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Re-assessment of a large archosaur dentary from the Late Triassic of South Wales, United Kingdom

Owain Evans [a,b], Cindy Howells [c], Nathan Wintle [d], Michael J. Benton [a,*]

[a] School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, UK
[b] Cell and Developmental Biology, University College London, Anatomy Building, G23 Gower Street, London WC1E 6BT, UK
[c] Palaeontology, National Museum Cardiff, Cathays Park, Cardiff CF10 3NP, UK
[d] 13 Highbury Crescent, Bridgend CF31 4RD, UK

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ABSTRACT

A large jaw of a predatory archosaur from the latest Triassic of South Wales, named *Zanclodon cambrensis*, has long intrigued vertebrate palaeontologists. Could it be the oldest large theropod dinosaur? Here we reanalyse the specimen based on a new 3D digital reconstruction. We confirm first that it is indeed latest Triassic in age, most likely extracted from sandstones of the Cotham Member of the Lilstock Formation (Penarth Group, Rhaetian). Anatomically it shows features of theropod dinosaurs rather than other large non-dinosaurian predatory archosaurs of the Triassic. It shares general characteristics with European coelophysoids of similar age such as *Liliensternus* and *Dracoraptor* but is considerably larger. It is not a megalosauroid, as suggested previously, but it is unclear whether it might be an averostran or tetanuran. Its close similarity to *Dilophosaurus* suggests that this left-hand mandible specimen represents a more derived basal neotheropod and we assign it to a new genus, as *Newtonsaurus cambrensis*.

1. Introduction

Examples of large theropod dinosaurs in the Triassic are rare, and indeed it is often asserted that large flesh-eating dinosaurs only emerged in the Middle Jurassic, with forms such as *Megalosaurus* (Rauhut and Hungerbühler, 1998; Griffin and Nesbitt, 2020). The role of large predators was taken in the Late Triassic by rauisuchians, ornithosuchids, and other large pseudosuchian predators, on the lineage to crocodilians. Some footprints from the Late Triassic have been interpreted as those of large theropod dinosaurs, and many Late Triassic theropods known from skeletal remains may be immature individuals not yet at full adult size (Griffin and Nesbitt, 2020). Nonetheless there is a long span in the theropod record from their origin to the evidence of the first truly large forms. The large theropod mandible *Zanclodon cambrensis* from the latest Triassic of South Wales is then something of an anomaly.

The holotype specimen of *Zanclodon cambrensis* is the natural mould of a left dentary, showing both the interior (housed at the National Museum of Wales) and exterior surfaces (housed at the British Geological Survey), and supposedly extracted from rocks of Rhaetian age, the final stage of the Triassic, dating perhaps from 205 to 201 Ma. As Newton (1899, p. 92), its first describer, noted, “the resemblance which [the] jaw bears to the corresponding parts of *Megalosaurus* is so striking that the reference of the fossil to the same genus appears, at first sight, to be justifiable.” Despite these similarities, however, Newton assigned the jaw to the genus *Zanclodon*, established by Plieninger (1846) for a jaw of a carnivorous reptile from the Erfurt Formation (=Lettenkeuper), dated as late Ladinian, from the late Middle Triassic of Germany. *Zanclodon* was often allied with *Teratosaurus* in the Family Teratosauridae, widely regarded as an early diversification of theropod dinosaurs. By 1899, many species of *Zanclodon* had been established, mainly based on such jaw bones of late Middle to Late Triassic age. In a subsequent revision (Rauhut and Hungerbühler, 1998; Schoch, 2011), many of these *Zanclodon* species were re-identified as archosauriform indet., phytosaur, or rauisuchian. Newton (1899) allied the new jaw with *Megalosaurus* based on similarities in the strongly recurved tooth morphology, but he noted differences in the robustness and size of the dentary when compared to *Megalosaurus*. However, Newton (1899, p. 93) noted that he could not compare the jaw more widely because, apart from *Megalosaurus*, “no lower jaws are available for comparison.”

Newton's jaw fossil has been reviewed by many since. Waldman (1974) echoed Newton's initial observations that the dentary closely resembled that of *Megalosaurus*, with the only substantial morphological differences being found in the teeth. Later authors concurred with this interpretation, noting resemblances with the dentaries of a variety of megalosauroid theropods (Storrs, 1993, 1994; Galton, 1998, 2005), listing some potential synapomorphies (Molnar et al., 1990). However,

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[*] Corresponding author.
E-mail address: mike.benton@bristol.ac.uk (M.J. Benton).

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more recent studies concur that the supposed synapomorphies have a more general distribution, being present in all Neotheropoda (Rauhut and Hungerbühler, 1998). The specimen was then tentatively placed in Coelophysoidea based on the low-lying interdental plates (Naish and Martill, 2007, p. 500) and the presence of only one Meckelian foramen (Benson, 2010). Generally, the absence of diagnostic features has left *Zanclodon cambrensis* as a *nomen dubium*. It was however named informally as a new genus '*Newtonosaurus*' by Molnar et al. (1990).

Despite these short contributions, the specimen is of remarkable quality, even though it is only a rock mould, and no original bone remains. Further, if it is truly Rhaetian in age, it is an unusually early large predatory archosaur. It is associated with a diverse array of other reptiles including dinosaurs from a variety of locations in South Wales (Yates, 2003; Galton, 2007; Whiteside et al., 2016; Spiekman et al., 2023), and theropods have already been reported from the Rhaetian of Aust Cliff (Reynolds, 1946) and Lavernock Point (Galton, 1998). Using photogrammetry, we have generated new, three-dimensional images of the specimen, and we test the key questions of the true age of the specimen, whether it is a dinosaur or something else, and if it is a dinosaur and a theropod, what kind of theropod?

