The terrestrial fauna of the Late Triassic Pant-y-ffynnon Quarry fissures, South Wales, UK and a new species of *Clevosaurus* (Lepidosauria: Rhynchocephalia)

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A B S T R A C T

Pant-y-ffynnon Quarry in South Wales yielded a rich cache of fossils in the early 1950s, including articulated specimens of new species (the small sauropodomorph dinosaur *Pantydraco caducus* and the crocodylomorph *Terrestrisuchus gracilis*), but no substantial study of the wider fauna of the Pant-y-ffynnon fissure systems has been published. Here, our overview of existing specimens, a few described but mostly undescribed, as well as freshly processed material, provides a comprehensive picture of the Pant-y-ffynnon palaeo-island of the Late Triassic. This was an island with a relatively impoverished fauna dominated by small clevosaurs (rhynchocephalians), including a new species, *Clevosaurus cambrica*, described here from a partially articulated specimen and isolated bones. The new species has a dental morphology that is intermediate between the Late Triassic *Clevosaurus hudsoni*, from Cromhall Quarry to the east, and the younger *C. convallis* from Pant Quarry to the west, suggesting adaptive radiation of clevosaurs in the palaeo-archipelago. The larger reptiles on the palaeo-island do not exceed 1.5 m in length, including a small carnivorous crocodylomorph, *Terrestrisuchus*, and a possible example of insular dwarfism in the basal dinosaur *Pantydraco*.

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1. Introduction

The Late Triassic fissure deposits of the southwest of England and southern Wales have long been known to yield well preserved remains of the fauna that inhabited the area around 208–200 Ma. The first finds came in the 1830s, when bones of a dinosaur were unearthed on Durdham Down, Clifton, Bristol, named

Thecodontosaurus in 1836, only the fourth dinosaur, and the first sauropodomorph, ever to be named (Benton, 2012). After many reports of additional fossiliferous fissure sites around Bristol and in South Wales, a related dinosaur was described from fissure-fill sediments from Pant-y-Ffynnon Quarry, named *Pantydraco* (Galton et al., 2007), a close relative of *Thecodontosaurus*, the genus to which it had originally been assigned (Kermack, 1984; Yates, 2003).

The fissure deposits of the Late Triassic/Early Jurassic palaeo-archipelago on both sides of the Bristol Channel have produced important fossils that contribute to our understanding of the early evolution of rhynchocephalians, crocodylomorphs, and basal sauropodomorph dinosaurs as well as some of the world's oldest mammals (reviewed, Whiteside et al., 2016). In addition, the various sites, representing several distinct palaeo-islands, have yielded at least five species of the rhynchocephalian *Clevosaurus*.

Commercial quarrying of the host Carboniferous limestone uncovered most of the fissure deposits in South Wales. Teams from University College London (UCL), under the direction of Professor Kenneth Kermack (1919–2000), were able to collect large volumes of fissure sediment with bones from Pant-y-ffynnon and other quarries, including Pant and Pontalun. These samples were later stored in the Natural History Museum, London (NHMUK), but some rocks that were to be discarded by UCL when it terminated its

vertebrate palaeontology teaching in the early 1990s were transferred by Glenn Storrs to the University of Bristol.

Although most fossils from the Bristol–South Wales fissure deposits are fragmented or isolated bones (Whiteside et al., 2016), there are notable exceptions that include Cromhall Quarry, which has yielded articulated *Clevosaurus* specimens (Fraser, 1988; Whiteside et al., 2016) and Pant-y-ffynnon Quarry, where articulated *Pantydraco* (Kermack, 1984; Galton and Kermack, 2010) and *Terrestrisuchus* (Crush, 1984) were found. The Pant-y-ffynnon fossils themselves often show an excellent level of preservation with much detail retained.

The first mention of fossil finds from Pant-y-Ffynnon Quarry was Kermack (1956), a report of a Linnean Society meeting held on October 8th, 1953, in which he reported the discovery of five species of Triassic reptiles, with a brief description of a small agile crocodile represented by articulated skeletons as well as isolated bones. This was later described and named *Terrestrisuchus gracilis* by Crush (1984). From that original collection of bones, Kermack (1984) described *Thecodontosaurus*, as well as a coelophysoid and 'thecodont' in her thesis (Warrener, 1983; quoted in Galton and Kermack, 2010). The Pant-y-ffynnon *Thecodontosaurus* was subsequently named *T. caducus* by Yates (2003), and assigned to the new genus *Pantydraco* by Galton et al. (2007).

The presence of small diapsids ('lepidosaurs') at Pant-y-ffynnon, including *Clevosaurus* and *Kuehneosaurus*, was noted by Crush (1984), and D. Kermack (Galton and Kermack, 2010) reported that these taxa are the second most abundant fossils. Fraser (1994) also recorded the probable occurrence of *Clevosaurus*

at Pant-y-ffynnon, but both these genera were omitted as members of the fauna in table 1 of Edwards and Evans (2006; however, their text suggests that *Clevosaurus* is present); instead they identified the possible presence of the rhynchocephalian *Planocephalosaurus*. Evans and Kermack (1994) quoted Crush's thesis (1981), which suggested that *Gephyrosaurus* was a faunal constituent. Whiteside et al. (2016) noted the presence of *Clevosaurus* and, from earlier reports, *Kuehneosaurus*, but also, from direct observations, *Diphydontosaurus*. These variable reports of small diapsids from Pant-y-ffynnon show the need for first-hand reassessment.

Here, we examine the terrestrial fauna of the Pant-y-Ffynnon quarry fissures. We consider the described specimens, but focus for the first time on a quantitative assessment of microvertebrate remains of all taxa, especially the small diapsids. We find that most identifiable fossils can be attributed to the genus *Clevosaurus*, including a new species with a distinctive dentition.

2. Geological setting

2.1. Geological setting of the fissures

The Late Triassic-Early Jurassic tetrapod-bearing fissures of the Bristol area and South Wales are distributed in clusters representing postulated palaeo-islands (Fig. 1). The fissures are karstic voids such as dolines or caverns formed by solution, often with some tectonic control (Robinson, 1957, 1971; Whiteside and Marshall, 2008; Whiteside et al., 2016). These voids were then infilled with sediments, some with associated vertebrate remains, washed in by
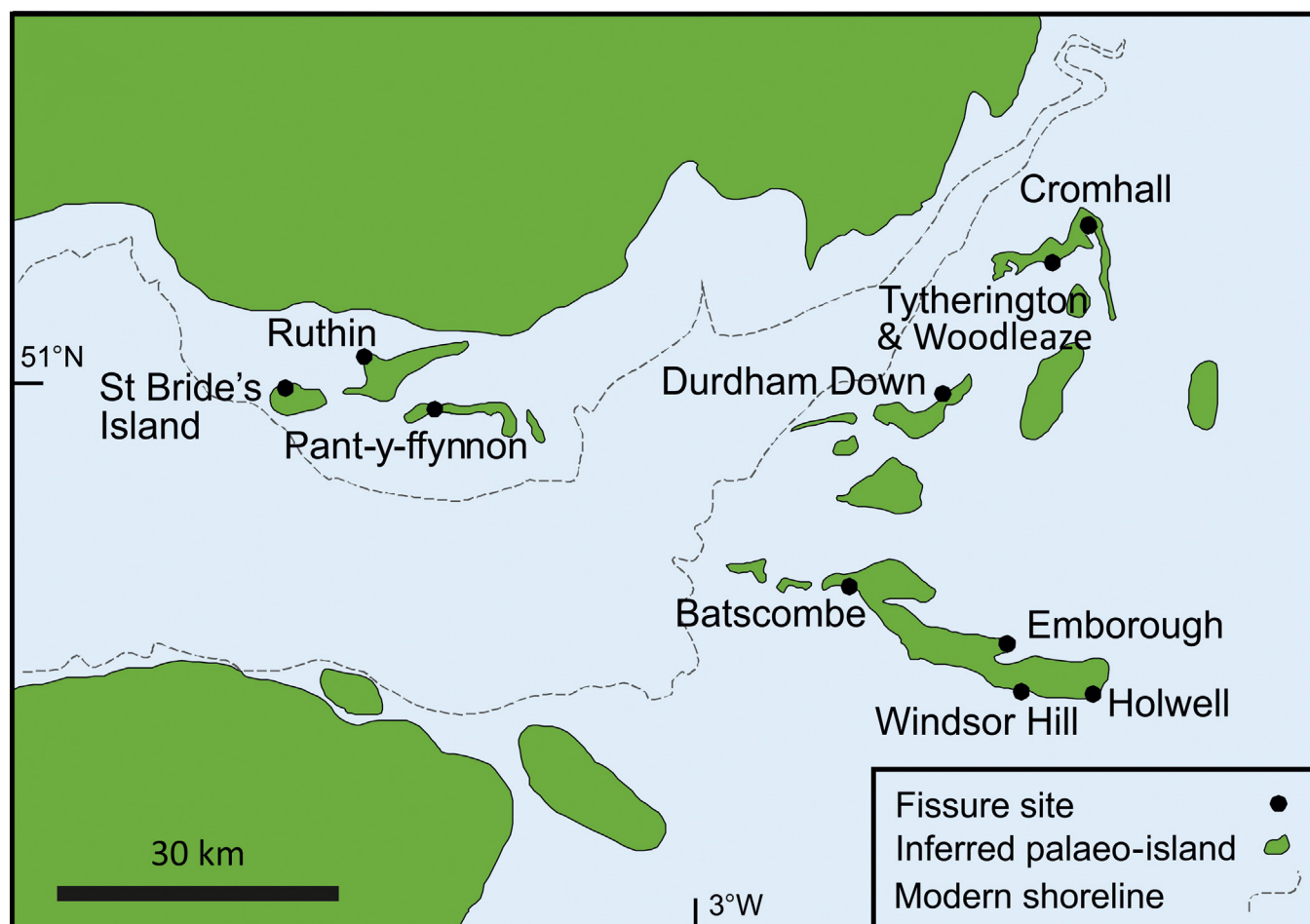
Fig. 1. Map of the Late Triassic and Early Jurassic fissure localities of the south-western U.K. with reconstructed palaeo-islands shown in green. Modified from Whiteside and Marshall (2008) and Morton et al. (2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

heavy rainfall (Whiteside and Robinson, 1983; Whiteside and Marshall, 2008). The earlier reptile-dominated 'sauropsid' fissure fills are Late Triassic, whereas those with a significant mammaliamorph component are principally Early Jurassic, although some may be Rhaetian in age (Whiteside et al., 2016).

The Pant-y-ffynnon deposits have a typical sauropsid fauna, comprising a 'prosauropod', a coelophysoid, a terrestrial crocodylomorph, and lepidosaurs (all mentioned by e.g. Fraser, 1994; Galton and Kermack, 2010). This assemblage is generally closely comparable with the well documented fissures of Cromhall (Robinson, 1957; Fraser, 1985; Walkden and Fraser, 1993; Fraser, 1994), Tytherington (Whiteside, 1983, 1986; Whiteside and Marshall, 2008), Woodleaze (Klein et al., 2015), Durdham Down (Foffa et al., 2014), Emborough and Batscombe (Robinson, 1957) in the Bristol area, and probably Ruthin in South Wales. The fissures of St Brides (Kermack et al., 1973; Evans and Kermack, 1994) in South Wales additionally yield numerous mammaliamorphs, thus differing from the sauropsid fauna, and are usually considered to be younger, probably Early Jurassic. The fauna of Holwell quarry (Whiteside and Duffin, 2017) links these two assemblages.

There is an issue with the location of the fossiliferous fissure(s) of Pant-y-ffynnon, as modern maps (Fig. 2A) show northern and southern quarries (UK grid references ST 046 742 and ST 046 740 respectively) on either side of an unclassified road. The smaller northern quarry is the older, as it alone is shown on Ordnance Survey maps from the 1910s to 1960s. From the analysis of those maps, and the notes of Kenneth Kermack and Dr Pamela L. Robinson (1919–1994), it is apparent that the productive fissure(s) were probably in the northern, north-eastern or western faces of the northern quarry (Fig. 2B). Kermack's notes show that he and his UCL team regularly revisited the quarries from 1962–1982 and documented the expanding work at the new southern quarry, initially at a rather slow speed before expanding to yield, each year, an estimated 100,000 tons of Carboniferous limestone.

The geological map (Fig. 2B) shows that the quarry was operating mainly within the Friars Point Limestone Formation dolomite, and the southern quarry also touched on the Friars Point Limestone Formation itself (both parts of the Black Rock Limestone Subgroup). These are typical Lower Carboniferous crinoidal limestones, widely quarried in South Wales and around Bristol as road metal, and sometimes as building stone. The proximity of Mercia Mudstone Group (marginal facies) and Penarth Group strata to the Carboniferous Limestone is like the situation at the Late Triassic fissure localities of Tytherington (Whiteside and Marshall, 2008), Durdham Down (Foffa et al., 2014), Woodleaze (Klein et al., 2015) and Cromhall (Morton et al., 2017), and marks the edge of the palaeo-island.

The timing of deposition of the Triassic fissures, including Pant-y-ffynnon, has been widely debated, with past researchers dating some of them as Carnian or Norian (Shubin and Sues, 1991; Benton, 1994; Benton and Spencer, 1995), based on the supposed primitive nature of many of the reptile fossils. Robinson (1971) and Crush (1984) suggested that the Pant-y-ffynnon fissure deposits were Norian, whereas Warrener (1983), quoted in Evans and Kermack (1994), suggested they were 'Rhaeto-Liassic', possibly Hettangian. However, Whiteside and Marshall (2008), based on palynological assemblages at Tytherington and faunal similarities, dated the Late Triassic 'sauropsid' fissure localities, including Pant-y-ffynnon, as Rhaetian, post-dating the initiation of the Rhaetian (Westbury Formation) transgression. Galton and Kermack (2010) accepted a Rhaetian dating for the Pant-y-ffynnon deposits. Whiteside et al. (2016), considering additional evidence from geomorphological and mapping relationships, also suggested a Rhaetian date. They further demonstrated that Pant-y-ffynnon shared 86% of its tetrapod fauna with Tytherington. Morton et al. (2017) demonstrated from conchostracan biostratigraphy that at least some

Cromhall Quarry infills are late Rhaetian (equivalent to the Cotham Member, Lilstock Formation) and a solitary conchostracan, *Euestheria* cf. *brodieana* (Morton et al., 2017, fig. 12g), from a Pant-y-ffynnon fissure deposit with the same lithology as the tetrapods, perhaps indicates a similar age.

