in NMS G 1992.47, and the positioning of the internal carotid foramina within the hypophysial fossa which are further posterior in this specimen. These may be examples of ontogenetic or intraspecific variation, or indicate that the assemblage from Kirtlington includes a different species to the specimens described here.

Phylogenetic analysis. Earlier studies have resulted in two hypotheses on the affinities of *Marmoretta*. Evans (1991) interpreted *Marmoretta* as a non-lepidosaurian lepidosauromorph, outside of the crown-group split between rhynchocephalians and squamates, based on material from Kirtlington, Oxfordshire. New data from specimens collected from the Isle of Skye (Waldman and Evans 1994) and subsequent analyses (Evans and Borsuk-Białynicka 2009; Evans 2009, Evans & Jones 2010; Jones *et al.* 2013) have generally re-iterated this view. The recent phylogenetic analysis of Schoch and Sues (2018) also recovered *Marmoretta* as a stem-group lepidosaur, as sister to the Middle Triassic *Fraxinisaura rozynekae*. In contrast to this hypothesis, Simões *et al.* (2018) recovered *Marmoretta*, along with *Megachirella* from the Middle Triassic of Italy, as a stem-group squamates, within Lepidosauria, using both parsimony analysis and Bayesian inference.

To evaluate the phylogenetic position of *Marmoretta* based on the new data, we used a modified version of the 347 characters in the morphological dataset of Simões *et al.* (2018). We added 32 new characters and removed two characters (these were replaced with new characters to reduce ambiguity in the squamosal descriptions, see below for more details), making a total of 377 characters. These changes are based on an extensive review of their dataset and published comparative literature and our modifications are described more completely in the Supplementary Data. Of the 32 new characters, two replaced existing characters and describe distinctive aspects of similarity among the squamosals of squamates that are absent outside the squamate crown-group (e.g. Evans 2008). Overall, our additions mostly reflect comparative observations that were framed by older literature, but were not included in the original character list of Simões *et al*. (2018). These observations document variation among early crown-group reptiles and especially among early lepidosauromorphs, encoding character state variation that has been influential for existing phylogenetic hypotheses (e.g. Camp 1923; Parrington 1958). We also revised the scores of several taxa, focusing on those that have previously been considered as early lepidosauromorphs (e.g. *Megachirella, Sophineta, Palaeagama, Gephyrosaurus and Diphydontosaurus*) or potentially closely related taxa *,(e.g. Kuehneosaurus* and *Pamelina*). We omitted some taxonomic units, and added others such as *Fraxinisaura*. A list of these modifications together with explanatory notes is included in Supplementary Data.

We performed a non-time calibrated Bayesian analysis of the resulting data using the Mkv model with using MrBayes v.3.2.5. as described in Supplementary Data 1, using a maximum clade credibility tree (MCC) to summarize the results of this analysis (Fig. 20).

The MCC tree recovers *Marmoretta* as a stem-group lepidosaur (i.e. a non-lepidosaurian lepidosauromorph), in agreement with some previous studies (Evans 1991, Jones *et al.* 2013). We also find *Marmoretta* as a sister taxon of the Middle Triassic *Fraxinisaura*, within an early diverging and geologically long-lived clade of non-lepidosaurian lepidosauromorphs. This is consistent with the phylogenetic hypotheses posited by Schoch and Sues (2018), who noted the striking similarity of the maxillae of *Marmoretta* and *Fraxinisaura*, which both possess a low, triangular facial process and elongate anterior process. We find this group (*Marmoretta* + *Fraxinisaura*) is supported by three unambiguous synapomorphies (the absence of the premaxillary process of the maxilla c.20.1, the absence of a parietal foramen c.73.1 and the absence of an infraorbital foramen on the palatine c.101.1) The clade comprising *Marmoretta* + *Fraxinisaura* also possesses several lepidosauromorph synapomorphies, including a reduced lacrimal (under deltran c.360.1), pleurodont implantation of maxillary dentition (under acctran c.213.0), a quadratojugal foramen (unambiguous c.42.1) and an 'hour-glass' shaped frontal (under acctran c.354.1).