Repository abbreviation: **AMNH**, American Museum of Natural History, New York, New York, USA; **BYU**, Brigham Young University Vertebrate Paleontology, Provo, Utah, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **GSM**, British Geology Survey, Keyworth, Nottinghamshire, UK; **LFKL**, Dinosaur Fossil Research and Protection Center of Lufeng City, Lufeng, Yunnan, China; **MB**, Humboldt Museum, Berlin, Germany; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **MNHN**, Museum National d'Histoire Naturelle, Paris, France; **MSM**, Mesa Southwest Museum, Mesa, Arizona, USA; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; **OUMNH**, Oxford University Museum of Natural History, Parks Row, Oxford, UK; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **SAM**, Iziko South African Museum, Cape Town, South Africa; **SIDMM**, Sidmouth Museum, Sidmouth, UK; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TMM**, Texas Vertebrate Paleontology Collections, The University of Texas at Auatin, Austin, Texas, USA; **TTU-P**, Texas Tech University Paleontology, Lubbock, Texas, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA; **UFRGS-PV**, Paleovertebrate Collection of the Laboratório de Paleovertebrados of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **UMNH**, Utah Museum of Natural History, Salt Lake City, Utah, USA; **UUVP**, Utah Museum of Natural History, University of Utah, Salt Lake City, Utah, USA; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

2. Geological setting

Newton (1899, p. 89) reported that the specimen "was obtained by Mr. John David, of Porthcawl (Glamorganshire), from a mason, who was engaged in preparing stone for building a wall, at Stormy Down, near Bridgend." Newton attempted to identify the location and horizon from which the fossil had been obtained, noting that "Stormy Down is within the boundary of the Penarth or Rhaetic Beds on the old edition of the Geological Survey map; but whether the bed which yielded the fossil lies above or below the *Avicula contorta*-shales is a point still under investigation". We confirm Newton's (1899, p. 89) observation of several bivalve impressions on the block (Fig. 1), and despite the poor preservation, these can be identified as species of *Pteromya* from their overall shape ('subovate, sub-equilateral or inequilateral to a varying extent, not strongly inflated… umbones broad, protruding very little; postero-dorsal and posterior margins forming continuous, strongly convex curve'; Ivimey-Cook et al., 1999, p. 123). A key feature, the 'obtuse ridge passing from the umbo to the postero-ventral corner of the shell, separating a flattened postero-dorsal area, with a well-defined, obtuse outer angle, from the flank of the shell' (Cox, 1963, p. 583) cannot be discerned. The two bivalves are probably *P. langportensis* and *P. crowcombeia* respectively (David Martill, pers. comm.), the first being typical of the Langport Member of the Lilstock Formation and the second occurring in the Westbury Formation and Cotham Member of the Lilstock Formation of the Rhaetian (Richardson and Tutcher, 1916; Cox, 1963; Ivimey-Cook et al., 1999, pp. 123–126). The bivalves then suggest that the block containing the jaw is probably late Rhaetian and equivalent to the Lilstock Formation of the Penarth Group.

Fig. 1. Poorly preserved bivalves, right valve of *Pteromya langportensis* (left) and left valve of *Pteromya crowcombeia* (right), in the matrix of GSM 6532. These confirm a Rhaetian (Penarth Group) age, and presumed assignment to the sandstones of the Cotham Member of the Lilstock Formation, exposed widely on Stormy Down, where the specimen was originally collected.

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This confirms earlier suggestions (Storrs, 1994; Galton, 1998) that the block lithologically matched one of the sandstones of the Lilstock Formation. Stormy Down exposes sections of the Cotham Member of the Lilstock Formation, and the general lithology of the block containing the dentary mould matches horizons of the lower Lilstock Formation (Ivimey-Cook, 1974; Wilson et al., 1990): the matrix around the jaw is a lightly coloured fine-grained sandstone, with darker patches of lenticular bedding that vary between brown and buff in colour. However, it is difficult to distinguish the Cotham Member from some harder beds in the upper Westbury Formation, as in South Wales the transition is gradual (Wilson et al., 1990). Nonetheless, these are all Rhaetian in age, and quite distinct from the mudstone–limestone interbeds of the uppermost Rhaetian and overlying Jurassic.

The sandstone block is characteristic of a marginal marine environment, possibly a lagoonal or beach deposit (Wilson et al., 1990). The lower Lilstock Formation comprises rocks that were deposited in varying terrestrial and marine environments, with short periods of transgression and regression, and with some evidence of storm deposition (Ivimey-Cook, 1974; Wilson et al., 1990). This is consistent with the incorporation of a terrestrially derived fossil such as a dinosaur bone into marine sediments (Evans et al., 2024).

3. Digital reconstruction

Identifying osteological features on this specimen is problematic as it is a natural mould. To make identification more rigorous, a three-dimensional digital reconstruction was generated. Both specimens were first scanned using an Artec Space Spider industrial 3D scanner, and the surface scan images were imported into Blender 4.0 (Blender Online Community, 2024). Following this, sections of the matrix present on the model were cut away digitally to reveal the negative of the mould, which is representative of the original bone. Matrix was then continuously deleted, ensuring that a small area of polygons remained around the dentary to prevent the loss of anatomical detail around the edges. Both sides of the dentary were then imported into the same scene and placed alongside each other, aligned at the largest tooth. Ambient occlusion was then applied to aid the identification of smaller anatomical features. From this, characters could be readily identified, as well as providing a better perspective on some areas of the bone that are difficult to analyse on the mould, such as the ventral and distal surfaces.

