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THE LATE TRIASSIC AND EARLY JURASSIC FISSURE FAUNAS FROM BRISTOL AND SOUTH WALES: STRATIGRAPHY AND SETTING

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The famous vertebrate-bearing fissures of the Bristol area in southwest England and in south Wales were traditionally referred to "upland" environmental settings, and assigned an overall time range of some 60 Myr; we reject both of these viewpoints. In terms of the environmental setting, based upon the evidence of palaeogeography, sediments, and fossils, we show that all the Triassic-aged fissures were near-coastal and embedded in karst formed on palaeo-islands in a subtropical archipelago. Further, the dates of these fissure fills in both regions do not span the Carnian to Rhaetian, as commonly supposed, but instead they are probably all Rhaetian. We update information on the Charles Moore Holwell "*Microlestes*" fissure assemblage and demonstrate that the marine fauna confirms a Rhaetian age. As proposed by previous authors, younger fissure fills around the St. Brides area of South Wales were also formed on an island, but during the Hettangian–Sinemurian. The youngest fissure deposit in the region is Pliensbachian. The age range of the fissures thus shrinks to c. 20 Myr, and the first episode of tetrapod fissure infilling shifts from the time of the Carnian "pluvial" episode, to the early Rhaetian, when western Europe was undergoing major rifting associated with the beginning of the opening of the North Atlantic, and when the Rhaetian sea flooded over landscapes that had long been purely terrestrial and arid. We recognise clear changes in the faunal composition of the terrestrial vertebrate biota from the early Rhaetian, dominated by reptile taxa, with some mammaliamorphs, that then declined rapidly in diversity before the Hettangian. This herpetofauna was followed by three faunal assemblages in the Early Jurassic of St. Brides which became increasingly diverse following the end-Triassic mass extinction; each had prominent mammaliamorphs as well as high numbers, but few species, of rhynchocephalians.

Key words: Rhaetian, Triassic, Bristol fissures, Jurassic, Hettangian, Sinemurian, reptiles, mammaliamorphs.

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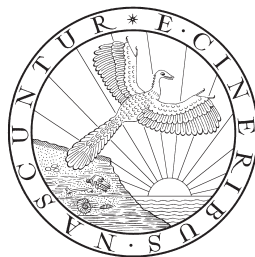
INTRODUCTION

The Late Triassic and Early Jurassic fissure fill deposits located on both sides of the Bristol Channel in southwest England and South Wales yield rich and unique vertebrate faunas (Robinson 1957; Kermack *et al.* 1973; Fraser 1994; Whiteside and Marshall 2008). The fissure fills, emplaced in Carboniferous Limestone, have produced many new vertebrate genera including fish, mammaliamorphs, and archosauromorph and lepidosauromorph reptiles. The tetrapods are of global importance as they span the end-Triassic mass extinction (ETE) and comprise well-preserved animals of small size that are not so commonly found in coeval deposits elsewhere. Two debated themes concerning the fissures are their ages and their environmental setting.

The earliest recorded find of Bristol fissure vertebrates was the small sauropodomorph dinosaur *Thecodontosaurus* Morris, 1843 from Durdham Down, Bristol (Riley and Stutchbury 1836, 1840), which was one of the first dinosaurs to be named (Benton *et al.* 2000). The geology and faunas of the fissures have been documented in reviews by Moore (1867, 1881), Robinson (1957), Savage (1993), and Benton and Spencer (1995). Other researchers have described specific fissure systems, including Windsor Hill (Kühne 1956), St. Brides Island quarries and additional South Wales localities (Kermack *et al.* 1973), Cromhall (Fraser and Walkden 1983; Walkden and Fraser 1993), and Tytherington (Whiteside 1983; Whiteside and Marshall 2008). The fissure faunas include some of the best known Mesozoic vertebrates that were first described from these localities and continue to be important in evolutionary studies and palaeogeography (Figs 1–3). The genera first described from the infills include mammaliaforms (*Morganucodon*, *Kuehneotherium*, *Microcleptes* [now *Thomasia*], *Bridetherium*, *Eozostrodon*, and *Paceyodon*), reptiles (*Thecodontosaurus*, *Clevosaurus*, *Gephyrosaurus*, *Planocephalosaurus*, *Diphydontosaurus*, *Sigmala*, *Pelecymala*, *Terrestrisuchus*, *Kuehneosaurus* [and *Kuehneosuchus*], *Tricuspisaurus*, *Variodens*, *Pantydraco*, *Agnosphitys*), and chondrichthyan fishes (*Duffinselache*, *Pseudocetorhinus*).