Our phylogenetic findings therefore differ from those of Simões *et al.* (2018), who recovered *Marmoretta* as a stem-group squamate, nested within Lepidosauria (i.e. as a member of the crown-group). Consistent with our recovery of *Marmoretta* in the stem-group, we observe various features that are present in crown-group lepidosaurs, but are absent in *Marmoretta*. These features include subolfactory processes of the frontals (unambiguous c.69.1) and the lateral conch of the quadrate (under deltran c.121.1). The absence of a lateral conch of the quadrate in *Marmoretta* may be plesiomorphic for lepidosauromorphs, with the lateral conch probably appearing closer to the divergence of the crown-group in more derived stem-lepidosaurs. The quadrate conch is present in squamates and early rhynchocephalians (Evans 1980, Whiteside 1986, Simões *et al.* 2018) and, probably, convergently in kuehneosaurs (Evans 2009). Unfortunately, the condition in the quadrate is unknown in *Fraxinisaura* (Schoch and Sues 2018). Further, *Marmoretta* possesses several features that are not found in squamates (e.g. quadratojugal present c.38.0, absence of a notch for the squamosal on the cephalic head of the quadrate c.123.0, the ventral exposure of the entry foramen for the internal carotid artery in the basisphenoid c.124.1), or in rhynchocephalians (e.g. the absence of frontal tabs on the parietal, c.78.1, the presence of a splenial c.176.1, the absence of a notochordal canal in adults, c.229.1).

Megachirella from the Middle Triassic of Italy, like *Marmoretta*, was originally reported as a non-lepidosaurian lepidosauromorph (Renesto & Posenato, 2003) but subsequently recovered as a stem-squamate inside of the lepidosaurian crown-group by Simões et al. (2018). Our MCC tree, recovers *Megachirella* as a stem-squamate, in accordance with Simões *et al* (2018). *Megachirella* shares several key features with lepidosaurs e.g. a lateral quadrate conch (c.121.1) and with squamates e.g. the loss of the anteroventral process of the squamosal (c.50), although both of these character states are also found in kuehneosaurs, which were not recovered as lepidosauromorphs in our analysis. We also recover *Sophineta*, which generally has been described as a non-lepidosaurian lepidosauromorph (Evans and Borsuk-Białynicka 2009, Jones *et al.* 2013), as a basal squamate (in the MCC tree). However, it is notable that support for both *Megachirella* and *Sophineta* as squamates is poor in the MCC tree (posterior probability = 0.36 and 0.08 respectively), and both taxa are found in a trichotomy with squamates and rhynchocephalians in the 50% majority rule tree from our posterior sample (see Supplementary Data).

Our analysis also highlights substantial uncertainties regarding to the phylogenetic positions of other taxa traditionally interpreted as basal lepidosauromorphs, with *Paliguana* recovered outside Lepidosauromorpha in both tree topologies (Fig. 20 and Supplementary Data). The anatomy, affinities and evolutionary implications of this taxon require further investigation.

CONCLUSIONS

New anatomical data on the skull of *Marmoretta oxoniensis* from the Middle Jurassic of UK and Late Jurassic of Portugal has significantly added to our knowledge of this taxon. Based on these new data, our phylogenetic analysis recovers *Marmoretta* as a member of the lepidosaurian stem lineage, and a sister taxon to the Middle Triassic *Fraxinisaura.* This differs from the hypothesis proposed by Simões *et al.* (2018) who recovered *Marmoretta* as a squamate, within the lepidosaurian crown-group. As a Middle Jurassic taxon, *Marmoretta* remains significantly younger than other stem-group lepidosaurs, including its closest known relative *Fraxinisaura*. Both taxa are members of a clade that co-existed with the crown-group for at least 80 million years, and likely became extinct before the end of the Mesozoic, leaving rhynchocephalians and squamates as the sole representatives of the lepidosaurian line.