4. Description

The holotype specimen, GSM 6532, is a well-preserved natural mould of a dentary bone from the left-hand side split into two halves, separating the lateral and medial surfaces into two blocks. The medial surface (Fig. 2A) preserves an impression of the dentary up to the dentary–surangular suture, where there appears to be a break in the original bone — suggesting that the posterior end of the mandible broke away and was buried separately. The lateral surface (Fig. 2B) is preserved in less detail, with the impression becoming faint towards the ventral margin of the anterior surface, leading to some difficulty in interpreting the morphology of the dentary tip. The block preserving the lateral impression has been broken diagonally approximately 15 cm along the original length. This break is visible on the medial impression block (Fig. 2A) but seems to have been reattached. There is little taphonomic distortion on either impression, with only a few thin

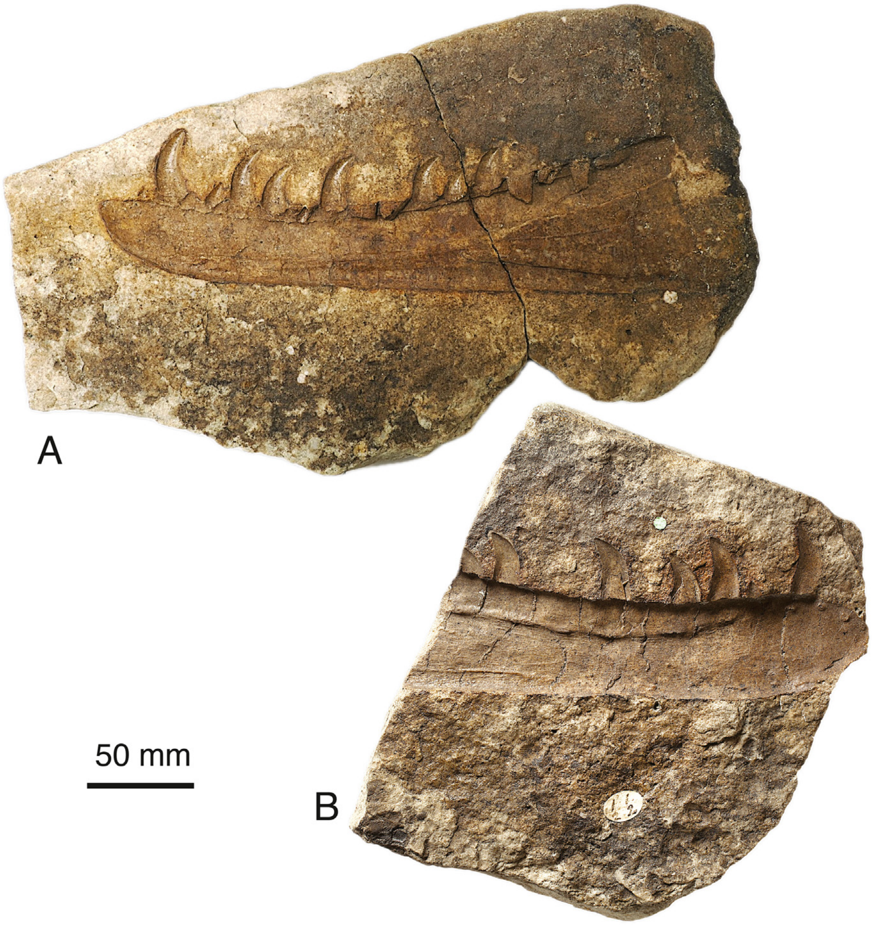

Fig. 2. The two separate blocks containing the jaw impression of the Stormy Down archosaur (GSM 6532) that make up the holotype: (A) The medial impression and (B) the lateral impression.

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compression cracks along the surfaces, and a loss of detail of the anterior tip on the lateral side. A very fine degree of anatomical detail is in fact preserved, including what we assume to be original striations along the bone on the lateral impression as well as denticles preserved on teeth four, five, seven and ten.

The dentary as preserved is 28 cm long on the medial block (Fig. 2A), and 13 cm on the lateral block (Fig. 2B). This is approximately the same length as the dentary of *Liliensternus* (MB.R.21751.8; von Huene, 1934). By comparison with *Liliensternus*, *Dilophosaurus*, and other early theropods, the preserved portion of the mandible, terminating at the final tooth position of the dentary, represents about half the length of the mandible, which then would have been 56 ± 5 cm long, corresponding to a total body length of 5–7 m.

GSM 6532 is similar in proportions to the anterior *Dilophosaurus* mandible (TMM 43646-1), but more robust than *Coelophysis bauri* (NMMNH P-50529); relative maximum depths of mandibles to lengths are 17.8 % for GSM 6532, 18.5 % for *Dilophosaurus*, and 12.2 % for *Coelophysis*. In lateral view, the ventral margin is flat, gradually curving dorsally towards the anterior tip. This morphology is common amongst Triassic–Jurassic carnivorous theropods, except in some megalosauroid taxa such as *Megalosaurus bucklandii* (OUMNH J.13505; Benson, 2010) and *Dubreuillosaurus valesdunensis* (MNHN 1998-13; Allain, 2005), which both have a slight concavity at the posterior end of the dentary, and a slight convex curve towards the anterior tip. The ventral morphology of the Stormy Down mandible is similar to that found in *Dilophosaurus wetherilli* (TMM 43646-1; Marsh and Rowe, 2020) and *Liliensternus liliensterni* (MB.R.2175.1.8), in which the flat ventral margin begins to curve gradually opposite the fourth alveolus.