The dating of the fissures has been contentious: many authors have assumed that the fissures fills represent a long time range, perhaps as much as 60 Myr, spanning from the Carnian (*e.g.*, Simms and Ruffell 1990; Benton and Spencer 1995; Fraser and Sues 2010) to the Mid Jurassic (Savage 1977). Most authors have distinguished two age categories of vertebrate-bearing fissures of Bristol; the predominantly reptile-bearing "sauropsid" fissures and the mammal-bearing fissures (Robinson, 1957), also termed the "complex A" and "complex B" fissures respectively (Shubin and Sues 1991). Robinson (1957) interpreted the former as infilled underground water-courses that pre-dated the Rhaetian transgression and perhaps spanned the Late Triassic, from Carnian to Norian — though in a later paper, Robinson (1971) suggested that these fissures were more precisely upper Norian based on two sets of evidence. First, she perceived lithological similarities between the older fissure deposits and the red and green Norian mudstones in the local Blue Anchor Formation. Second, she projected from geological relationships that the nearby "Rhaetic" would have once capped the Emborough "sauropsid" fissure and thus post-dated the infill. Finding two *Kuehneotherium* teeth in the Emborough deposit, Fraser *et al.* (1985) used Robinson's age assignment to report the first "pre-Rhaetic" "therian" mammal. This dating of Emborough was contradicted by Whiteside and Marshall (1985, 2008) who deduced that the fissure infill post-dated the Rhaetian transgression. Kermack *et al.* (1973), Whiteside (1983), and Whiteside and Marshall (2008) also argued that any suggested lithological similarities with the Blue Anchor Formation were spurious; "the lithological evidence is useless" said Kermack *et al.* (1973), "except to warn against the red is Norian fallacy" said Evans and Kermack (1994). Indeed, Whiteside and Marshall (2008) depicted a red and green-banded rock interspersed with black laminae from fissure 2 at Tytherington that yielded Rhaetian palynomorphs. The younger, mammal-bearing fissures have generally been assigned a "Rhaeto-Liassic" age (Kermack *et al.* 1973; Evans and Kermack 1994) based on the palaeobotanical evidence of Harris (1957) and Lewarne and Pallot (1957), or on palaeogeography (Robinson 1971).