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AUTHOR CONTRIBUTIONS

Elizabeth Griffiths carried out investigation and formal analysis of the µCT data and visualisation of 3D models into manuscript figures, as well as writing of the original manuscript draft. David Ford carried out formal analysis of the phylogenetic data and wrote the phylogenetic discussion in the manuscript as well as the supplementary data. Susan Evans wrote parts of the supplementary data, contributed to character matrix scoring and validation, and the validation of anatomical comparisons. Roger Benson conceptualised, managed and supervised the project. All authors assisted in review and editing of the manuscript.

DATA ARCHIVING STATEMENT

Data for this study are available in [the Dryad Digital Repository]: / https://datadryad.org/stash/share/ZoQIqYgXRaPshFaNQ3rPS3514iErx5idKbLebzezwR0.
MorphoSource project: www.morphosource.org/projects/000349957 [login not necessary, project is open access] **[please note that the data for this paper are not yet published and this temporary link should not be shared without the express permission of the author]**

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FIG. 1. A, NMS G 1992.47.1a. B, renderings of tomographic data showing transparent blocks of specimen NMS G 1992.47.1a&b with segmented bones shown inside the semi-transparent blocks, C, segmented bones in preserved position shown enlarged. Scale bar = 10mm.

FIG. 2. Digital skull reconstruction of *Marmoretta oxoniensis*, using information from NMS G 1992.47.1a and CAMSM X9991, in A–B, lateral, C–D, dorsal and E–F ventral views. Grey shading is used in line drawings (B,D,F) to provide information on depth. Abbreviations: an = angular; ar = articular; cor = coronoid; d = dentary; ect = ectopterygoid; fr = frontal; j = jugal; mx = maxilla; pa = palatine; par = parietal; pbp = parabasisphenoid; pmx = premaxilla; po.f = postfrontal; po.or = postorbital; pr.a = prearticular; prf = prefrontal; ptg = pterygoid; qu = quadrate; s.a = surangular; sq = squamosal. Dashed lines indicate broken/restored regions of the cranium. Scale bar = 1mm.

FIG. 3. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Right maxilla in A, lateral, B, dorsal, C, medial, and D, ventral views. Right premaxilla in E, lateral, F, dorsal, and G, ventral views. Abbreviations: alv.b = alveolar border; d.p = dorsal process; j.f = jugal facet; m.f = maxilla facet; ne.f = neurovascular foramina pa.f = palatine facet; sac.e = superior alveolar canal entrance; sn.r = subnarial ramus. Dashed lines indicate broken/restored regions of the bone. Scale bar =1mm.

Fig. 4. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Cross section (A) and interpretive drawing (B) of tooth implantation in the maxilla and dentary. Abbreviations: bp = basal plate; d(lab) = dentary labial wall; d(lin) = dentary lingual wall; dt = mature dentary tooth; f = nutrient foramina; m(lab) = maxilla labial wall; m(lin) = maxilla lingual wall; mt = emerging maxillary tooth.

FIG. 5. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Right prefrontal in A, dorsal, B, ventral, and C, lateral views. Abbreviations: fr.f = frontal facet; l.f = lacrimal facet; mx.f = maxillary facet; orb.b = orbital border; p.p = palatine process. Scale bar = 1mm.

FIG. 6. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Right jugal in A, lateral, B, dorsomedial oblique and C, medial views. Abbreviations: ect.f = ectopterygoid facet; mx.f = maxillary facet; po.f = postorbital facet; pv.p = posteroventral process. Scale bar = 1mm.

FIG. 7. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Right postorbital in A, lateral, B, anterolateral oblique and C, medial views. Abbreviations: j.f = jugal facet; orb.b = orbital border; pf.f = postfrontal facet; sq.f = squamosal facet. Dashed lines indicate broken/restored regions of the bone. Scale bar = 1mm.