The Rhaetian sea level and, as a consequence, the water table, would have been far higher than today (currently about 50 m below the limestone surface in Pant-y-ffynnon), and Late Triassic phreatic caverns formed within a few metres of the surface of the Carboniferous Limestone in, for example, Tytherington (Whiteside and Marshall, 2008). The presence of a filled mudcrack (NHMUK R36942) with a lepidosaur bone found in one fissure, and Triassic caverns within the Carboniferous Limestone (K.A. Kermack notes, NHMUK), also indicate similar high-water table conditions during fissure infilling at Pant-y-ffynnon.

2.2. Palaeoenvironment

It is clear from the disarticulation and isolation of most bones found in the South Wales-Bristol fissure deposits that some degree of transport was involved before the bones were deposited and became fossilized (Whiteside et al., 2016). However, the bones themselves are often well preserved, if fragile, meaning that although there was transport before the bones found their resting place, it must have been short—perhaps only a few tens of metres. Pant-y-ffynnon and Cromhall quarries are important localities that have produced the best examples of complete or near-complete tetrapod skeletons and, in the case of the former, unique examples of articulated archosauromorphs such as *Terrestrisuchus* (Crush, 1984). The animals might have walked into the caves, or died nearby and been washed in, but in the absence of further detail about the original fossiliferous caverns, it is impossible to say. It is likely however, that if agile and generally small animals that were adapted to karstic terrains wandered into fissures they would usually have been able to walk back out.

This good preservation allows for reasonably confident identification and an assumption that the collection comprises a substantial representation of the fauna of a particular palaeo-island. For all localities, it is assumed that the fossils came to rest below, at or near a high standing water table (Whiteside et al., 2016). The white bones, such as those from the rock associated with *Pantydraco*, would have been deposited in oxic conditions, in the vadose zone or above the halocline, whereas the dark grey or black bones (usually in a yellowish limonitic matrix) formed in an anoxic environment at or just below that feature (Whiteside and Marshall, 2008). Articulated or partially articulated specimens were probably from animals that fell into the fissure or with minimal transport from the land surface. It is likely that articulated fossils occur most commonly near the entrance of a fissure, as any significant transport would separate and damage the bones. Reworked limestone clasts and separated bones are often of similar sizes, suggesting that that they possessed similar hydrodynamic properties, and were transported together (Whiteside et al., 2016).

The UK Late Triassic fissures were evidently formed near the sea, as indicated by marine fish fossils associated with the terrestrial reptiles, as well as the palynomorph/dinocyst assemblage (Marshall and Whiteside, 1980) and the presence of a glauconitic clay (Whiteside and Robinson, 1983) in a fissure at Tytherington. This evidence is supported by the presence of the Rhaetian actinopterygian *Pholidophorus* in the Tytherington and Cromhall deposits (Whiteside, 1986) as well as conspicuous cavern formation at Tytherington, Cromhall and Pant-y-ffynnon quarries; both point to a high sea level during fissure infilling. These observations on the likely palaeotopography, coupled with the evidence for a Rhaetian age, mean that most of the redbed fissures were formed on palaeo-islands amidst the transgressive Rhaetian
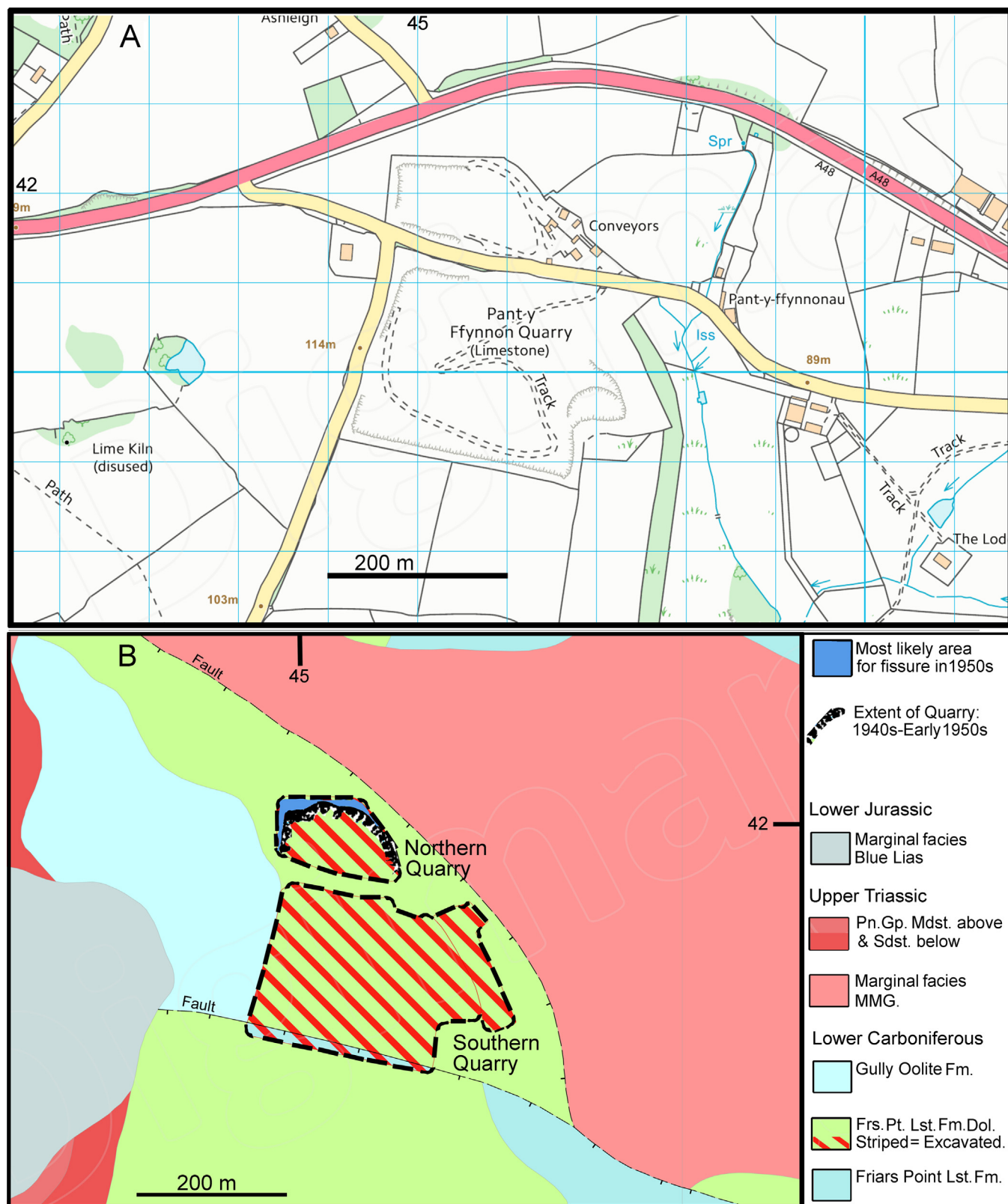
Fig. 2. Maps of the Pant-y-ffynon locality. (A) Current Ordnance Survey map of the vicinity around the quarry. (B) Geological map of the area. The tetrapod bones described in this paper all derive from the Northern quarry which probably ceased limestone extraction in the late 1950s or early 1960s. Abbreviations: Dol., Dolomite or Dolomitised; Fm., Formation; Frs. Pt., Friars Point; Gp., Group; Lst., Limestone; MMG., Mercia Mudstone Group; Mdst., mudstone; Pn., Penarth; Sdst., sandstone. (based on BGS 1:10 000 digimap © 2017 https://digimap.edina.ac.uk/).
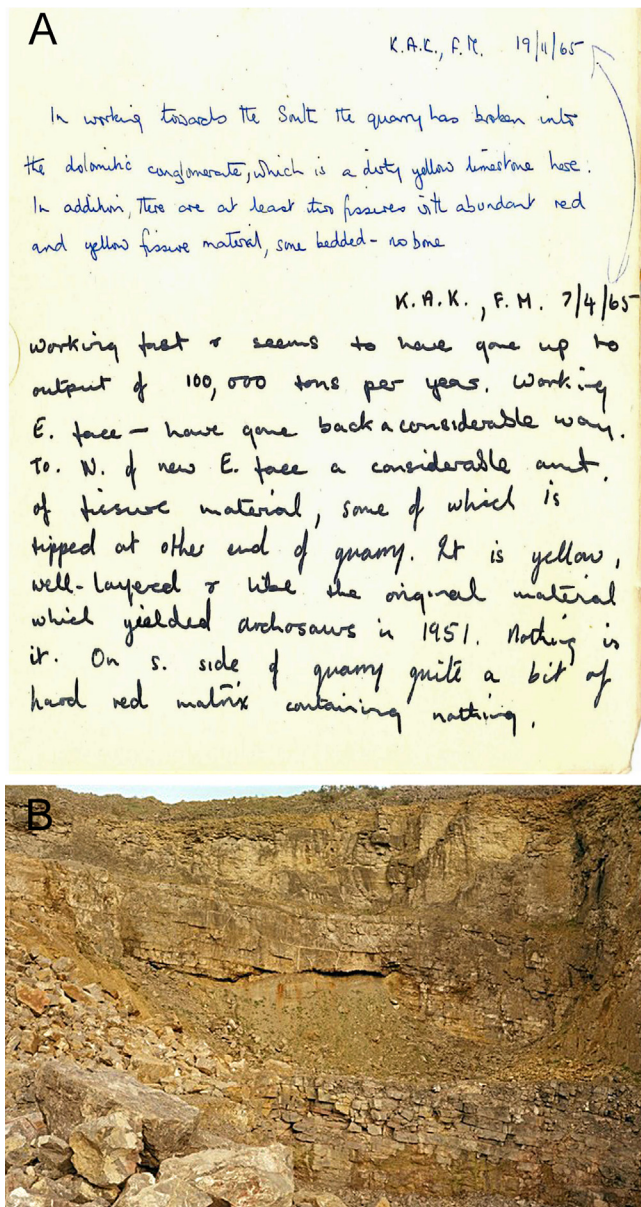
Fig. 3. Historical information about Pant-y-ffynnon. (A) Extract from notes of Kenneth A. Kermack (K.A.K) and Francis Mussett (F.M.) from 1965, discussing lack of finds in the new (Southern Quarry) and referring to the original finds in the early 1950s. (B) Photograph P007812 from BGS geoscenic images taken in 1983 by C.J. Jeffery, of a Pant-y-ffynnon southern quarry fissure reported as a 'Triassic swallow-hole in the Black Rock Carboniferous Limestone. The cavern is infilled by a sequence of laminated grey-green and yellowish-brown silts and fine sands of Triassic age.' The estimated height from horizon to bottom of the photograph is 15 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Materials and Methods

3.1. Collection of materials

We considered the registered and unregistered collections of small and large rocks from Pant-y-ffynnon held by the NHMUK. These include large rocks with the type specimens of *Pantydraco* and *Terrestrisuchus* and smaller hand specimens containing fossils still surrounded by matrix.

Our quantitative study is based on processing of a sample of the considerable amount of Pant-y-ffynnon fissure matrix in the NHMUK and BRSUG. The seven fossiliferous blocks (five from NHMUK, two from BRSUG) were collected from Pant-y-ffynnon, possibly in 1951 (K.A. Kermack notes and the date on the envelope of unpublished notes of Pamela Robinson, NHMUK), although Kermack (1956) and Robinson (1957) state that the year was 1952. Articulated tetrapods were certainly collected in 1952 (Kermack, 1956; Kermack et al., 1973; Crush, 1984). Notes made by Kenneth Kermack and his team on later visits suggest that no vertebrate fossils were collected after at least 1962 (K.A. Kermack, unpublished field notes, NHMUK), and indeed there is no evidence that any specimens we have seen were collected after the early 1950s. During these visits, no finds are recorded, with 'no bone found' regularly stated, and the fissures with red matrix seem to have been barren (Fig. 3A).

The specimens were collected from dumped material at the sides of the quarry tracks rather than *in situ* (Robinson notes and Kermack notes, NHMUK; Robinson, 1957; Crush, 1984; Kermack, 1984). Robinson (1957) states that 'the fossiliferous material from Pant-y-ffynnon Quarry was found on the tip. No trace remained of the fissure which had housed it. Another winter's exposure to the weather would have resulted in complete disintegration of the material'. Crush (1984), while affirming that the fossils came from the 'old quarry', further emphasized that the specific location of the original fissure that yielded the fossils, including the articulated specimens, is unknown. However, Diane Kermack (in Galton and Kermack, 2010, p. 396) reported that the articulated and associated *Pantydraco* material was found in the 'same spoil heap on the same day'. Kenneth Kermack et al. (1973) designated a 'fissure system 1' for the source of the reptile fossils, but they did not describe it and it is probably just a nominal assignment. There are no figures or photographs from the 1950s of the fissures in the northern quarry, but the Triassic fissure shown in Fig. 3B from the eastern side of the southern quarry is typical of the upper quarry level fissures found in other localities such as Tytherington.

The texture of the rocks varies, with some being fissile and laminated and others massive, although all contain lithic or mineralised clasts 3–100 mm in size, the smaller clast sizes being most common. There is also a range of lithologies and colours. The two BRSUG rocks are crumbly, yellow and limonitic, and of the type mentioned by Kermack in his notes. The rocks from the NHMUK include a block of yellow/buff matrix that had yielded *Pantydraco* bones studied by Diane Kermack (then Warrener, 1984) and a dark grey and brown block with black bones (see Fig. 4A, B) as well as the counterslab (Fig. 4C; these rocks were originally named '*Glevosaurus*' A and B; now NHMUK R36939 and NHMUK R36940 respectively). The remaining material is a collection of hand-sized, yellow, harder rocks and a brown specimen with a distinctive mudcrack that contained a lepidosaur long bone in the matrix that fills the crack. Based on descriptions of fissures elsewhere, such as Tytherington (Whiteside and Marshall, 2008) and Cromhall (Walkden and Fraser, 1993), it is possible that all the rocks came from the same fissure, as implied by the 'fissure system 1' designation of Kermack et al. (1973).