The environments represented by the fissure deposits have also been debated, and the traditional view, widely promulgated is that they represent a distinctive "upland" biota based on the small size of the tetrapod species, including dinosaurs, and their supposed occurrence in Mesozoic hilly limestone "caves" (Robinson 1957; Tarlo 1962; Halstead and Nicoll 1971; Halstead and Halstead 1981). However, this concept was challenged by Marshall and Whiteside (1980), Whiteside (1983), Whiteside and Robinson (1983), and Whiteside and Marshall (2008), who used palynological, fish and glauconitic clay evidence to demonstrate that the sauropsid fissures at Tytherington were formed and infilled in limestone islands set in a marginal marine location.
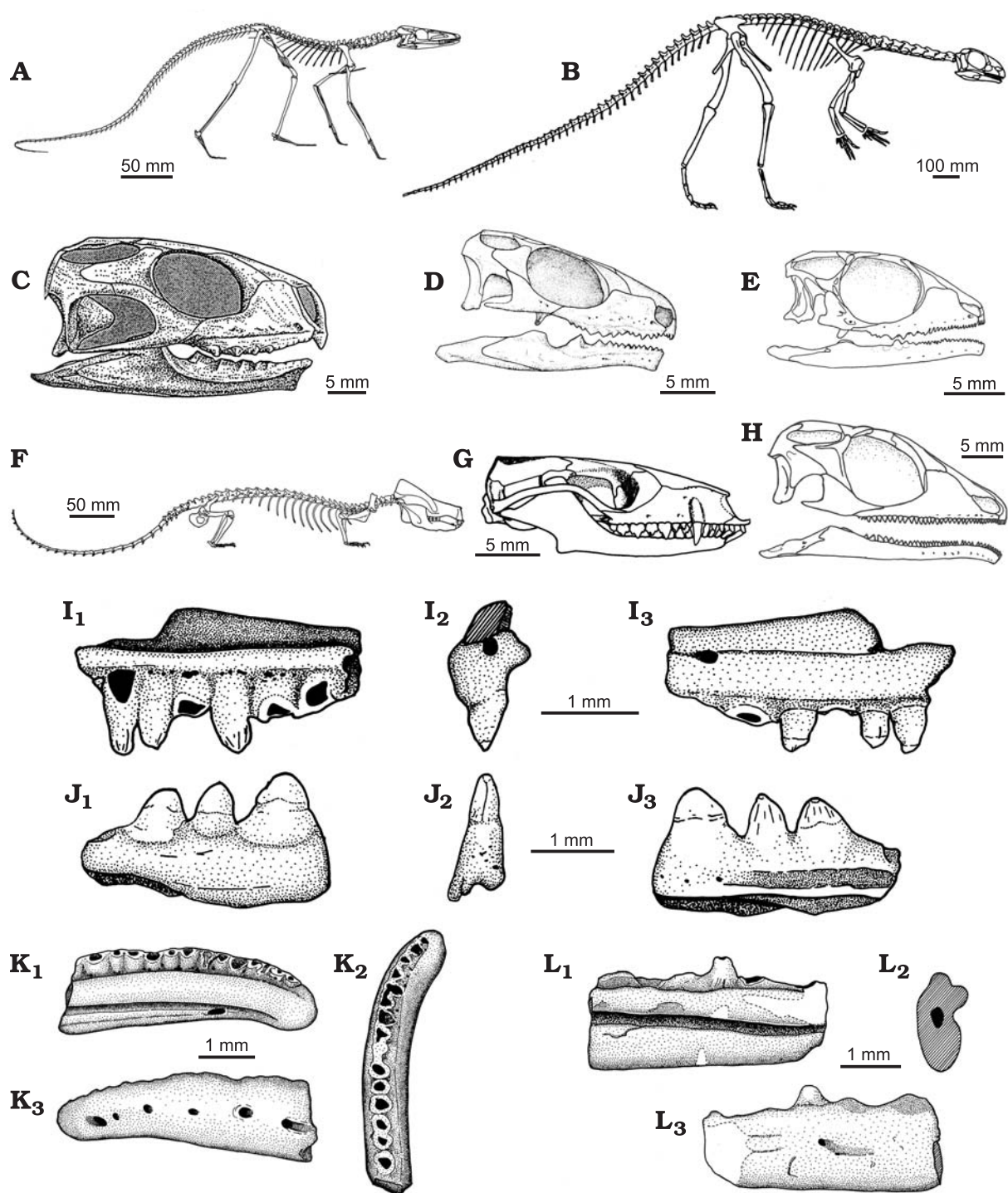
Fig. 1. Characteristic taxa found in the Triassic and Jurassic fissure faunas and new lepidosaur specimens from Holwell. **A–E**. Taxa typical of Rhaetian sauropsid fissures. **A**. *Terrestrisuchus* from Pant-y-ffynnon (from Crush 1984). **B**. *Thecodontosaurus* (based on *Pantydraco*) from Durdham Down (from Kermack 1984). **C**. *Clevosaurus hudsoni* from Cromhall, lateral view of skull and lower jaw (from Fraser 1994). **D**. *Planocephalosaurus* from Cromhall, lateral view of the skull and lower jaw (from Fraser 1982). **E**. *Diphydontosaurus* from Tytherington, lateral view of the skull and lower jaw (from Whiteside 1986). **F–H**. Taxa typical of St. Brides Early Jurassic fissures. **F**. *Oligokyphus* from Windsor Hill (from Kühne 1956). **G**. *Morganucodon*, lateral view of skull and lower jaw from a variety of St. Brides quarries (from Evans and Kermack 1994). **H**. *Gephyrosaurus*, lateral view of skull and lower jaw from Pontalun (from Evans 1980). **I–L**. Lepidosaur remains from Holwell (Moore Collection, BATGM). **I**. CD7, undetermined pleuracrodont rhynchocephalian maxilla fragment in medial (I_1), anterior (I_2), and lateral (I_3) views. **J**. C126, jaw fragment with posterior acrodont teeth of cf. *Diphydontosaurus* sp. in lateral (J_1), posterior (J_2), and medial (J_3) views. **K**. CD2, left dentary anterior fragment of ?