FIG. 8. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Frontal in A, dorsal, B, oblique right posterolateral, C, ventral and D, anterodorsal views. Dashed lines show estimated outlines of original bone before breakage, and are used to indicate broken regions. Dotted line in C estimates the ventral portion of the bone. Abbreviations: c.c = cristae cranii; n.f = nasal facet; pf.f = postfrontal facet; prf.f = prefrontal facet. Scale bar = 1mm.

FIG. 9. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Right postfrontal in A, lateral, B, medial and C, ventromedial views. Abbreviations: fr.f = frontal facet; orb.b = orbital border; par.f = parietal facet; po.f = postorbital facet. Scale bar = 1mm.

FIG. 10. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Parietal in A, dorsal, and B, right lateral views. Abbreviations: acs.f = ascending flange ; ml.c = midline crest; tu = tubercle. Dashed lines are to highlight the depressions between the domes as well as broken/estimated bone outlines. Scale bar = 1mm.

FIG. 11. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Right squamosal in A, lateral, B, medial and C, posterior views. Abbreviations: po.f = postorbital facet; qu.f = quadrate facet. Scale bar = 1mm.

FIG. 12. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Right quadrate and quadratojugal in A, lateral, B, medial, C, ventral, D, anterior, E, posterior and F, dorsal views. Abbreviations: pt.f = pterygoid facet; quj = quadratojugal; quj.f = quadratojugal foramen; sq.f = squamosal facet. Dashed lines indicate broken/restored regions of the bone. Scale bar = 1mm.

FIG. 13. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Left and right palatine in A, ventral view and B, dorsal view. Abbreviations: max. ram = maxillary ramus; subo.f.m = suborbital fenestra margin; t = teeth. Scale bar = 1mm.

FIG. 14. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Left and right pterygoids in A, ventral and B, dorsal views. Abbreviations: b.a = basal articulation; md.f = midline facet; pa.f = palatine facet; pp = palatal plate ; qp = quadrate process; tp = transverse process. Dashed lines indicate broken/restored regions of the bone. Scale bar = 1mm.

FIG. 15. *Marmoretta*, Skye, specimen NMS G 1992.47.1a Right maxilla, jugal and ectopterygoid in medial view A without ectopterygoid showing facet on jugal, B with ectopterygoid and C dorsal view. Abbreviations: ect.f = ectopterygoid facet; ect = ectopterygoid; j = jugal; mx = maxilla. Scale bar = 1mm.

FIG. 16. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Parabasisphenoid in A, dorsal, B, ventral and C, posteroventral views. Abbreviations: bpt.p = basipterygoid processes; cv = cristae ventrolaterales; hf = hypophysial fossa; ica = internal carotid foramen; ppw = posterior parasphenoid wing; psr = parasphenoid rostrum. Dashed lines indicate broken/restored regions of the bone. Scale bar = 1mm.

FIG. 17. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Basioccipital in A, dorsal, B, ventral and C, posterior views. Abbreviations: bt = basal tubera; eo.f = exoccipital facet; oc = occipital condyle. Scale bar = 1mm.

FIG. 18. *Marmoretta*, Skye, specimen NMS G 1992.47.1a. Right dentary in A, lateral, B, dorsal, C, medial, and D, ventral views. Abbreviations: alv.s = alveolar shelf; cor.f = coronoid facet ; M.g = Meckelian groove; t = teeth. Scale bar = 1mm.

FIG. 19. *Marmoretta oxoniensis*, referred specimen CAMSM X9991. Right lower jaw approximately as preserved, with slight reconstruction to move the prearticular, splenial and angular into place. A dorsal, B, lateral, C, ventral and D, medial views. Abbreviations: an = angular; ar = articular; c = coronoid; d = dentary; pr.a = prearticular; s.a = surangular; sp = splenial. Scale bar = 1mm.

FIG. 20. Maximum clade credibility tree recovered from Bayesian analysis using non-time calibrated Mkv model. Figures adjacent to nodes are the posterior probability value of the node.