The pale bones of one rock associated with the *Pantydraco* collection may be the earliest collected in 1951 (though the only

seas (Whiteside et al., 2016). The lower parts of the fissures penetrated below the Rhaetian sea level, perhaps with a saline influence in some locations, though it is likely that deposits situated further inland would have formed in freshwater lenses below sea level (Whiteside and Robinson, 1983; Whiteside and Marshall, 2008; Klein et al., 2015). Three of the rocks that we acid prepared have a yellowish, limonite-rich matrix and all have yielded at least some light or dark grey fossils; in these regards they are similar to the fossiliferous deposits of Tytherington fissure 13, which Whiteside and Marshall (2008) suggested was a flank margin cavern on the edge of the palaeo-island.

record of this seems to be a pencil inscription on the rock itself but this might be simply a sample number) and its specific location is not known. Its fossil content is different from the yellow rocks, with more archosauromorph remains, and the white or cream colour of those bones suggests a more oxic environment of deposition than the other, mainly lepidosaur specimens, which are a darker grey or even black.

3.2. Preparation

Before preparation, each rock and visible bone within the sediment was photographed at a range of distances with a Nikon Coolpix P530. Many already prepared specimens at the NHMUK were also photographed, and the best small specimens were photographed with photostacking equipment in the Angela Marmont Centre on site at the NHMUK. Small specimens prepared at the University of Bristol were photographed with a Leica photomicroscope and stacking software. Photographs were edited for clarity and consistency in Adobe Photoshop Elements 7©.

The rocks were prepared at the University of Bristol mainly using acetic acid. The fossiliferous Triassic fissure sediments have a large calcium carbonate component that varies between lithologies, and possibly between fissures, as shown by the differing times it took for different fissure-fill rocks to break down. Rocks were placed in a 2–5% solution of acetic acid buffered with a 1:3 mixture of tri-calcium di-orthophosphate precipitate and sodium carbonate anhydrous respectively overnight before being removed (Viegas and Benton, 2014) and washed over four sieves of sizes 850 μm, 500 μm, 180 μm and 90 μm. Residue caught in the sieves was drained and dried on filter papers before being picked through under the microscope to separate fossils from residue. After being in acid, large pieces were placed in water with some alkaline washing-up liquid to neutralise any acid left on them for the same or double the time they were in acid (Viegas and Benton, 2014). Fossil fragments were kept in separate pots, labelled with their origin and size to aid later identification and cataloguing.

Bones that became visible on the surface during acid digestion were coated with a 10% solution of dissolved Paraloid B72 beads and acetone to consolidate and protect them from further acid damage (Klein et al., 2015). Paraloid was used as it is clear, protective and if necessary can be removed by solution in acetone (Klein et al., 2015). Some specimens that were very fragile and had become sufficiently exposed were left in situ so as not to risk any further acid erosion. After acid treatment was finished, some specimens were cleaned with acetone and a small paintbrush to remove excess Paraloid or sediment that had become stuck to them. Some specimens, particularly those that were white, became slightly yellowed by the combination of Paraloid and acid treatment. This is most clear on NHMUK R36973 (see Fig. 12C, D) where one side was Paraloid treated and exposed to acid and shows darkened colour, but the other side had none of this exposure and instead simply popped out of the rock upon mechanical preparation and so retains its original white colour.

Articulated specimens were left in situ and Paraloid treated before being exposed to a 1% acetic acid solution for a maximum of ten minutes at a time. Water was used to clean the fossil surface thoroughly to expose a greater area of specimen without disturbance. Where possible, the rocks with articulated sections were trimmed with a rock saw, and the excess material could be acid processed.

3.3. CT scanning

The articulated specimen, on counterslabs NHMUK R36939 and R36940, was CT-scanned at the University of Bristol on a Nikon XTH225ST CT Scanner. Scans were left running for 2.5 h, sufficient time because of the high contrast between bone and soft matrix.

The scans were visualized and volume rendered in Avizo 8.0 software. For the skull bones in NHMUK R36940, and to achieve greater detail in the images of the articulated limb in NHMUK R36939, individual slices were labelled by hand on a Wacom Cintiq 24HD tablet to build the 3D image manually. This allowed some confusing edges to be clarified, especially to manage inorganic fragments in the somewhat heterogenous rock matrix.

4. Systematic descriptions

4.1. Clevosaurus cambrica *sp. nov*

Superorder: Lepidosauria, Duméril and Bibron, 1839 (sensu Evans, 1984)
Order: Rhynchocephalia, Günther, 1867 (sensu Gauthier et al., 1988)
Suborder: Sphenodontia, Williston, 1925 (sensu Benton, 1985)
Family: Clevosauridae Bonaparte and Sues, 2006 (sensu Hsiou et al., 2015)
Genus: *Clevosaurus* Swinton, 1939
Type Species: *Clevosaurus hudsoni* Swinton, 1939
Included species: *C. minor* from southern England (Fraser, 1988); *C. bairdi* from Nova Scotia, Canada (Sues et al., 1994); *C. convallis* from south Wales (Säilä, 2005); *C. brasiliensis* from southern Brazil (Bonaparte and Sues, 2006); *C. sectumsemper* from southern England (Klein et al. 2015); and possible species *C. mcgilli*, *C. petilus* and *C. wangi* all from Yunnan, China (Wu, 1994). Note that '*Clevosaurus' latidens* from southern England (Fraser, 1993) is not considered part of the clevosaur clade by most recent authors (e.g. Martínez et al., 2013) because it has transversely widened teeth quite distinct from members of the Clevosauridae, and it has been assigned to a new opsithodont genus by Herrera-Flores et al. (2018).

Clevosaurus cambrica sp. nov. Figs. 4–7.

4.1.1. Derivation of species name
Latin meaning 'Welsh', referring to the country in which the animal was found

4.1.2. Holotype
A left maxilla, NHMUK R37016, showing the diagnostic flanged teeth and largest tooth in mid-row position (Fig. 5A).

4.1.3. Referred specimens
A left dentary, NHMUK R37015 (Fig. 5C; on the same block as a key *Terrestrisuchus* specimen Fig. 5D); a right maxilla, R37042 (Fig. 5B); partial skull and right lower jaw, vertebrae, and left scapulocoracoid and forelimb, NHMUK R37014 (Figs. 4C, 6), NHMUK R37013 (Figs. 4A, B, 7). NHMUK R37013 is the new registered number of the skull and associated bones in rock specimen NHMUK R36939, whereas newly registered NHMUK R37014 is found in rock specimen NHMUK R36940.

4.1.4. Type locality and horizon
Upper Triassic (Rhaetian) fissure infill within Lower Carboniferous Limestone, Pant-y-ffynnon Quarry, near Bonvilston, Vale of Glamorgan, South Wales, UK (NGR ST 046742)

4.1.5. Diagnosis
A species of *Clevosaurus* with five prominently flanged additional teeth on the posterior region of the maxilla and six additional teeth on the dentary. Distinguished from *C. brasiliensis*, *C. bairdi, C. minor, C. hudsoni,* and *C. sectumsemper* by a greater number of flanged maxillary and additional dentary teeth. Unlike
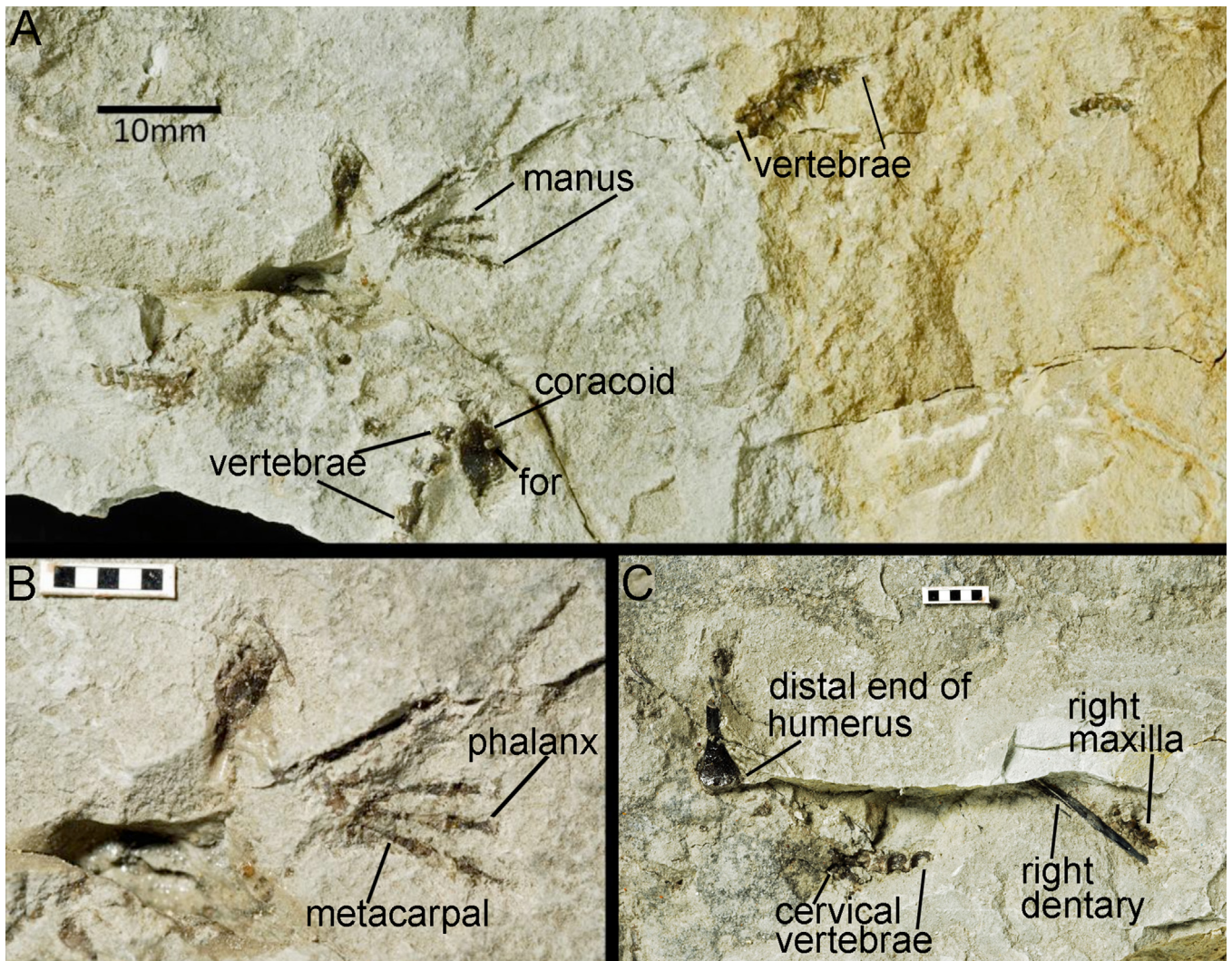
Fig. 4. *Clevosaurus cambrica* sp. nov. rock specimen NHMUK R36939 photographs, showing a hand and several columns of vertebrae (A) and a close-up of the manus (B), and (C) the counterslab rock NHMUK R36940 with the dentary and maxilla (newly registered NHMUK R37014) also shown in CT scan of Fig. 6. Scale bars in B and C = 5 mm. Photographs by Simon Powell.

the latter two species, the largest tooth is not the posteriormost of a sequence of increasing size. Distinguished from *C. convallis* by a greater development of the anterolateral flanges on dentary teeth; *C. cambrica* also lacks the very small posteriormost dentary teeth of *C. convallis* recorded by Säilä (2005). The prominent anterolabial flange on each posterior dentary tooth further distinguishes *C. cambrica* from Chinese *Clevosaurus* specimens, which show little development of the structure (Jones, 2006). The posteriormost large flanged maxillary teeth of *C. cambrica* have little or no overlap but can have continuous cutting edges between individual teeth (Fig. 5A; holotype), which contrasts with the slightly overlapping dentition of the Chinese *Clevosaurus*, as well as *C. convallis*, and *C. bairdi*. No maxillary specimen of *C. cambrica* has the two or three subconical teeth that lie posteriorly to the last flanged tooth recorded in the largest specimens of *C. hudsoni* by Fraser (1988). In contrast to *C. cambrica*, posterior subconical maxillary teeth are also present in mature specimens of *C. minor* (Fraser, 1988), *C. brasiliensis* and *C. convallis* (which can have up to four of these teeth; Martínez et al., 2013 and Säilä, 2005 respectively), as well as some Chinese clevosaurs (Jones, 2006). Unlike *C. minor* (Fraser, 1988) there are no teeth that could be 'successional' on the anterior of the maxilla. Although the bases of the dentary teeth of specimen NHMUK R37014 (but not in specimen NHMUK R37015) do become progressively more ventral posteriorly, the feature is less pronounced than in *C. sectumsemper*.

4.1.6. Remarks

The proposed species is known from two dentaries (Figs. 5C, D, 6C–E) and three maxillae (Figs. 5A, B, 6A, F). In the CT scan of the more complete specimen, NHMUK R37014, Fig. 6A) there is a single tooth placed medially to the anterior of the lateral palatine tooth row, a clevosaur clade autapomorphy (Hsiou et al., 2015). Therefore, the new species belongs to the genus *Clevosaurus*, based on two diagnostic characters, the presence of a single anterior, medially-positioned palatine tooth (Hsiou et al., 2015), and the similarity of the prominent posterolingual and antero-lateral flanges on, respectively, the large maxillary and dentary teeth to the type species *C. hudsoni* (Fraser, 1988). Although no specimen of the premaxilla has been found, the maxilla (Fig. 5A, B) shows a key clevosaur characteristic of the anterior end, which is excluded from the external nares by a process of the premaxilla, as in *C. hudsoni* (Fraser, 1988).