These features of size and shape are only suggestive and not diagnostic. The same is true for the dorsal margin and anterior end of the dentary (Figs. 2, 3). The dorsal margin is concave, with shallow arc shape in which the anterior tip is elevated. The anterior tip is convex, forming a distinctive dorsal expansion, with its apex at the third tooth. This feature has been noted in several Triassic–Jurassic archosaurs and has been referred to as a 'chin' in *Dilophosaurus*, where the expansion is particularly pronounced (Marsh and Rowe, 2020) both dorsally and laterally. Across archosaurs, the extent of this expansion is however variable. Notably, this anterior dentary bulge is associated with a notch between the maxilla and premaxilla, resulting in an arched diastema, in several archosaurian taxa including *Dilophosaurus wetherilli* (TMM 43646-1), *Sinosaurus triassicus* (LFKL-004; Zhang et al., 2023) *Coelophysis kayentakatae* (MNA V2623; Rowe, 1989), *Eustreptospondylus oxoniensis* (OUMNH J.13558; Sadleir et al., 2006), *Liliensternus liliensterni* (MB.R.2175.1.8), and the sauropodomorph *Eoraptor lunensis* (PVSJ 512; Sereno et al., 2012), as well as the crocodylomorph *Sphenosuchus acutus* (SAM 3014; Walker, 1990) and the rauisuchian *Batrachotomus kupferzellensis* (SMNS 80260; Gower, 1999). This anterior dorsal hump is also present in the poposauroid *Arizonasaurus babbitti* (MSM 4590; Nesbitt, 2005), but it is significantly shallower when compared to dinosaurs. The convex dorsal margin of the Stormy Down specimen is common amongst archosaurs, both dinosaurs and pseudosuchians, particularly in *Prestosuchus chiniquensis* (UFRGS-PV-0629-T; Mastrantonio et al., 2024), *Postosuchus kirkpatricki* (TTU-P 9000; Weinbaum, 2011) and *Hesperosuchus agilis* (AMNH FR 6758; Clark et al., 2001).

In dorsal view (Fig. 3C) the dentary curves laterally towards the anterior tip. This curvature is caused by a lateral expansion of the anterior section of the dentary to accommodate the large second alveolus. A similar expansion is present in the dentaries of theropods such as *Dubreuillosaurus valesdunensis* (MNHN 1998-13), *Eustreptospondylus oxoniensis* (OUMNH J.13558), *Sinosaurus triassicus* (LFKL-004), *Liliensternus liliensterni* (MB.R.21751.6) and *Dilophosaurus wetherilli*

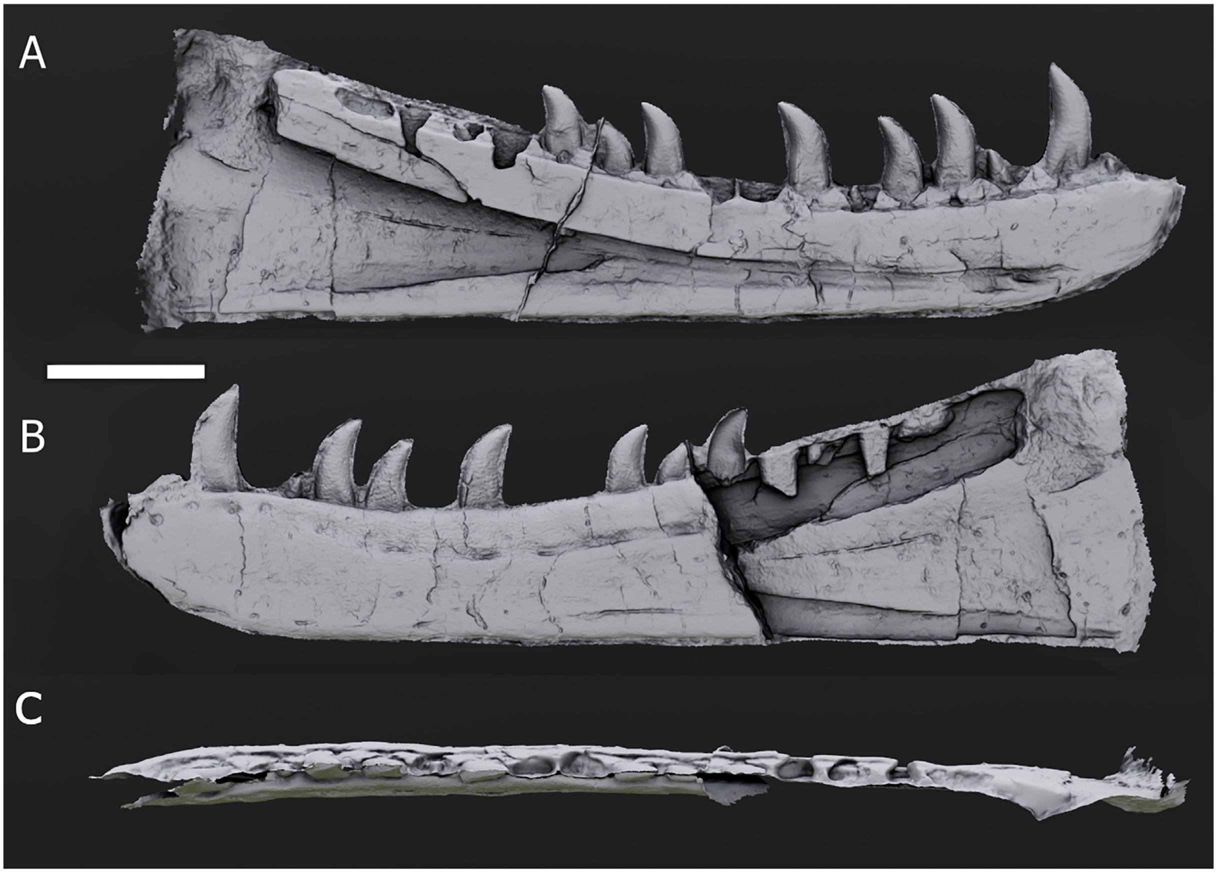

Fig. 3. Digital reconstruction of the holotype specimen GSM 6532, developed by combining photogrammetry images of both slabs. In presenting the 3D model here, what were moulds in the rock become solid surfaces of the dentary. (A) In medial view, (B) in lateral view, and (C) in dorsal view.