*Diphydontosaurus* sp. in lateral (K_1), medial (K_2), and occlusal (K_3) views. **L**. CD6, left dentary fragment of *Diphydontosaurus* sp. in medial (L_1), cross-sectional (L_2), and lateral (L_3) views.
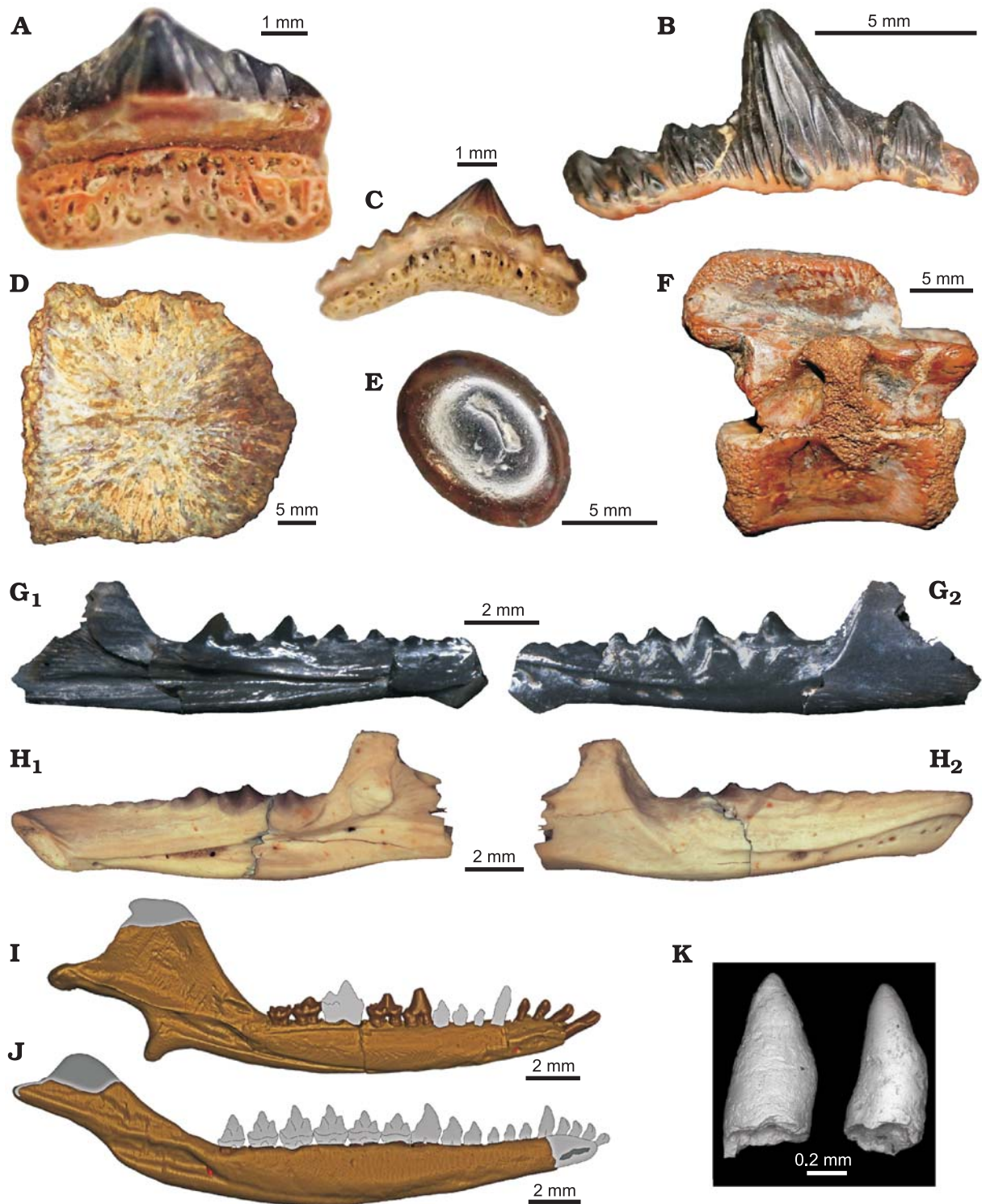
Fig. 2. Specimens from the Rhaetian and Early Jurassic fissures of the Bristol region and South Wales. **A–F**. Holwell sharks and aquatic reptiles from the Moore collection in BATGM. **A**. M64, tooth of *Lissodus minimus* in lingual view. **B**. M192, tooth of *Hybodus cloacinus* in labial view. **C**. M183, lateral tooth of *Synechodus rhaeticus* in lingual view. **D**. CD10, osteoderm of *Psephoderma alpinum* in surface view. **E**. M193, tooth of *Psephoderma alpinum* in occlusal view. **F**. C28, vertebra of *Pachystropheus rhaeticus* in lateral view. **G–J**. Tooth-bearing lower jaws. **G**. *Clevosaurus sectumsemper*, a reconstructed left dentary from Woodleaze quarry in medial (G_1) and lateral (G_2) views (after Klein *et al.* 2015). **H**. *Clevosaurus* aff. *sectumsemper*, a reconstructed right dentary from Fissure 2 at Tytherington in lateral (H_1) and medial (H_2) views (after Van den Berg *et al.* 2012). **I**. A reconstructed left lower jaw of *Morganucodon*, with paler areas missing (after Gill *et al.* 2014). **J**. A reconstructed left lower jaw of *Kuehneotherium*, with paler areas missing (after Gill *et al.* 2014). **K**. SEM image of two aff. *Gyrolepis* teeth (BRSMG CC 6087) from a Cromhall terrestrial fissure.
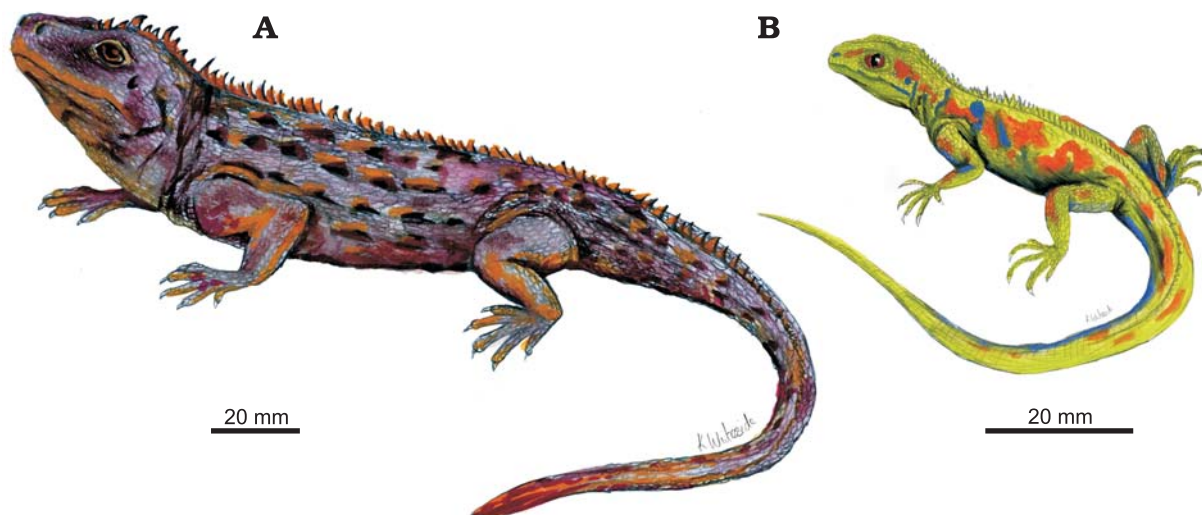
Fig. 3. Life reconstructions of *Clevosaurus hudsoni* and *Diphydontosaurus avonis*. **A**. *Clevosaurus hudsoni*, based on Fraser (1988a, 1994). **B**. *Diphydontosaurus avonis*, based on Whiteside (1983, 1986). Drawings by Katharine Whiteside.