As noted, *C. cambrica* has five flanged teeth, akin to carnivore sectorial teeth comprising shearing molars and premolars (White-side, 1983) on the maxilla, differing from the condition in *C. sectumsemper* and *C. hudsoni*, where four flanged teeth are present
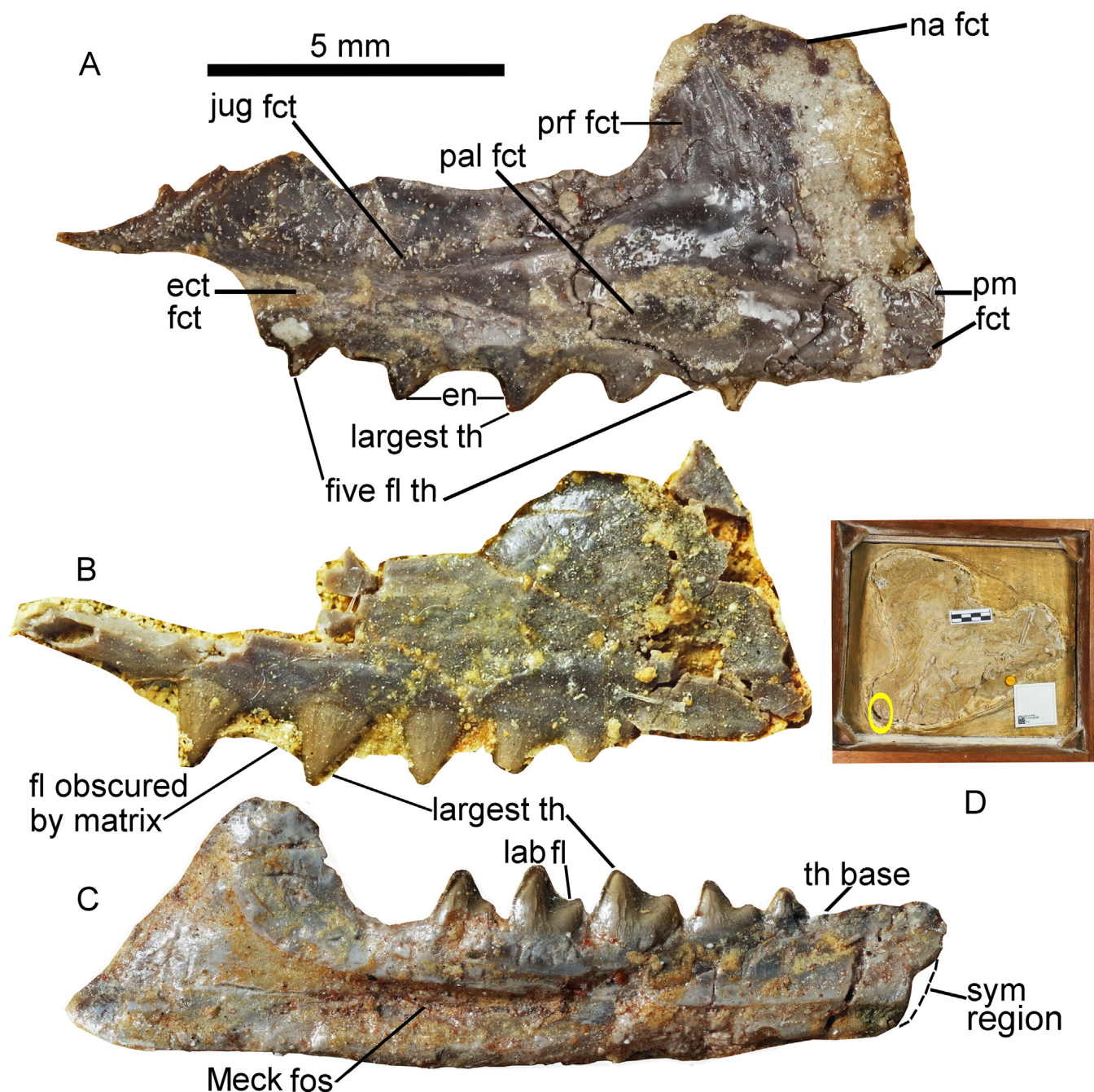
Fig. 5. The rhynchocephalian *Clevosaurus cambrica* sp. nov. (A) Holotype left maxilla of *C. cambrica*, NHMUK R37016, in medial view; note that the largest flanged tooth is in mid region of the flanged dentition. (B) Right maxilla of *Clevosaurus cambrica* sp. nov. NHMUK R37042, showing nature of surrounding matrix and fragility of the bones following acid preparation, in lateral view with largest additional tooth in mid region. (C) Left dentary NHMUK R37015 from the *Terrestrisuchus* slab NHMUK R7571, medial view; note that the largest flanged tooth is in the mid region. (D) *Terrestrisuchus* slab BMNH R7571 showing location of *C. cambrica* dentary. Scale bar for A, B and C = 5 mm. Each rectangle in D = 10 mm. Photograph B by Simon Powell.

in mature individuals (Fraser, 1988 for *C. hudsoni*), and from *C. convallis*, which has six (Säilä, 2005). Also, as noted, the maxillary teeth do not increase in size uniformly posteriorly. In fact, in our specimens, the largest *C. cambrica* tooth in the series is either the penultimate tooth or antepenultimate; the most posterior tooth can be relatively small. In this respect, the species is like *C. convallis*. A similarity to *C. sectumsemper* is that the cutting edges of maxillary teeth can be fused or near fused (Klein et al. 2015, Fig. 3D). The dentary flanged teeth of *C. cambrica* also do not increase in size uniformly, with the largest tooth in the penultimate or antepenultimate position; this is like *C. convallis*,

but contrasts with *C. sectumsemper* and *C. hudsoni* where the largest flanged tooth is the most posterior.

The assignment of NHMUK R37014 to *Clevosaurus cambrica* is based on the five large flanged teeth on the maxilla, with the largest mid-region, as well as the fact that it also comes from Pant-y-ffynnon.

4.1.7. Description of bones

4.1.7.1. Maxilla. The most complete maxilla (Fig. 5A), the holotype, is 15 mm long and another with some breakage (Fig. 5B) is 13 mm
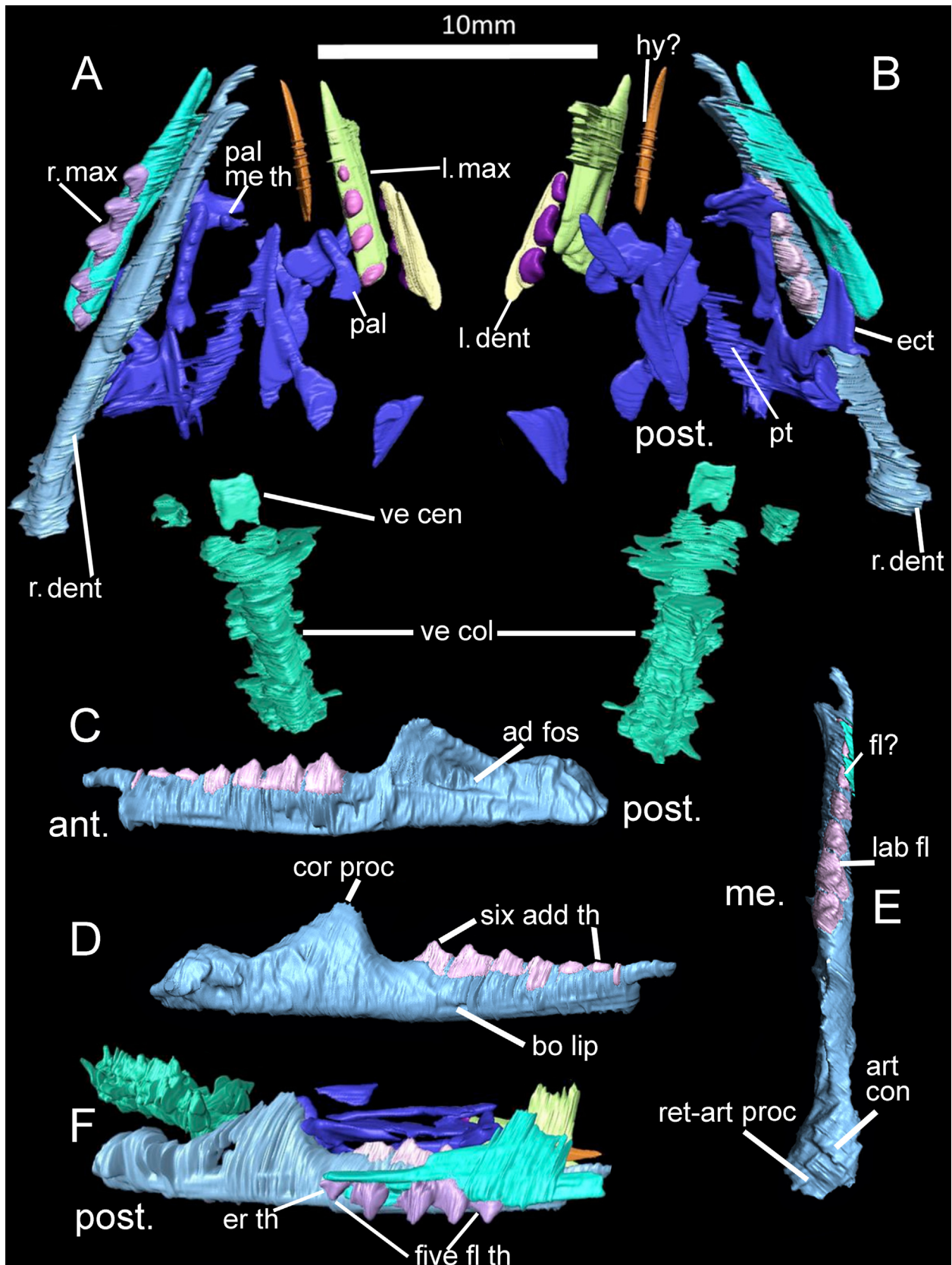
Fig. 6. *Clevosaurus cambrica* sp. nov, NHMUK R37014, CT scans of skull and lower jaw. (A) Ventral view showing palatine teeth. (B) Dorsal view. (C–E) Right dentary in, respectively, lateral (C), medial (D) and occlusal (E) views. (F) Lateral view of jaw, highlighting the diagnostic five flanged maxillary teeth with the largest in the toothed mid region. Turquoise and lime (with lavender and pink teeth respectively) elements are maxillae; yellow and pastel blue (with purple and lilac teeth respectively) are dentaries; dark blue is the palate; seafoam green is a string of cervical vertebrae.
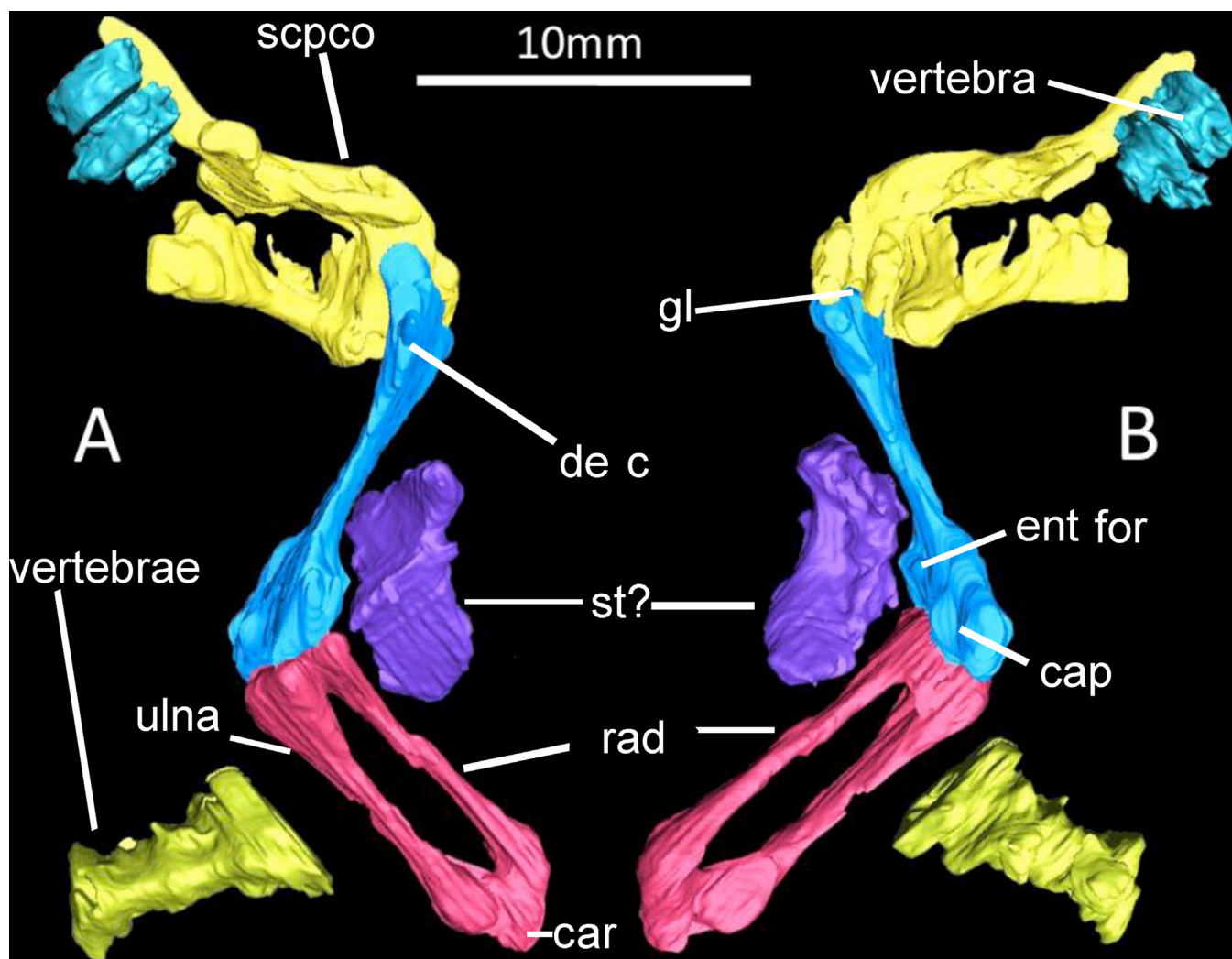
Fig. 7. *Clevosaurus cambrica* sp. nov., NHMUK R37013, CT scans of a left forelimb, in postero-lateral (A) and postero-medial (B) views. Yellow represents the scapulocoracoid; purple, a symmetrical element, perhaps the sternum; blue is the humerus; the radius and ulna possibly with some wrist bones preserved are shown in pink. There are also two pairs of vertebrae, in turquoise and green, at the top and bottom of the images.

long. The maxilla is a hatchet-shaped element, comprising a somewhat square dorsal or nasal process, and an elongate parallel-margined posterior process. The ventral margin is slightly curved and bears teeth, and there is a rounded anterior margin curving to a straight dorsal margin around the nasal process. The posterodorsal margin then sweeps down and backwards to a posterior point best shown in the holotype (Fig. 5A). Some contacts for the jugal, ectopterygoid, prefrontal and the prominent palatine facet are clear, but others are less so; the maxilla likely contacted the premaxilla along the anterior margin and the nasal dorsally.