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(TMM 43646-1), as well as the pseudosuchians *Sphenosuchus acutus* (SAM 3014) and *Postosuchus kirkpatricki* (TTU-P 9000). Sixteen alveoli are present on the specimen, with seven bearing fully erupted teeth, and with replacement teeth clearly present in alveoli 1, 3, 6, and 14. There were likely seventeen alveoli in total as in *Dilophosaurus wetherilli* (UCMP 37303), but the anteriormost alveolus has not been preserved on the specimen, leaving only a slight impression on the dorsal surface. The alveoli are transversely compressed, oval in outline, and generally of the same or similar size. The second alveolus, which would likely have been the third in the complete dentary, is significantly larger, and is transversely expanded, which is accommodated by the transverse expansion of the anterior jaw tip, giving the alveolus a more circular impression. This pattern is common in archosaurs with one or two larger anterior teeth.

Five fully erupted teeth are present in alveoli 2, 4, 7, 10, and 12 (Fig. 3). The second (third) tooth is the largest, as in *Liliensternus liliensterni* (MB.R.21751.6), *Dilophosaurus wetherilli* (TMM 43646-1) and other coelophysoids. In the Stormy Down specimen, this may also have formed the apex of a tooth rosette. Additionally, the largest tooth is also slightly distally procumbent, a feature seen in non-averostran neotheropods (Hendrickx et al., 2019).

The teeth are transversely compressed, strongly apically recurved and distinctly homodont, only decreasing in size slightly posteriorly. Although many archosaurs possess recurved teeth, the dental morphology of the Stormy Down archosaur has greatest similarity to that of *Liliensternus liliensterni* (MB.R.21751.6) and *Dracoraptor hanigani* (NMW 2015.5G.1a; Martill et al., 2016), in which the apex of the tooth crown is heavily recurved and the section above the cervix, but below the apex, remains straight. This tooth morphology was noted by Newton (1899) as a contrast with megalosauroid taxa, the teeth of which show a gentle recurvature along the whole crown, except in *Dubreuillosaurus valesdunensis* (MNHN 1998-13). Caudal denticle impressions are preserved on teeth 4, 5, 7, and 10 on the distal side of the mould, extending down to just above the cervix (Fig. 4). Poor preservation means that it is difficult to determine the exact pattern of serration on GSM 6532, and whether both the caudal and distal carinae were serrated as in *Liliensternus liliensterni* (MB.R.21751.6) and *Dracoraptor hanigani* (NMW 2015.5G.1a).

Ten interdental plates are clearly preserved on the specimen (Figs. 2A, 3A, 5A); they are sub-pentagonal and unfused. This morphology is common in early theropod dinosaurs, but less so in pseudosuchians. In the rauisuchians *Fasolasuchus tenax* (PVL 3851; Nesbitt et al., 2013), *Postosuchus kirkpatricki* (TTU-P 9000) and *Teratosaurus suevicus* (ZPAL Ab III 563; Brusatte et al., 2009), the interdental plates fuse to form a sheet of bone. In the Otter Sandstone archosaur (SIDMM G 1 2010) and the poposauroid *Arizonasaurus babbitti* (MSM 4590), the dental plates are unfused but have a significantly more oval outline. Similarly unfused interdental plates are present in the dentaries of *Sphenosuchus acutus* (SAM 3014) and *Terrestrisuchus gracilis* (NHMUK PV R 38290b; Spiekman et al., 2023), but these are triangular. Amongst Triassic–Jurassic theropod dinosaurs, it is notable that the interdental plates in ceratosaurs, specifically *Ceratosaurus nasicornis* (UUVP 158; Madsen and Welles, 2000), *Genyodectes serus* (MLP 26-39; Otero and Reguero, 2013) and *Majungasaurus crenatissimus* (FMNH PR 2100; Sampson and Witmer, 2007), are fused. A narrow paradental groove separates the dental plates from the medial side of the dentary and, although poorly preserved, appears to be open for its entire length as in *Dilophosaurus wetherilli* (UCMP 37303), *Allosaurus fragilis* (BYU 8901; D'Emic et al., 2019) and *Magnosaurus nethercombensis* (OUMNH J.12143/1a–b; Benson, 2010). The groove is distorted between alveoli 6 and 9, associated with two compression cracks in the specimen.

The medial surface of the dentary (Figs. 2A, 3A, 5A) is split into two elevated sections of bone, the supradentary and the splenial contact, separated by the broad Meckelian fossa. The dorsal and ventral surfaces meet towards the anterior tip of the Meckelian groove to form a mediolaterally flattened symphysial area. The dorsal supradentary section is bordered by the interdental plates dorsally, and the Meckelian fossa ventrally. The alveoli penetrate this section, but not through to the Meckelian fossa. The ventral portion tapers to a point posteriorly and is medially convex, forming the splenial contact. The Meckelian fossa is deep and broad, transferring into the Meckelian groove below the sixth alveolus, where the depth gradually diminishes. A single

Fig. 4. Close-up of two teeth of GSM 6532, showing fine preservation of serrations along the posterior carina. Scale bar is 10 mm.