In this review we provide our analysis, with new evidence, of the fauna, geology, dating and palaeo-environment of the suite of "sauropsid" and mammaliamorph-bearing fissures in South West Britain, the nature of their infill and their fossil content. As emphasised by Whiteside and Marshall (2008), there is no *prima facie* evidence that any of the "sauropsid fissure" infills in southwest Britain (and their contained tetrapods) date from pre-Penarth Group (Rhaetian) times. The age and environment of the principal mammaliaform-bearing fissures of Holwell and particularly St. Brides Island are re-considered based on faunal comparisons, geological relationships, and palynological findings. The dating and palaeoenvironment of the fissure fishes, reptiles and mammaliamorphs reveal a coherent picture of a vertebrate biota that inhabited the karst at or near the marine margins of small islands around the Triassic–Jurassic boundary.

Fig. 4. Late Triassic–Pliensbachian fissure localities in the Bristol area and in South Wales. A simplified Rhaeto-Liassic geography of the palaeo-archipelago. Light grey is the region of sauropsid fissures and dark grey that of the principal mammaliamorph localities. Note proximity of Emborough to dark area. Upper left inset is a close up of the quarries in the St. Brides area, from Evans and Kermack (1994), and lower left inset shows the position of the localities within the UK. Modified from Whiteside and Marshall (2008) and Klein *et al*. (2015).