There are five additional teeth along the ventral margins of the right and left maxillae (Fig. 5A, B); the anterior dentition has been largely worn away. In the holotype left maxilla (Fig. 5A) the most anterior additional tooth is broken and only the posterior flange of that tooth remains with an imprint of the cusp in the matrix. It is noticeable that the thick enamel, present on all the flanged teeth, runs continuously from the first additional tooth to at least the penultimate tooth (it is unclear if it runs continuously to the posteriormost tooth) producing a long cutting blade about half the length of the maxilla. This cutting blade resembles that of a serrated steak knife. In the right maxilla (Fig. 5B), the largest maxillary tooth is the second from most posterior (penultimate), whereas in the holotype left maxilla (Fig. 5A) it is the third most

posterior (antepenultimate). The teeth are composed of an anterior cone in lateral view, with a trailing posterolingual (or posteromedial) flange. The teeth are fused to the maxillary ventral margin, the acrodont implantation condition typical of rhynchocephalians.

4.1.7.2. Dentary. The isolated dentary, NHMUK R37015, is largely complete, but the margins are slightly abraded and a probable anterior additional tooth is missing. In medial view (Fig. 5C), the anterior symphysis is missing, but as in other clevosaurs would presumably have been a slightly excavated elongated inclined surface that would have expanded slightly anteriorly and ventrally to form the junction with the right-hand mandible. Behind this, a horizontal rim marks the upper margin of the Meckelian fossa. The Meckelian fossa widens posteriorly below the three posteriormost teeth. The dentary expands substantially dorsally behind the tooth row as the coronoid process, and the posterior margin terminates in a triangular shape. The upper margin would have formed the contact with prearticular and surangular in life, and the angular would have run forward and contacted the ventral margin of the dentary.

The dentary preserves at least five well defined flanged additional teeth with another one represented by a tooth base

anteriorly (Fig. 5C). In front, there would have been the remnant hatchling teeth (definition of Robinson, 1976) but these typically wear away as the animal grows and the dentary changes shape. The posteriormost four dentary teeth show a pronounced saddle-shaped form. All these teeth possess a posterior conical portion that is linked by a U-shaped cusp to a smaller anterior crest (the flange) that points forwards. The deep U-shaped cusps in these teeth presumably occluded with the matching conical maxillary teeth.

The dentary specimen NHMUK R37014, analysed from the CT scan (Fig. 6C–E), has six additional teeth with clear flanges in the posteriormost four, but the anterior two also appear to show pronounced apices with rudimentary flanges. The largest tooth is the penultimate in the row, whereas in NHMUK R37015 it is the antepenultimate. In both specimens, as in C. hudsoni (Fraser, 1988), the posterior flange of the last tooth is less well developed than in the large preceding teeth.

4.1.7.3. Skull.

Further description of the skull is based on NHMUK R37014, from its external appearance (Fig. 4C) and the CT scans (Fig. 6). The specimen comprises a skull and lower jaws from the palate down, including maxillae, dentaries, and palatine, all with teeth preserved. Some cervical vertebrae are preserved posterior to this (Fig. 4C).

The skull bones on the right side (Fig. 6) are rather more complete than those on the left, and so measurements are taken from the former side. In right lateral view (Fig. 6F), the posterior region of a right maxilla, with five teeth, sits in front of the mandible and other elements. The maxilla is slightly less complete than those in Fig. 5, but the tooth shapes also show some development of a slightly saddled appearance, not so clear in the isolated maxillae (Fig. 5A, B). The teeth also have distinctive ridges that run apically; prominent dental ridges were recognized as a feature of Clevosaurus by Whiteside (1986). The incomplete maxilla measures 11 mm in length, the partial dentary 19 mm; what is preserved of the row of palatine teeth is approximately 6 mm long. The mandible is more or less complete, lacking the anterior margin of the dentary. The dentary bears six teeth (Fig. 6C–E). The posterior elements of the mandible are also present, the prearticular, surangular, articular, and presumably the angular ventrally, but sutures cannot be discerned. The articular region that articulated with the quadrate is present, and the retroarticular process appears relatively short, although the scan may be incomplete in this region. An unregistered specimen of the articular region in the NHMUK collection of a probable Clevosaurus suggests that the region is similar in C. cambrica to C. hudsoni. There is no separate coronoid bone. Overall, the mandible shows the elongate canoe shape typical of most rhynchocephalians.

Among the elements of the palate, highlighted in blue in Fig. 6A, B, the right palatine is approximately in life position relative to the right maxilla, with six small teeth (Fig. 6A) apparent, though there may be a possible seventh at the anterior end. The left palatine is slightly rotated towards the right palatine, and bears just discernible teeth. Behind and medial to these are portions of both pterygoids. The right ectopterygoid is present, with the maxillary process in near proximity to the maxilla. The palatine teeth seemingly curve less medially than described in C. hudsoni (Fraser, 1988) and the Chinese Clevosaurus (Jones, 2006), but the single, larger, medial palatine tooth is common to all. Like C. cambrica, six palatine teeth are present in the lateral rows of C. hudsoni (Fraser, 1988) and C. sectumsemper (Klein et al., 2015), whereas there are eight in C. brasiliensis, five in C. convallis (Säilä, 2005) and four in C. minor (Fraser, 1988).

The dorsal view of the skull (Fig. 6B) shows the occlusal views of the left and right dentaries. The right dentary lies, as in life, inside the right maxilla, but the left dentary has been displaced post mortem so that it lies laterally to the left maxilla. On the right-hand side, the elements of the palate seem to be in near natural connection, showing the palatine lateral process that contacted the medial face of the maxilla. The flange formed from the ectopterygoid and pterygoid that guided the dentary during occlusion can be discerned. The bones of the palate on the left-hand side are more jumbled, and it is harder to identify individual elements. One rod-like element between the dentaries (Fig. 6A, B) cannot be identified, unless it is a displaced hyoid element.

4.1.7.4. Vertebrae.

It was hard to segment the short portion of cervical vertebral column in NHMUK R37014 (Fig. 6A, B, pale green), but there seem to be four or five vertebrae, all quite short and in close contact. The two anterior elements could be isolated portions of the atlas (possibly the centrum fused with the axis centrum and intercentrum), or the atlas may be represented by the connected set of three possible ossifications at the front of the short column. Another possibility, although less likely, is that they are portions of the braincase, such as the basioccipital. In ventral view (Fig. 6A), four definite centra can be distinguished, each as long as wide, slightly keeled and laterally pinched, and with expanded margins around the articular faces.

Two series of vertebrae are also seen in the digital model of NHMUK R37013 (Fig. 7). Two broad, short centra are seen isolated, near the scapular blade, and a further set of two occurs beside the forearm elements. These latter vertebrae have elongate centra, with narrow keels (Fig. 7A).

4.1.7.5. Shoulder girdle.

The left scapulocoracoid (part of NHMUK R37013) is preserved slightly distorted, but with the humeral head in place in the glenoid. The scapula has a 14 mm long strap-like blade, with a distinct embayment on the anterior margin, placed about halfway along its length (Fig. 7A). The glenoid appears to have substantial crests anteriorly and posteriorly (Fig. 7B), located just above the humeral head.

The coracoid extends antero-ventrally, seemingly rotated slightly upwards, as a curved element, terminating in a rounded posterior margin. It is about 10 mm long. There is a suggestion of the coracoid foramen in another specimen shown as a rounded opening on the dorsal margin seen most clearly in the specimen photograph (Fig. 4C), where the fuller shape of the coracoid is seen. It has a curved ventral margin, as is usual in rhynchocephalians, and the possible coracoid foramen, nearly 1 mm across, is located near the dorsal margin, but entirely surrounded by bone.

A symmetrical winged element located beside the inside of the elbow (Fig. 7A, B) may be a sternal plate, marked by a distinct longitudinal crest along the midline (ventral surface) and a curved dorsal surface. The lateral margins are robust. Ossified elements in the sternal region are present in Sphenodon, and a nearly identical bone was present in the Late Jurassic Homoeosaurus (Cocude-Michel, 1963). Note, however, that rhynchocephalian sterna are usually not ossified, and if they are, they are generally thin and flat.

4.1.7.6. Forelimb.

The left humerus is a straight element, 14 mm long, and with expanded ends. In antero-lateral view, there is a pointed deltopectoral crest (Fig. 7A) proximally, and a narrow ectepicondylar process distally. In postero-medial view (Fig. 7B), the capitellum, a pronounced convex condyle, is in contact with the proximal head of the radius. There is a bulky entepicondylar crest, but the detail of some distal articular facets, such as the trochlea, cannot be seen. There is evidence of an entepicondylar foramen, and although the ectepicondylar foramen present in Clevosaurus hudsoni (Fraser, 1988, fig. 29) is not apparent, its presence is probable as the feature is found in all rhynchocephalians. The epiphysis anterior and posterior margins appear sharp.

The left ulna and radius are also preserved articulated, and in close contact with the distal end of the humerus (Fig. 7). Both elements are about the same length, 13 mm, and of similar dimensions, the ulna sitting on the outside of the elbow (Fig. 7A) and having a heavier proximal end. Both ulna and radius have expanded articular ends and narrow epiphyses.

At the distal end of these elements is at least one proximal wrist bone, possibly the intermedium or centrale. There is an articulated manus, most clearly visible on the surface of NHMUK R36939 (Fig. 4A, B); it is possibly in plantar view as the middle metacarpal displays a hemicylindrical condyle with expanded ends. It is approximately 8 mm long at its longest point and shows the three central digits (II, III, IV) in natural position, each with a metacarpal of similar length, possibly 4 mm, and a further primary phalanx in contact. Digits I and V are likely to have been shorter than the three pictured and may be buried in the rock.

4.1.7.7. Size. There is enough material of *Clevosaurus cambrica* to estimate its original size, by comparison with more complete remains of related species, in particular *C. hudsoni* (Fraser, 1988). The CT scan dentary is 19 mm long and suggests a skull about 18 mm long (the retroarticular process projects behind the occiput). However, the holotype *C. cambrica* maxilla indicates, by comparing proportions (about 60% the length of the skull) with *C. hudsoni* described by Fraser (1988), that the skull may reach 24 mm in some individuals. The calculated skull length range is therefore about 18–24 mm. This means that *C. cambrica* was larger than *C. sectumsemper*, but smaller than *C. hudsoni*, whose skulls were 14–18 mm (Klein et al. 2015) and 40 mm long (Fraser, 1988) respectively. Further, the humerus, at 14 mm long, falls between the average lengths of the bone in *C. sectumsemper* and *C. hudsoni*, where it is 8.2 mm and 20.4 mm respectively (Klein et al. 2015). Therefore, the total body length of *C. cambrica* was probably about 15–17 cm in life, compared to 12 cm for *C. sectumsemper* and 25 cm for *C. hudsoni*.

4.2. Clevosaurus *sp.*

4.2.1. Cranial elements

By far the most common identifiable remains from Pant-y-ffynnon are clevosaur jaw elements, especially a range of morphotypes of the maxilla (Fig. 8). Most of these do not show diagnostic characters of any particular *Clevosaurus* species, and are not complete enough to distinguish between the new species *C. cambrica* and the two best known clevosaur species across the Late Triassic archipelago, *C. hudsoni* and *C. sectumsemper*. Some of the specimens have five additional teeth (Fig. 8A, C, G, I) and these may represent *C. cambrica*, but they are retained as *Clevosaurus* sp. for the present.

Several isolated maxillae (Figs. 8, 9B) show considerable variation in size, shown for example in comparing the flanged teeth of Fig. 8C and E. Some of the specimens are damaged, but others (e.g. Fig. 8B–G) show considerable detail of bone and teeth. These mainly lateral views (Fig. 8A, B, D, F–H) show a longitudinal ridge above the tooth row, and varying portions of the dorsal and posterior processes. The preserved teeth sometimes include, as in *C. cambrica*, the largest, mid-row tooth, whereas others (Fig. 8A, B, D, F and G), like *C. hudsoni* (Fraser, 1988) and *C. sectumsemper* (Klein et al., 2015), have teeth that appear to become progressively larger posteriorly. Generally, the juvenile dentition is removed by wear as the animal grows, but one maxilla (Fig. 8F) shows unworn alternating-sized anterior teeth, each small tooth being half the size, or less, than the tooth following behind; this dentition is the remnant hatchling series of Fraser (1988). Another specimen (Fig. 8E) displays a continuous cutting edge where the flange of one tooth joins, or almost joins the anterior 'cone' of the following

tooth. This is also a feature found in the *C. cambrica* holotype (Fig. 5A).

The typical flanged maxillary teeth of *Clevosaurus* can be seen in occlusal view in Fig. 9B. One maxilla (Fig. 8B) appears to have the wide spacing between the teeth, in lateral view, found in *C. sectumsemper* (Klein et al., 2015), but the flanges are not well preserved, so any tooth overlap is unclear.

In addition to the *C. cambrica* specimen on the *Terrestrisuchus* slab (Fig. 5C, D) and the articulated specimen (Fig. 6C–E), at least one isolated *Clevosaurus* dentary (Fig. 9D) is also known, and it includes the coronoid process and one large, flanged tooth. The large gap between this tooth and the coronoid process could be interpreted as the same as in *C. sectumsemper* (Klein et al., 2015), but there is no definitive evidence of that species, such as the increasingly lower bases of each successive posterior tooth. We cannot therefore assign this specimen to either species with certainty. The small fragment of dentary (Fig. 9A) also has three teeth with successively lower bases, but this is probably a juvenile, as the Meckelian fossa is relatively wide. Numerous isolated clevosaur teeth (e.g. Fig. 9C) probably resulted from damage during deposition or during preparation; they cannot be assigned to species.

Among other isolated cranial elements of rhynchocephalians is a left jugal of *Clevosaurus*, slightly smaller than that of *C. hudsoni*, and showing the anterior, dorsal, and posterior processes (Fig. 10A). There is also a quadrate, probably of *Clevosaurus*, with the articular surface visible (Fig. 10B).