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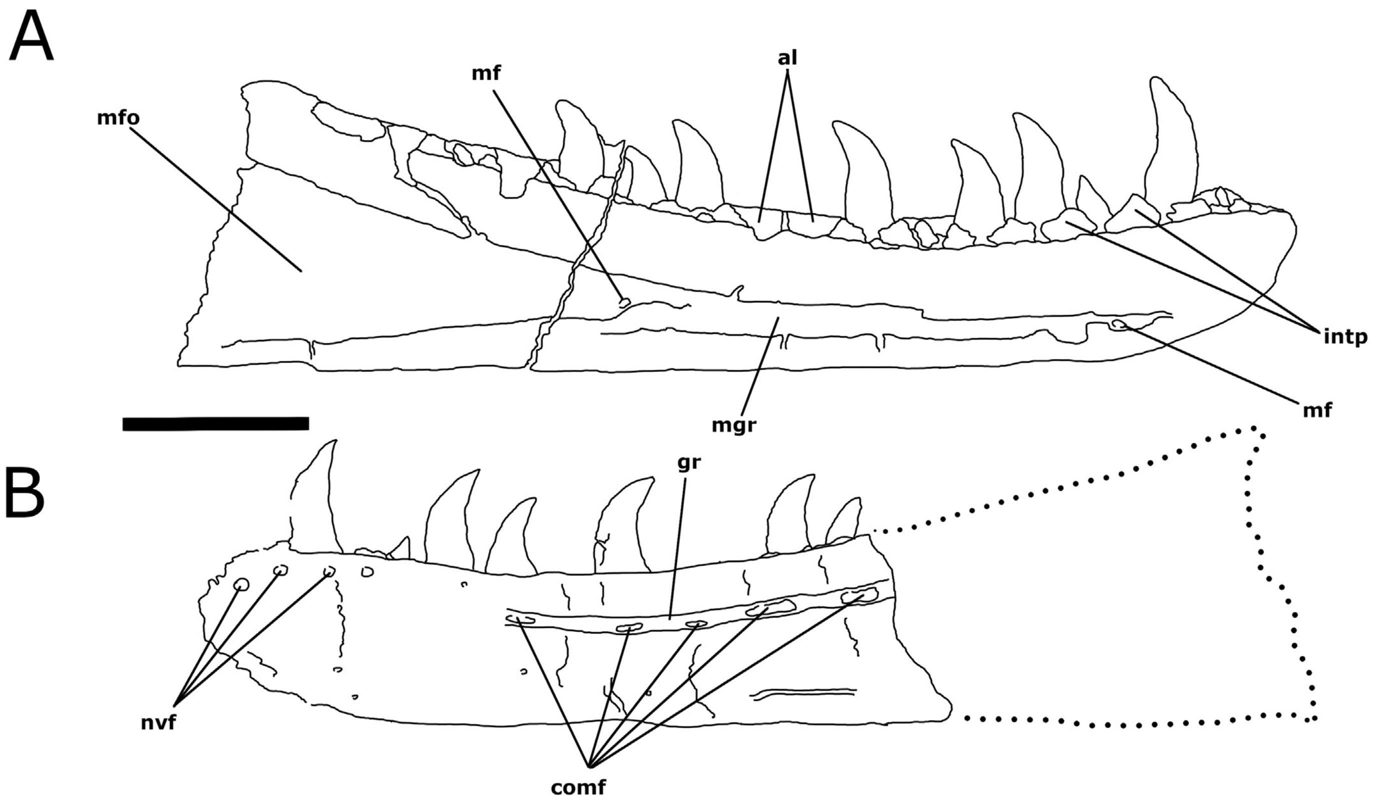

Fig. 5. Interpretive drawing of the Storm Down specimen. (A) In medial view and (B) in lateral view; mfo, Meckelian fossa; mf, Meckelian foramen; al, alveoli; mgr, Meckelian groove; intp, interdental plate; comf, compressed foramina; nvf, neurovascular foramina; gr, groove. Scale bar represents 50 mm.

Meckelian foramen is present at the terminal anterior end of the groove, level with the third alveolus. A second possible foramen may be present at the margin between the Meckelian fossa and the Meckelian groove, but it is difficult to distinguish because of the state of preservation. Two anterior foramina are a common feature of megalosauroids, whilst *Ceratosaurus nasicornis* (UUVP 158), *Majungasaurus crenatissimus* (FMNH PR 2100) and possibly *Dilophosaurus wetherilli* (TMM 43646-1) have only one.

A row of four large circular foramina follows the anterior dorsal margin on the lateral surface of the dentary (comf, Figs. 3B, 5B). The identification of foramina on the anterior margins is dependent on preservation, and GSM 6532 lacks the random arrangement of foramina seen in many archosaurs. Although there may be a taphonomic bias towards larger foramina, the arrangement here is identical to that found in *Liliensternus liliensterni* (MB.R.2175.1.8), where four circular foramina also follow the dorsal margin. A groove runs antero-posteriorly along the lateral surface, with five dorsoventrally flattened foramina within the groove. In *Dilophosaurus wetherilli* (UCMP 37303), *Dubreuillosaurus valesdunensis* (MNHN 1998-13), *Magnosaurus nethercombensis* (OUMNH J.12143/1a–b), *Eustreptospondylus oxoniensis* (OUMNH J.13558), *Majungasaurus crenatissimus* (FMNH PR 2100) and *Torvosaurus tanneri* (BYU 2003; Britt, 1991), foramina also sit in a similar groove, but in these taxa, the foramina open either posteriorly or anteriorly. In GSM 6532, the circular foramina appear to be elongated, seemingly their undistorted shape and with no evidence of dorso-ventral compression. This morphology is not present in any other taxa and may be autapomorphic.