THE LOCALITIES

The main sauropsid localities (Fig. 4) with a diverse fauna are situated in South Wales at Pant-y-ffynnon and Ruthin and also to the north of Bristol at Durdham Down, Tytherington, and Cromhall, the last of which has the most recorded genera. Other sauropsid sites are Woodleaze (near Tytherington), Emborough, and Batscombe, which are in the Mendip Hills to the east and south of Bristol. Twyn-yr-Odyn, near Cardiff, has only been recorded as yielding fishes (Howgate 1976), but is considered here as a sauropsid-type fissure locality from its palaeogeography and the fact that fishes from similar fissure fills have been found in Cromhall and Tytherington.

Mammaliamorph-bearing fissure fills are found in the neptunian dykes at Holwell and Windsor Hill in the Mendip Hills, but the main finds derive from the quarries of Ewenny, Pontalun (currently known as Lithalun) and Pant, north of St. Brides Major in South Wales (Fig. 4). All the fissures are found within the Carboniferous Limestone of the region, and their locations are given in Table 1.

GEOLOGY

The vertebrate-bearing fissures of the Bristol region and in South Wales are emplaced in Carboniferous Limestone of Early Carboniferous (Mississippian) age. The fissures follow vertical joints and fractures

Table 1. List of key fissure localities around Bristol, and in South Wales, with UK grid references. Information is from Fraser (1994) and current analysis.

	Locality	UK grid reference
Bristol region	Cromhall	ST 704 916
	Tytherington	ST 660 890
	Woodleaze	ST657 885
	Durdham Down	ST573 747
	Emborough	ST 623 505
	Batscombe	ST 460 550
	Windsor Hill	ST 615 452
	Holwell	ST 727 452
South Wales	Twyn-yr-Odyn	ST 116 738
	Pant-y-ffynnon	ST 046 743
	Ruthin	SS 975 796
St. Brides palaeo-island quarries	Cnap Twt	SS 911 753
	Duchy	SS 906 757
	Ewenny	SS 902 768
	Pontalun	SS 895 765
	Pant	SS 893 760