4.2.2. Postcranial elements

A complete left femur (Fig. 9E, F) is approximately 25 mm long. It is similar to the restored right femur of *Clevosaurus hudsoni* (Fraser, 1988, fig. 33) in proportions, and in showing an elongate, strong lateral trochanter at the anterior end (Fig. 9E). An isolated proximal head of a femur (Fig. 9H) is clearly smaller, though there is not enough preserved to estimate its full length. A right tibia (Fig. 9G) is 18 mm long, slightly longer than the mean tibia length observed in *C. sectumsemper* (17.4 mm) and so it is possible this could have come from the new species which, from cranial bone comparisons, is slightly larger. Although it seems anatomically similar also to the tibia of *C. hudsoni* (Fraser, 1988, fig. 34), the proximal and distal regions are 30–40% wider than expected in that species. The cnemial crest is also quite pronounced and it is possible that this tibia derives from another taxon, possibly not even a rhynchocephalian.

Fragments of tiny long-bone shafts were among the most common fossils extracted by acid digestion. Their differing sizes could reflect the variation in size among individuals of different ages as well as possibly between species of *Clevosaurus*. Most such limb bone elements could not be identified because they lack terminal ends. Specimens that can be identified include specimens on small rocks at the NHMUK. Those shown in Fig. 9 are a small rhynchocephalian partial ulna, 9.5 mm long, and possibly 13–14 mm when complete (Fig. 9I) and a partial humerus, 8.4 mm long (Fig. 9K). A possible radius (Fig. 9J) is 7 mm long, although it may have been slightly longer before breakages.

There are some good isolated specimens of *Clevosaurus* scapulocoracoids in the NHMUK collection (Fig. 10C, D); particularly noticeable is the fused suture (Fig. 10D) between the two elements and the glenoid where the humerus would have articulated.

4.3. Diphydontosaurus *sp.*

Although some poorly preserved material has been found in our preparation, the collections at the NHMUK have some better examples of *Diphydontosaurus* fossils from Pant-y-ffynnon
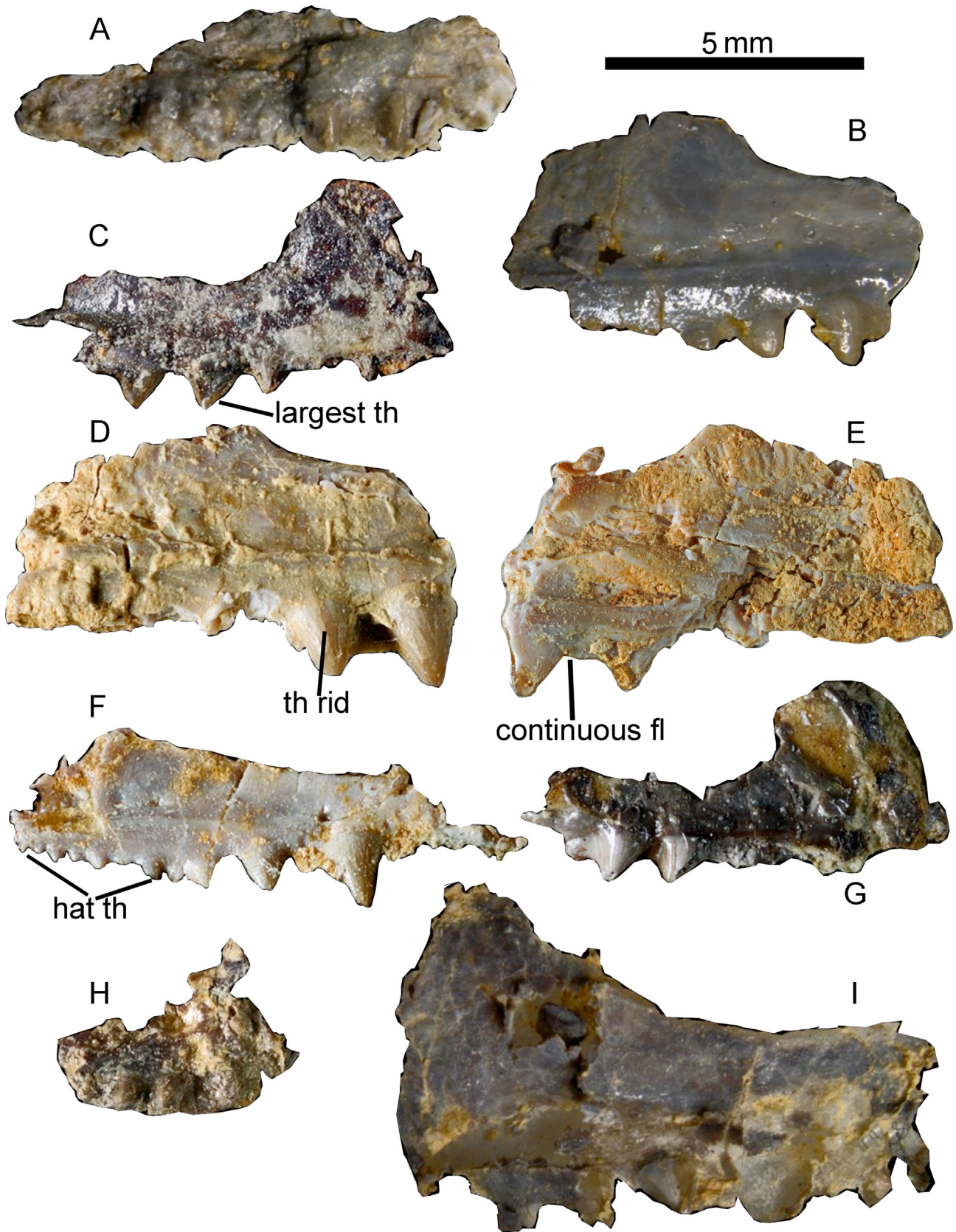
Fig. 8. Maxillae of *Clevosaurus* sp. showing the range of morphotypes of the genus at Pant-y-ffynnon; all in lateral view except the medial views of C, E and I. (A) Crushed *Clevosaurus* sp. left maxilla, NHMUK R37039. (B) *Clevosaurus* left maxilla, NHMUK R37040. (C) *Clevosaurus* (probably *C. cambrica*) left maxilla, NHMUK R37028. (D and E) *Clevosaurus* sp. left maxilla, NHMUK R37032 with near continuous flange in E. (F) *Clevosaurus* sp. left maxilla, NHMUK R37029, showing alternating-sized hatchling dentition. (G) *Clevosaurus* sp. right maxilla, NHMUK R37038, with indications of additional teeth similar to *C. hudsoni*, increasing in size posteriorly. (H) *Clevosaurus* left maxilla fragment, NHMUK R37023. (I) *Clevosaurus* right maxilla, NHMUK R37041.

Fig. 9. Rhynchocephalian cranial and postcranial elements. (A–D) Dentary fragments and isolated teeth of *Clevosaurus* sp. (A) *Clevosaurus* medial view of juvenile dentary fragment, NHMUK R37033. (B) *Clevosaurus* maxilla fragment, occlusal view, NHMUK R37028. (C) *Clevosaurus* isolated cracked tooth in occlusal view showing enamel NHMUK R37050. (D) *Clevosaurus* sp. with some similarities to *C. sectumsemper*; posterior of dentary, medial view with coronoid process, NHMUK R37037. (E-K), rhynchocephalian long bones. (E, F) *Clevosaurus* left femur in dorsal (E) and ventral (F) views, NHMUK R37030. (G) ?*Clevosaurus* right tibia in anterior view, NHMUK R37045. (H) Proximal head of *Clevosaurus* femur, NHMUK R37046. (I) *Clevosaurus* ulna, NHMUK R37019. (J) Small unidentifiable rhynchocephalian radius, NHMUK R37047. (K) Unidentifiable rhynchocephalian humerus, NHMUK R37034. Top scale bar refers to A–D and lower scale E–K.
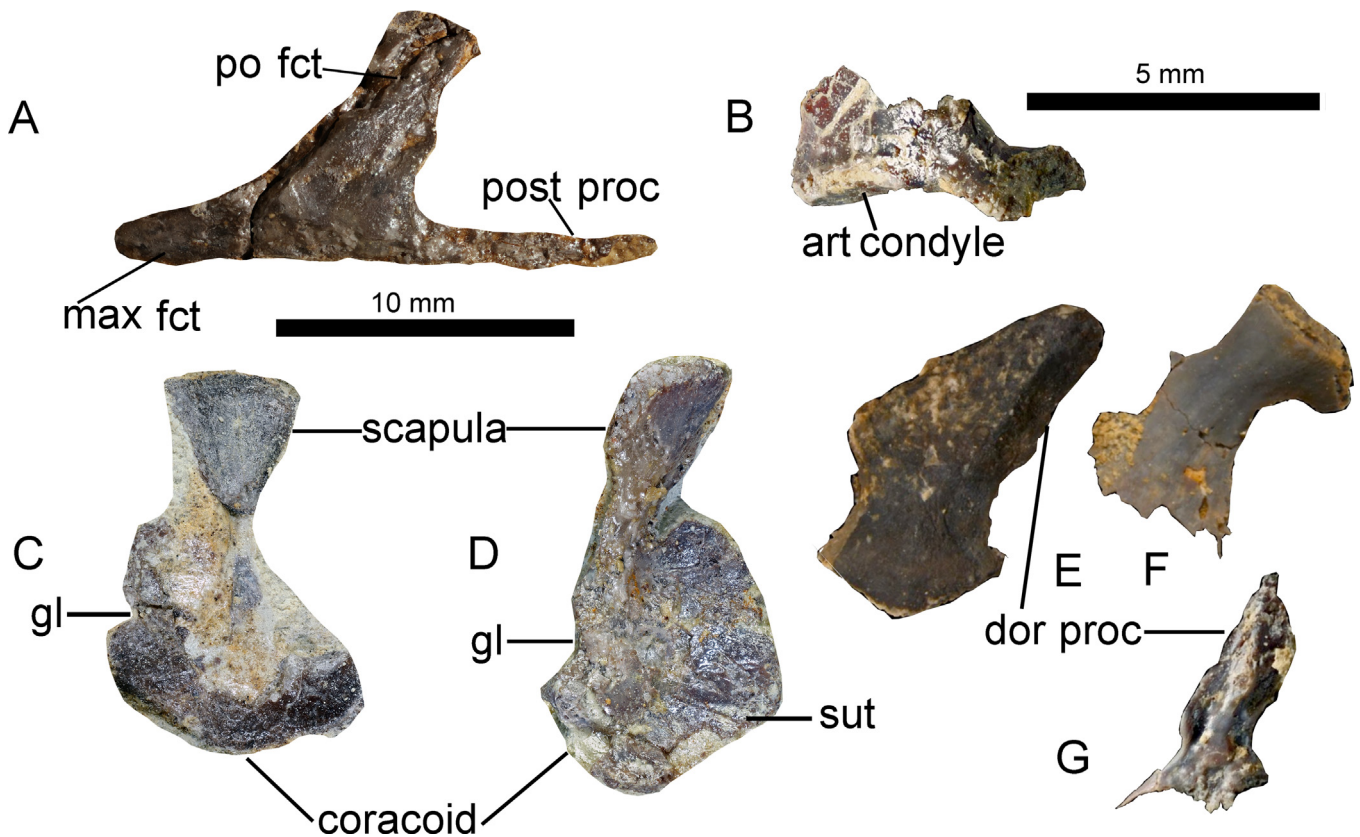
Fig. 10. Rhynchocephalian cranial and postcranial elements. (A) NHMUK R37017, left jugal in lateral view of a *Clevosaurus* sp. of similar size to *C. hudsoni*. (B) Rhynchocephalian quadrate, NHMUK R37027, probably of a large sphenodontian such as *Clevosaurus* sp., with articular surface of ventral region shown. (C) Right scapulocoracoid of *Clevosaurus* sp. in lateral view, NHMUK R37020. (D) Left scapulocoracoid of *Clevosaurus* sp. in medial view, NHMUK R37021. (E) Right ilium of *Clevosaurus* or *Planocephalosaurus* sp. in medial view, NHMUK R37049. (F) BRSUG 28381-4, Left ischium of?*Planocephalosaurus* sp. in medial view. (G) Right ilium of a small rhynchocephalian medial view, NHMUK R37026. 10 mm scale bar refers to A, C and D, and 5 mm scale bar refers to B, E–G.

(Fig. 11A–D). The substantially broken but impressive left dentary (Fig. 11A) provides significant information. It is identified as *Diphydontosaurus* as there are posterior acrodont teeth (sitting on the crest of the jaw) with an anterior dentition that, although damaged, appears to be pleurodont. Between the larger acrodont and small pleurodont teeth there is a transitional region with teeth of intermediate size but with a deeper lingual base than the posterior dentition. There appears to be an edentulous region on the crest of the jaw behind the triangular acrodont teeth, which is typical of *Diphydontosaurus* (Whiteside, 1986), but the area is damaged and there are calcite crystals growing there. The specimen is similar in length (*c.* 15 mm), general shape and with the rounded symphysis of the *D. avonis* holotype of Whiteside (1986). However, the coronoid is pronounced, which suggests that either the reconstruction of the region in *Diphydontosaurus* by Whiteside (1986) underestimated its height, or it is a different species of the genus or closely related taxon. The Pant-y-ffynon specimen probably has more teeth (estimated at 26–27) than *D. avonis*, but this is uncertain as the dentition is not sufficiently well preserved.

A parietal (Fig. 11G) is slightly smaller than the unpaired bone of *Diphydontosaurus avonis*, but we cannot be sure that this specimen is unpaired as the bone is fractured, including in the midline, with matrix filling the cracks. A larger parietal (Fig. 11F), but of similar size to that of *Diphydontosaurus avonis*, with a prominent central foramen, is unpaired but has a ridge suggesting an ontogenetically late fusion; that is a characteristic of *Diphydontosaurus* (Whiteside, 1986) and is therefore referable to the genus. Although we cannot be sure as the underside is inaccessible and the facets are not

discernible, we tentatively ascribe a poorly preserved bone to an unpaired frontal (Fig. 11E) which is a characteristic of *Diphydontosaurus* (cf. Whiteside, 1986, fig. 10). In contrast, *Clevosaurus* has paired frontal bones and the frontal of *Planocephalosaurus* has a transversely relatively thicker mid region.

4.4. Additional rhynchocephalian specimens

A few fossils can be ascribed to a third rhynchocephalian genus, possibly a basal sphenodontian somewhat larger than *Diphydontosaurus*.