5. Discussion

5.1. Classification background

GSM 6532 has proved hard to classify. Newton (1899) compared it with many Triassic taxa that he referred to as generally ‘megalosauroid,’ but which now would mostly be described as *nomina dubia*: *Teratosaurus suevicus*, *Palaeosaurus cylindrodon*, *Cladyodon lloydi*, *Avalonia sanfordi* and *Picrodon herveyi*. All were based on isolated teeth and so were hard to compare with other taxa. *Teratosaurus suevicus* is now understood to be a rauisuchian (Benton, 1986; Brusatte et al., 2009), whilst both *Avalonia sanfordi* (=*Avalonianus*) and *Palaeosaurus* were revealed to be chimeric specimens comprising skeletal remains from a prosauropod, and isolated teeth from an indeterminate archosaur (Galton, 1998, 2007). *Cladyodon* and *Picrodon* both remain poorly defined and are generally ascribed to an unspecified archosaurian predator.

The taxonomic position of *Zanclodon* was revised by subsequent authors. In his review of Triassic archosaurs, von Huene (1908) stated that the genus name *Zanclodon* must be reserved only for the specimens initially identified by Plieninger (1846). von Huene instead referred the South Wales specimen to *Plateosaurus*, which now seems extraordinary as a wealth of specimens of the latter from Germany shows it was clearly an early diverging sauropodomorph. Schoch (2011) re-evaluated the status of *Zanclodon*, assigning all the diagnostic material to the species *Zanclodon laevis*. The most notable diagnostic character, as agreed by several previous authors, was the lack of serrations on all teeth (Galton, 2001; Hungerbühler, 2001). GSM 6532 preserves impressions of serrations on four teeth. Therefore, this material cannot be placed within *Zanclodon*, and *Zanclodon cambrensis* can no longer be considered a member of that genus. In their review of Tetanurae, Carrano et al. (2012, p. 257) reported various earlier assignments of *Z. cambrensis* to Megalosauridae but concluded that it “is substantially different from *Megalosaurus*, indeed from tetanurans generally, and is an indeterminate theropod outside Averostra or a more basal predatory archosaur”.

5.2. Diagnostic characters

A key question is to determine whether GSM 6532 is a dinosaur or something else. It appears to be a dinosaur, based on several features.

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The interdental plates are unfused, quite unlike those of rauisuchians, which generally exhibit a fused interdental plate. Additionally, the pentagonal morphology on the interdental plates differs from the unfused interdental plates of *Arizonasaurus babbitti*, *Sphenosuchus acutus* and *Terrestrisuchus gracilis*. Such unfused pentagonal interdental plates are found across most Dinosauria, except ceratosaurs, where the interdental plates are fused. It cannot be determined whether the additional articulation in the lower jaw between dentary and post-dentary elements, diagnostic of Theropoda, was present or not.

If the specimen is a theropod, can it be assigned to any of the major clades by reference to diagnostic characters? Attempting to place GSM 6532 in Neotheropoda based on current phylogenies is impossible, as amongst autapomorphies 28–47 listed by Carrano et al. (2012, table S3), none refers to the dentary or teeth. As for Averostra, there are no dentary characters amongst the 12–33 apomorphies. The same is true for Tetanurae, comprising Megalosauroidea and all subsequent theropods, for which the 14–38 apomorphies do not include any pertaining to the dentary or its teeth.

Of the 351 theropod characters listed by Carrano et al. (2012), GSM 6532 shows the subcircular third dentary alveolus (character 121(1), shared also with Coelophysoidea and Megalosauria); the dentary shape in dorsal view curving anteromedially (character 122(1), shared with various tetanurans, but not diagnostic of the clade); longitudinal groove housing a dorsally situated row of neurovascular foramina present on lateral surface (character 124(1), seen in Megalosauroidea and several other derived tetanuran clades); and single Meckelian foramina (character 125(0), as in Coelophysidae and various tetanurans).

We can say GSM 6532 is probably not *Megalosaurus* because it lacks several apomorphic features noted by Carrano et al. (2012, p. 236), namely the presence of 13–14 dentary teeth (our specimen has 16–17), the unexpanded third dentary alveolus, and dentary straight in dorsal view with unexpanded symphyseal area. Further, the paradental groove is narrow (character 123(0)), unlike in Megalosauria in which it is wide anteriorly defining a distinct gap between the medial dentary wall and the interdental plates.

Allocating Late Triassic and Early Jurassic theropods to the two major clades, the Coelophysoidea and Averostra (plus stem averostrans), has proved difficult. Some of the taxa, such as *Coelophysis*, *Liliensternus liliensterni*, and *Dracoraptor*, are coelophysoids, whereas *Dilophosaurus wetherilli* and *Sarcosaurus woodi* are close to Averostra, but in the stem (Marsh and Rowe, 2020; Ezcurra et al., 2021). Therefore, it is not unexpected that it was difficult to allocate GSM 6532 unequivocally to one or other clade.

5.3. Comparisons

Can the Stormy Down mandible be assigned to any of the existing named Late Triassic and Early Jurassic theropod genera? First to consider are taxa of similar age from Europe, including *Liliensternus liliensterni* from the mid-Norian of Germany (von Huene, 1934). As noted through the descriptions above, the general shape of the dentary is similar, although considerably smaller — the entire mandibles of the two specimens are given as 7 cm and 12 cm long (von Huene, 1934, p. 145), whereas the current dentary bone is 28 cm long, equivalent to a complete mandible length of 40–45 cm. Further, *Liliensternus liliensterni* has 22 mandibular teeth, compared to 16–17 in the Welsh specimen.