developed in the limestones, particularly of the Black Rock Limestone Subgroup and/or Gully Oolite Formation (*e.g.*, Cromhall, Tytherington, Pant-y-ffynnon, St. Brides quarries, Woodleaze and Windsor Hill). Other localities show fissures in the Clifton Down Limestone Formation, including Durdham Down (Foffa *et al.* 2014) and Holwell (Savage 1977), the Hunts Bay Oolite Group (*e.g.*, Ruthin), younger sections of the Pembroke Limestone Group (High Tor Limestone; western side of Pant and Pontalun quarries) and the Hotwells Limestone (now termed the Oxwich Head Limestone Formation), as at Emborough (Savage 1977). The nature of these different Carboniferous Limestone formations probably constrains the morphology of the fissures, and it may be that the types of caverns observed at Cromhall (Fig. 5A) and Tytherington, for example, reflect the material properties of the massive Black Rock Limestone.

Where documented, the fissure systems generally trend W-E or NW-SE, but few fissure systems have been observed as the quarry face is progressively worked. As an exception, Robinson (1957) depicted a fissure at Cromhall quarry with a N-S orientation. Whiteside and Marshall (2008, fig. 9) described the change in cross section of the NW-SE trending fissure 2 at Tytherington quarry, and they noted that other Tytherington reptile-bearing fissures were oriented W-E. Moore (1867) recorded the fissures at Holwell as trending W-E, and Savage and Waldman (1966) reported WNW-ESE directions for fissure fills left standing after quarrying. Savage (1977) also recorded the Windsor Hill fissure as trending W-E. Kermack *et al.* (1973) reported that the fissures in Duchy and St. Brides Pant 2 were W-E whilst PGG has observed that the fissures in Ewenny, St. Brides Pant 4 and 5, and Pontalun also lie W-E. The W-E and NW-SE trends of these fissures accord with the same trends of fractures reported by Wall and Jenkyns (2004) and Woodcock *et al.* (2014) for the main Late Triassic dilatational openings and infillings. Extension of the fractures and sediment fill probably continued until at "least the early Cretaceous" (Woodcock *et al.* 2014).

Some of the fissures, particularly those at Holwell and Windsor Hill, are regarded as neptunian dykes which are near-vertically sided, tectonically generated openings under a marine but near-shore environment and contain significant proportions of aquatic as well as terrestrial fauna.