Three small postcranial elements include a sphenodontian right ilium (Fig. 10E) and left ischium (Fig. 10F) that are similar in morphology and size to those figured by Fraser and Walkden (1984) and therefore, may be from a *Planocephalosaurus*-type sphenodontian. However, the ilium was found in NHMUK R36939, which yielded partially articulated *C. cambrica* bones, and the element may derive, more probably, from a small individual of the new clevosaur. A small, somewhat crushed, right ilium (Fig. 10G) may derive from a *Diphydontosaurus*-sized rhynchocephalian.

Two specimens of dentary (Fig. 11B–D) are referable to another small basal rhynchocephalian, which we designate taxon A. The specimen (Fig. 11C, D) is damaged in the mid region and detail is missing there, but the dentition is clearly more homodont along the length of the dentary than in *Diphydontosaurus*. The anterior extremity of the dentary is relatively more robust than in *Diphydontosaurus* and has the distinctive flanged appearance typical of sphenodontians (Fig. 11D). In particular, the anterior teeth are sturdy and the overall dentition could be considered as
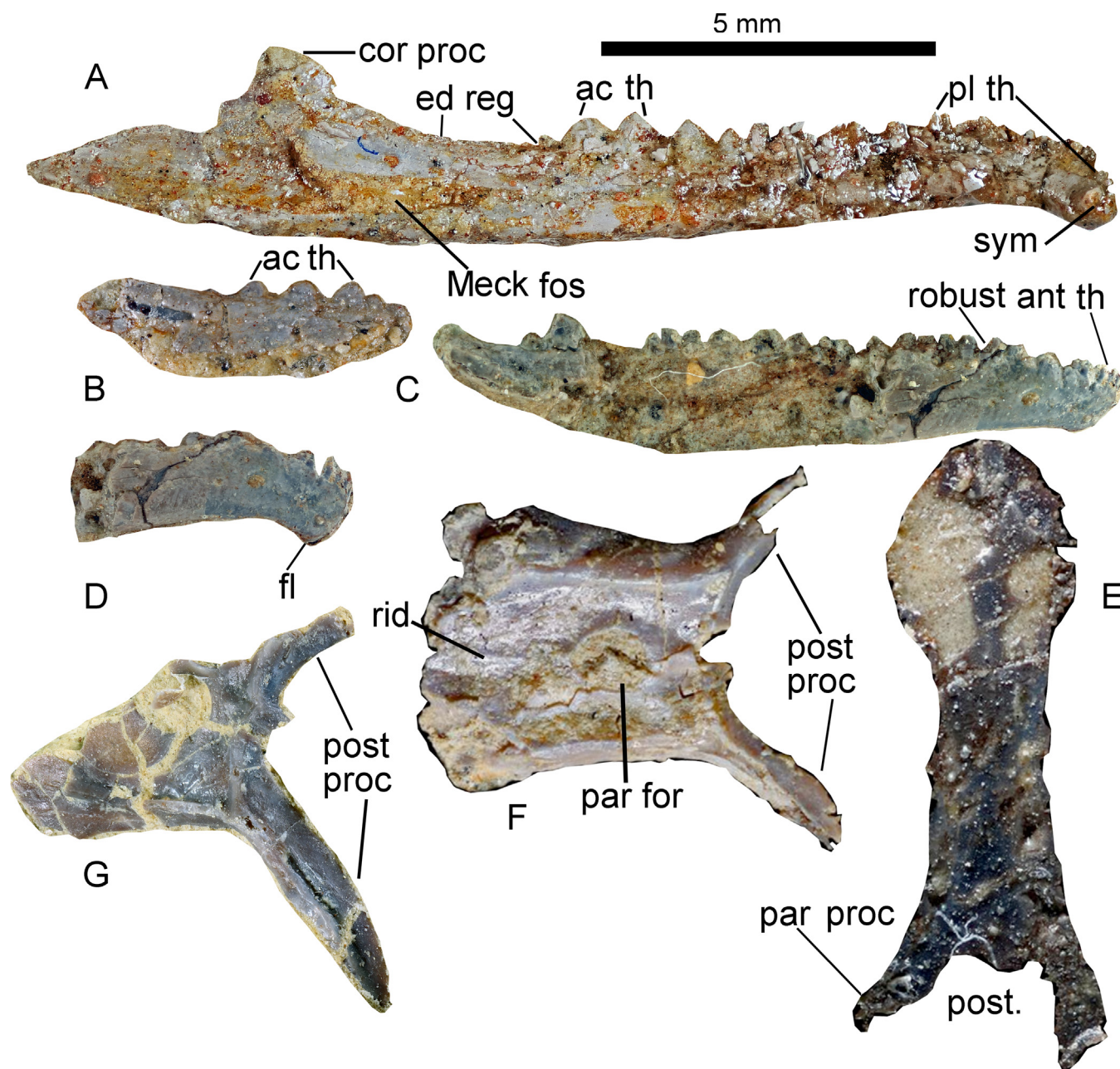
Fig. 11. Rare rhynchocephalians from Pant-y-ffynnon. (A) *Diphydontosaurus* sp., left dentary in medial view, showing high coronoid region, NHMUK R37024. (B) Posterior fragment of taxon A dentary showing acrodont teeth, NHMUK R37035. (C) Right dentary of taxon A in lateral view showing relatively robust anterior teeth, NHMUK R37022. (D) Same as C in a slightly different lateral orientation, showing flange. (E) Possible *Diphydontosaurus* frontal, NHMUK R37025 in dorsal view. (F) *Diphydontosaurus* parietal, in dorsal view, NHMUK R37031. (G)?*Diphydontosaurus* parietal, in dorsal view, NHMUK R37018.

reminiscent of *Planocephalosaurus*. However, there is no sign of the very large posteriormost tooth found in *Planocephalosaurus* (Fraser, 1982), and we consider that the specimen more closely resembles *Whitakersaurus bermani* described by Heckert et al. (2008) from the late Norian–Rhaetian Chinle Group of the USA. *Whitakersaurus* has a similar relatively robust anterior dentition and the specimen is the same size (10–11 mm) as the largest dentary depicted by Heckert et al. (2008). The Pant-y-ffynnon specimen has *c.* 25 teeth, more than in *Whitakersaurus*, and because of the damage and fragility of the specimen, we cannot determine whether the tooth apices have the radial ridges and mesio-distal trough of the American taxon. Furthermore, although the posterior dentition

appears to be acrodont, the medial side is hidden in matrix and therefore we cannot establish the type of implantation of anterior teeth (described as pleurodont for *Whitakersaurus* by Heckert et al., 2008). We refer specimen NHMUK R37035 (Fig. 11B) to taxon A as it seemingly lacks the edentulous posterior region of *Diphydontosaurus*.

4.5. Pantydraco caducus *(Yates, 2003)*

Many isolated elements attributable to *Pantydraco* are in the NHMUK collection. These are in addition to the type specimen, a nearly complete skeleton, NHMUK P24, already described in detail

by Yates (2003), Galton et al. (2007) and Galton and Kermack (2010). Other remains pictured by those authors from the NHMUK collections include a *Pantydraco* right tibia (NHMUK P77/1, Fig. 12A), which is 63 mm long, and a right fibula (NHMUK P77/1, Fig. 12B), which is 56 mm long. The phalanx found by us (Fig. 12C, D) is less diagnostic of any taxon, but is the right size and shape to be assigned to *Pantydraco*. It is 13 mm long, far too large and robust to come from any of the lepidosaurs, and probably too short and broad to be assigned to *Terrestrisuchus*. A neural arch and centrum (Fig. 12E, F) could also be assigned to *Pantydraco*—the centrum is deep as in an archosaur, and the neural arch is slender, as seen in various *Pantydraco* vertebrae (Yates, 2003, Figs. 11–13).

In addition to some elements, including phalanges and vertebrae from our acid processing, two fragments of teeth from the two Bristol rocks came to light, BRSUG 28381-1 and BRSUG 28381-2 (Fig. 12G–J) that can be attributed to *Pantydraco* because they share the "leaf-like" overall shape and the sharp edges lined with broad denticles of *Thecodontosaurus antiquus* (Riley and Stutchbury, 1836; Benton et al., 2000). These are merely the tips of the crowns of the teeth, but the denticle shape and size is identical to that observed in the *Pantydraco* holotype (Yates, 2003, Fig. 9).

A small fragment of the posterior zygapophyseal region of a vertebra (BRSUG 28381-3; Fig. 12K, L) indicates the largest tetrapod in our sample. Scaling up the specimen by comparing *Pantydraco* and *Thecodontosaurus* dorsal vertebrae indicates an animal about 1.5 m long. That is slightly larger than the 1.3 m reconstruction of *P. caducus* by Galton and Kermack (2010).

4.6 Terrestrisuchus

It is difficult to distinguish isolated bones of *Pantydraco* from *Terrestrisuchus* because they are both slender-limbed archosaurs of similar size, and only certain elements show diagnostic characters (Crush, 1984; Galton et al., 2007). We show one of the key articulated specimens (NHMUK R7571; Fig. 5D) of *Terrestrisuchus* associated with the new species of *Clevosaurus*.

We recovered a left ilium (Fig. 12M) from the acid digestion of NHMUK R36973, which we ascribe to *Terrestrisuchus* as it has the long posterior process and is a dorso-ventrally narrow bone compared to the broader form of *Pantydraco*. It is the same size and morphology as the ilium figured by Crush (1984, Fig. 8C) but unfortunately the bone is damaged in the ventral acetabular region, so its crocodylomorph character is not certain.

4.7. Coelophysoid

Warrener (1983 in Galton and Kermack, 2010) and Rauhut and Hungerbuhler (2000) recorded a coelophysoid from Pant-y-ffynnon. These specimens, a left articulated pelvis, a left femur, parts of a sacrum and dorsal vertebrae, had previously been recognised as a 'coelurosaur' by Warrener (1983) in her thesis (Galton and Warrener, 2010). We could not locate these fossils in the NHMUK collections, nor did we find any examples of a coelophysoid in our samples.

4.8. 'Edgar'

Although it remains undescribed, it is worth mentioning the existence of a crurotarsan (pseudosuchian) archosaur at Pant-y-ffynnon. This is probably the 'thecodont' of Warrener (1983); quoted in Galton and Kermack, 2010). The vertebrae are amphicoelous, rather than amphicoelous-platycoelous, as in *Thecodontosaurus*, *Pantydraco* and *Terrestrisuchus*. The animal has long been termed 'Edgar' by the UCL team (they frequently gave informal first names to undescribed species) to distinguish it from

other taxa. We recovered no specimens referable to this taxon in our acid digestion sampling.

4.9. Kuehneosaur

Possible kuehneosaur remains were noted from Pant-y-ffynnon (Crush, 1984; Benton and Spencer, 1995; Galton and Kermack, 2010), but we found no specimen attributable to that taxon in our sampling, nor in the NHMUK collections.

4.10. Other remains

In addition to the fossils described above, it is worth mentioning that many crinoid ossicles were present in the matrix, but these are reworked clasts from the Carboniferous Friars Point Limestone, which hosts the fissures. This was clear from the different, more abraded, mode of preservation of the crinoids and the Triassic fossils. These ossicles range in diameter from 1–10 mm and are typical of similar fissure deposits, such as at Tytherington Quarry (Van den Berg et al., 2012) where the fissures are also embedded in the Carboniferous Black Rock Subgroup.

5. Faunal composition

Our acid-digested samples of seven rocks yielded over 1800 individual specimens and form the basis of an assessment of species diversity and approximate faunal composition (Fig. 13D). First, we excluded the crinoid ossicles and about half of the picked fossils, which could not be identified more precisely than simply 'bone fragment'. This left over 840 identifiable elements, each of which was used to signify one individual, except in cases where an articulated series of bones clearly came from the same individual (e.g. from rock specimen NHMUK R36940, Fig. 4C). The values are imprecise because we are dealing with isolated teeth and bones. However, it is worth recording that, although we found a few *Pantydraco* teeth, we recovered no *Terrestrisuchus* or teeth from any other archosauromorph; these teeth are within the size range of the bones so if present in the immediate habitat around the fissures we would expect to have found them.

Rhynchocephalians dominate, comprising 98% of the fauna, of which clevosaurs are by far the most abundant, with much rarer examples of *Diphydontosaurus* (*c.* 0.2%). The dinosaur *Pantydraco* is also rare (<2%), and the crocodylomorph *Terrestrisuchus* is rarer still. From our sampling and additional fossils held in the NHMUK collections, as well as the unfound coelophysoid, we record a minimum of eight tetrapod genera, including at least four sphenodontian taxa, in the Pant-y-ffynnon fauna. We regard the suggested presence of *Gephyrosaurus* (Crush, 1981, in Evans and Kermack, 1994) as a probable misidentification of *Diphydontosaurus*.

The occurrence at Pant-y-ffynnon of *Diphydontosaurus* with a sauropodomorph dinosaur (*Pantydraco*) parallels the association of the sphenodontian with *Thecodontosaurus antiquus* at Durdham Down (Foffa et al., 2014) and Tytherington (Whiteside and Marshall, 2008; Van den Berg et al., 2012). Also, as at Tytherington (Whiteside and Marshall, 2008), we find no confirmed evidence of *Kuehneosaurus* in the Pant-y-ffynnon NHMUK collections, nor in our processed materials.