Second to consider is the coelophysoid *Dracoraptor hanigani*, from the earliest Jurassic of South Wales (Martill et al., 2016), geographically close to the Stormy Down mandible. However, the specimen lacks the dentary and so cannot be compared. It is smaller, with a skull estimated at about 20 cm long. A third taxon to consider is *Sarcosaurus woodi* from the Lower Lias of England, perhaps 1–5 Myr younger, which is interpreted as a neotheropod and one of the closest sister-taxa to Averostra (Ezcurra et al., 2021). We cannot compare GSM 6532 to *Sarcosaurus woodi*, however, because the latter is based only on postcranial remains. The wealth of isolated theropod specimens from the latest Triassic (Rhaetian) of nearby Lavernock Point (Evans et al., 2024) confirms the likelihood of several theropod taxa but whether they were all coelophysoids or averostrans cannot be said.

Two taxa from North America that might be comparable are *Coelophysis bauri* from the later Carnian and early Norian of the southwest, some 25 Myr older, and *Dilophosaurus wetherilli* from the Early Jurassic of the same region, some 5 Myr younger. The mandible of the coelophysoid *Coelophysis bauri* is shallower and has a sharper anterior termination (*cf.*, Colbert, 1989, fig. 38) and the teeth are more slender and lack the mid-length bend seen in the Stormy Down specimen. *Coelophysis* has 26–27 mandibular teeth compared to 17 in our specimen, and it is smaller, with a skull length of 9–27 cm, compared to 40–45 cm.

The Welsh specimen might be said to have greatest affinity with the averostran outgroup taxon *Dilophosaurus wetherilli* (Marsh and Rowe, 2020). The dentary length is comparable to the paratype specimen of *Dilophosaurus wetherilli* (UCMP 37303), which is ~28 cm long. It also shares several dentary characters: an expansion of the anterior tip of the dentary, 16–17 dentary alveoli, the largest dentary tooth being found in the third alveolus, an open paradental groove for its entire length, and a lateral groove along the labial margin which contains a series of foramina. However, GSM 6532 differs from *Dilophosaurus* in several ways: the anterior expansion of the dentary is less pronounced than in *Dilophosaurus* in which it forms a characteristic bulge; the dentary is less deep than in *Dilophosaurus*, with a shallower bow shape; and the distance between the dentary–surangular suture and the base of the dentary is 7 cm in GSM 6532 and 19 cm in the paratype of *Dilophosaurus wetherilli*.

Therefore, we cannot assign the Stormy Down mandible to any existing taxon, and although we identify it as a coelophysoid, this is tentative. With future discovery of more material, by age and size, the likelihood is that the specimen belongs to an as yet unnamed species. The specific epithet *cambrensis* is valid, but as discussed, the species cannot be assigned to *Zanclodon* or *Megalosaurus*, or any of the other discussed genera. We therefore formally establish a new genus name, based on one earlier suggested informally (Molnar et al., 1990).

5.4. Systematics

Suborder Theropoda Marsh, 1881
Infraorder Neotheropoda Bakker, 1986
Genus: *Newtonsaurus* nov. gen.
Type and only species: "*Zanclodon*" *cambrensis* Newton, 1899
urn:lsid:zoobank.org:pub:344BCD1C-E12E-4464-ABD5-F094654E0811

Type specimen: GSM 6532.

Locality: Stormy Down, near Bridgend, Wales, United Kingdom.

Stratigraphy: Sandstone of the Cotham Member of the Lilstock Formation, mid to late Rhaetian (*c.*, 202 Ma).

Background of the name: The generic name *Newtonsaurus* is named in honour of Edwin Tully Newton (1840–1930), palaeontologist at the British Geological Survey who was first to report the specimen. The name *Newtonsaurus* has been discussed in various online fora, having been established in private documents by Stephen Pickering in 1999, and has been mentioned rarely in compilations of nomenclature (*e.g.*, Molina-Pérez and Larramendi, 2019, p. 25), but so far has been a *nomen nudum*, never having been proposed in a scientific paper.

Diagnosis: A unique combination of characters, with autapomorphy marked (*): expansion of anterior tip of dentary, but not bulbous; dentary relative depth midway between those of *Coelophysis bauri* and *Dilophosaurus wetherilli*; 16–17 dentary teeth; largest dentary tooth in the third alveolus; open paradental groove for its entire length; lateral groove along the labial margin which contains a series of foramina; distance from dentary–surangular suture to base of dentary is short; *anterior–posterior elongation of lateral foramina along the labial margin of dentary.

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Comment: The taxon stands as unique on the basis of the combination of characters noted, some seen in *Liliensternus liliensterni*, some in *Coelophysis bauri*, and some in *Dilophosaurus wetherilli*, but not in this combination in any previously named genus. The tentatively proposed autapomorphy refers to the foramina in the labial groove, below the tooth row (Figs. 2A, 3A, 5B, comf). Each foramen is ~1.5 cm in length and they are elliptical in shape. Those in *Dilophosaurus wetherilli* are circular, and less than 50 mm across — a similar condition to other theropods.

CRediT authorship contribution statement

Owain Evans: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Cindy Howells:** Writing – review & editing, Resources, Data curation. **Nathan Wintle:** Visualization. **Michael J. Benton:** Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pgeola.2025.101142.

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