The current study has adopted methods used before in studies of similarly-aged (Rhaetian) fissures at Tytherington (Van den Berg et al., 2012), Durdham Down (Foffa et al., 2014), and Woodleaze (Klein et al., 2015), and the faunal composition is similar in the preponderance of rhynchocephalians to Woodleaze which was even more spectacularly dominated by a *Clevosaurus* species (Fig. 13C). However, Pant-y-ffynnon has similar archosauromorphs in common with Tytherington fissure 2 (Fig. 13A) and Durdham
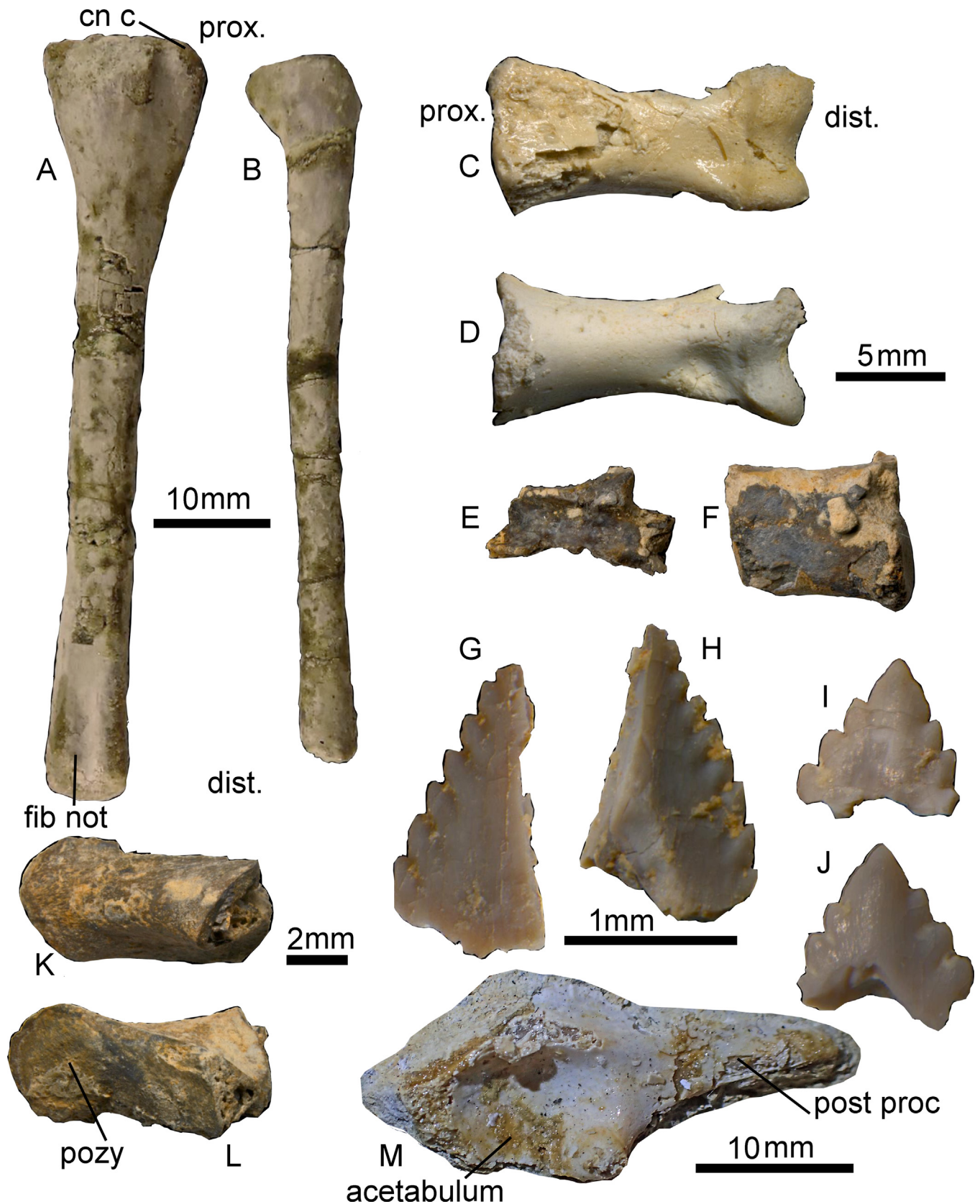
Fig. 12. Isolated elements of archosauromorphs including, (A–J), the sauropodomorph dinosaur *Pantydraco caducus*. (A) Right tibia, in lateral view, NHMUK P77/1. (B) Right fibula, in lateral view, NHMUK P77/1. (C, D) Phalanx in ventral (C) and dorsal (D) views, NHMUK R37043. (E, F) Part of neural arch NHMUK R37048a (E) and centrum NHMUK R37048b (F) of a laterally compressed archosauromorph vertebra, in lateral view. (G, H) Tooth fragments in lingual (G) and labial (H) views, BRSUG 28381-1. (I, J) Tooth fragments in lingual (I) and labial (J) views, BRSUG 28381-2. (K, L) BRSUG 28381-3, posterior zygapophysis of ?*Pantydraco* representing the largest individual archosauromorph known from Pant-y-ffynnon; (K) dorsal and (L) ventral views. (M) lateral view of left ilium of, probably, *Terrestrisuchus,* NHMUK R37044. Scale bars: 10 mm refers to A, B and M; 5 mm to C–F; 2 mm to K and L, and 1 mm to G–J.
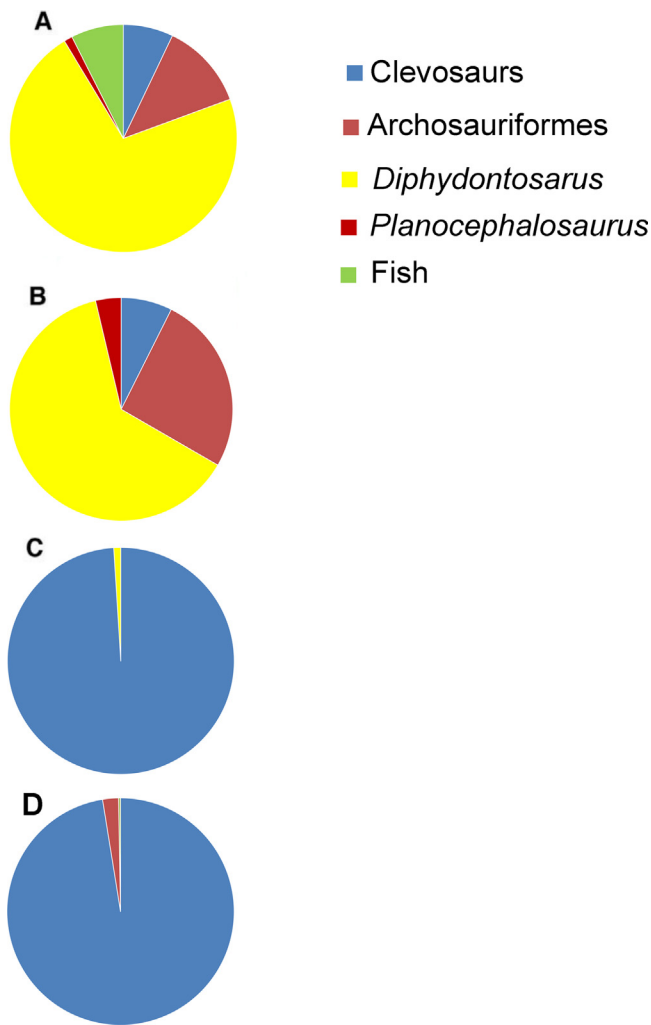
Fig. 13. Chart showing the relative abundance of prominent taxa from fissure deposits at Tytherington fissure 2 (A), Durdham Down (B) and Woodleaze (C) using previously published data (Van den Berg et al., 2012; Foffa et al., 2014; Klein et al., 2015) compared to Pant-y-ffynnon Quarry (D), which is based on 1815 processed specimens; 847 were identifiable. Unidentifiable fragments have been omitted and those bones that could have belonged to any of several species have also not been included. For full breakdown of species, see appendix.

Down (Fig. 13B), as well as geological field relationships (Whiteside et al., 2016). In contrast, those two Bristol localities are instead dominated by *Diphydontosaurus* (60–75%), with rarer *Clevosaurus* (10–15%), but a greater proportion of archosaurs.

6. Discussion

Clevosaurs were the most numerous group of Late Triassic tetrapods present at Pant-y-ffynnon. These small, lizard-like reptiles were most likely insectivorous, as indicated by their sharp but robust teeth (Figs. 5, 6, 8, 9), suitable for slicing through the chitin exoskeletons of insects (Fraser, 1988; Jones, 2009). Fraser (1988) suggested that *Clevosaurus hudsoni* might have become facultatively herbivorous in later life, and his evidence was the heavily worn dentary teeth especially in older adults. The wearing down of teeth as the animals aged led to a nipping "beak-like" dentition that could have been more suited to stripping leaves from plants than to hunting. However, this hypothesis is called into question when it is noted that the extant *Sphenodon* also acquires this beak-like dentition as it ages, but it remains carnivorous throughout life.

Klein et al. (2015) suggested that *Clevosaurus sectumsemper* was demonstrably carnivorous, with self-sharpening teeth ideally shaped for slicing prey and with a relatively large dorso-ventral tooth gap between the dentary and maxilla. This might have allowed it to tackle a greater array of prey, such as arthropods, molluscs and possibly small tetrapods such as young *Diphydontosaurus*. It is likely that the prominent flanged teeth of *C. cambrica* might also have been adapted to immobilize and dice similar prey. The best-preserved specimens and the CT imaging (Figs. 5 and 6) show that the posteriormost flanged teeth were smaller than those immediately in front, so it maintained a relatively large gap towards the back of the jaw as in *C. sectumsemper*.

The discovery of *Clevosaurus cambrica* has added to our knowledge of the adaptive radiation of the genus *Clevosaurus* on islands in the Late Triassic palaeo-archipelago around the present Bristol Channel area. On each palaeo-island, differences in palaeoenvironments and faunal compositions might have led to the evolution of distinctive species of clevosaur. *C. cambrica* has prominent large flanged posterior marginal teeth in common with *C. hudsoni* and *C. sectumsemper* of the Cromhall palaeo-island(s), but not their progressive distal increase in tooth size; rather the largest teeth are mid-dentition, as in the Early Jurassic *C. convallis* from St Brides palaeo-island. The number of large flanged *C. cambrica* additional maxillary teeth lies between the four of *C. hudsoni* and *C. sectumsemper* and the six less well-flanged teeth of *C. convallis*. Thus, *C. cambrica* appears to be intermediate in dental morphology between the earlier or contemporaneous *C. hudsoni* and *C. sectumsemper* from the Cromhall and Woodleaze palaeoislands to the east, and the younger *C. convallis* from fissure 4 at Pant Quarry, near to Pant-y-ffynnon (Säilä, 2005).

The other rhynchocephalians from Pant-y-ffynnon, *Diphydontosaurus*, taxon A and a possible larger basal sphenodontian, such as *Planocephalosaurus*, differed in size and probable diet. Whiteside and Duffin (2017) suggested that the anterior pleurodont teeth of *Diphydontosaurus* might have been appropriate to catch dipteran flies, but the shearing posterior teeth enabled it to tackle beetles or other hard arthropods with a harder exoskeleton. The diet of taxon A, due to its tiny size (smaller than *Diphydontosaurus*) and puncturing dentition, is likely to have been very small invertebrates. We found no teeth of any larger basal sphenodontian, so we will not speculate on its diet.

The slender crocodylomorph *Terrestrisuchus* had recurved, pointed teeth with a serrated edge (Crush, 1984). This was an obvious carnivore, and its slender body and relatively long legs would have made it an ideal pursuit hunter (Crush, 1984), likely preying on the clevosaurs, the adults of which would have been around one third its size. In fact, the *C. cambrica* dentary NHMUK R37015 next to the *Terrestrisuchus* specimen on NHMUK R7571 does bear many deep cuts and abrasions, including some covered by matrix, which we had originally attributed to action by the preparator. However, the profusion of these cuts and their localities near areas that would have borne soft tissue suggests that they could indicate predatory or scavenging action. *Terrestrisuchus* remains are far rarer in our sampling than those of *Clevosaurus*, which is to be expected when looking at a predator and its probable prey.

There had been controversy over the validity of *Terrestrisuchus*, with suggestions that it was a juvenile *Saltoposuchus*, the Norian genus from Germany (Fraser, 1994; Allen, 2003; Galton and Kermack, 2010). This has been disputed (Irmis et al., 2013) on the basis of the age and location of specimens, with *Terrestrisuchus gracilis* being geologically younger by 'several million years' (Irmis et al., 2013, p. 284). In addition, Irmis et al. (2013) argued that the bone histological evidence suggesting that *Terrestrisuchus* was a juvenile of *Saltoposuchus* would demand unusually fast growth rates, and so is unlikely.

Pantydraco was probably the only significant herbivorous vertebrate in the Pant-y-ffynnon ecosystem, and certainly the largest, at about 1–1.3 m long (Kermack, 1984; Galton and Kermack, 2010), and we have an indication from one bone fragment that it might have reached 1.5 m. On a small island in a palaeo-archipelago with potentially frequent forest fires (Harris, 1958; Whiteside and Marshall, 2008), the habitat might have been unable to support a viable population of much larger herbivores. In this regard, Galton and Kermack (2010) report that all *Pantydraco* fossils are from juveniles and regard the bodies of larger individuals (adults) as too big to fall into the limestone cracks. This seems an implausible suggestion, as the cracks are not particularly small (fissure entrances can be >1–2 m wide) and larger animals have small skeletal elements such as some cranial bones, teeth, phalanges, and caudal vertebrae, as well as fragments of larger bones, none of which have been recorded. Some of the *Pantydraco* features referred to as juvenile by Galton and Kermack (2010), such as its proportionally large skull with large orbits, are also characteristic of dwarfism, and it may be that the bones represent a small sauropodomorph living on a restricted island.

The diet of *Pantydraco* was probably like that of its close relative *Thecodontosaurus,* which is well established as an herbivore (Benton et al., 2000). The triangular teeth are often compared to those of extant iguanas, herbivorous, leaf-eating lizards. However, the coronoid process of the dentary is low in *Pantydraco* (Galton and Kermack, 2010), whereas *Iguana* has a high coronoid formed by the coronoid bone. Galton and Kermack (2010) therefore infer that *Pantydraco* would have been unable to shred tougher leaves and was facultatively omnivorous, as also suggested by Kermack (1984) and Barrett (2000). Galton and Kermack (2010) also comment that, although it was not found, a coronoid bone was probably present in *Pantydraco*, and if so that might have raised the coronoid area somewhat more than in their reconstruction. However, we consider that it is equally plausible that *Pantydraco* regularly browsed on the luxuriant vegetation around the moist entrances to the fissures; animals that died in that environment, perhaps during a drought or wildfire, would have been easily washed into the cavern.

Mammaliamorphs have not been recorded from Pant-y-ffynnon, and we found no evidence in our sampling. The presence of a clevosaur with large flanged teeth in an environment lacking mammaliamorphs is in accord with the suggestion of Whiteside and Marshall (2008) and Whiteside and Duffin (2017) that these taxa were likely ecological competitors, as both have a pronounced slicing dentition.

Although this is the most detailed study on the Pant-y-ffynnon fissure fauna to date, there is still more work to be done on taxa such as 'Edgar', which remains undescribed. 'Edgar' and the new clevosaur, *C. cambrica*, prove that, despite having been worked on since the 1950s, Pant-y-ffynnon Quarry may still yield new information on rare taxa of the latest Triassic.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.pgeola.2017.11.001.

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