Although there were clearly tectonic influences in the opening and widening of fractures in the Carboniferous Limestone, the host limestone often has matching bedding planes crossing the fissures, showing that there was no vertical movement on either side (see *e.g.*, Whiteside and Marshall 2008, fig. 8c). Many of the fissures have solutional features that were developed sub-aerially or in phreatic (below the water table) conditions below the limestone surface. Fluting or cusps have been recorded on the limestone walls of the fissures at Pant, Pontalun (Kermack *et al.* 1973), Cromhall (Walkden and Fraser 1993), and Tytherington (Whiteside 1983; Whiteside and Marshall 2008). Karstic features such as dolines, swallets or swallow holes have been described from Tytherington (Whiteside and Marshall 2008) and Emborough (Savage 1977), and a pipe that led to an infilled cavern can be seen in an old photograph of the Cromhall deposit (Fig. 5A). There is phreatic cavern development at Tytherington (Whiteside and Marshall 2008), Woodleaze (Klein *et al.* 2015), Pant-y-ffynnon and on St. Brides palaeo-island at Cnap Twt (Harris 1957), and Ewenny (Kermack *et al.* 1973).
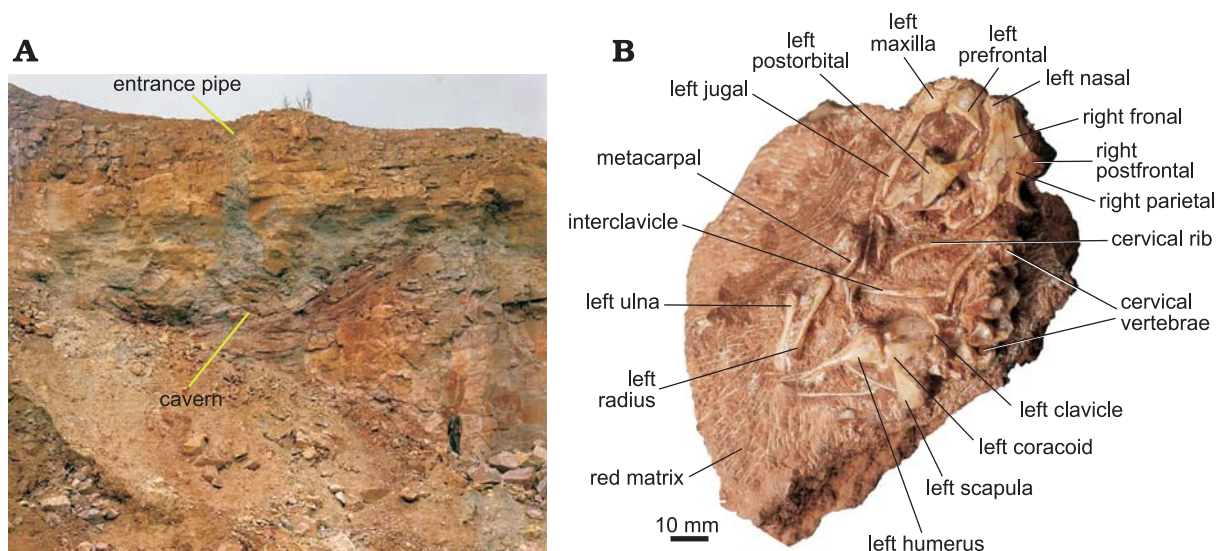
Fig. 5. Cromhall and its reptile fossils. **A**. Cromhall quarry fissure showing cavern development; note the upper green layers and the lower red beds. Both types of lithology have yielded terrestrial reptile bones. Note also the entrance pipe from the Carboniferous Limestone surface that is 3–4 m above the infilled cavern, The cavern extends on both the left and right sides; on the right-hand side the upper boundary of the cavern is about 2.5 m below the limestone surface. Photograph taken by C.A.F. Friend on 1/1/1965, from GeoScenic images, BGS archive. **B**. *Clevosaurus hudsoni* from Cromhall. This specimen (NHMUK PV R36832) in hard red marl has a skull that is dissociating into individual bones and the anterior skeleton consisting of cervical vertebrae, cervical ribs, pectoral girdle bones and parts of the left forearm. These articulated skeletons are rare but it is clear that this type of dissociation *in situ*, probably by bacterial action in subaqueous conditions, would produce great numbers of individual bones. The numerous bones may then be transported only short distances resulting in the jumbled conglomerations of disaggregated elements more typical of fissure deposits.

Whiteside and Marshall (2008) demonstrated that the Tytherington caverns or conduits were more plausibly formed in the fresh/saline water-mixing zone of freshwater lenses on small limestone palaeo-islands, rather than from flowing groundwaters dissolving limestone, as suggested by Simms and Ruffell (1990).

Fissure shapes and characteristics vary. Robinson (1957) described the Triassic reptile-dominated fissures as "underground water-course[s]", whereas Robinson (1971) and Kermack *et al.* (1973) identified the fissures of St. Brides palaeo-island as having a deep, narrow, "slot" morphology. However, these age-morphology distinctions are not clear-cut, as there are slot fissures at Cromhall (Walkden and Fraser 1993) and fissure 12 at Tytherington is a palaeo-doline (Whiteside and Marshall 2008), which looks slot-like in the exposure.

The sedimentary infills of the fissures comprise a great range of carbonate lithologies, including breccias, conglomerates, red, yellow and green marls, recrystallised limestones, and black and grey shales and siltstones, as well as calcareous sandstones. Dolomitised limestone breccias and/or limonitic deposits containing bones are found at Tytherington, Durdham Down and Pant-y-ffynnon; dolomitised limestone is recorded in the fissures at Cromhall (Fraser 1994), and pockets of ochre are also recorded from the near vicinity of the Emborough fissure (Robinson 1957; Savage 1977). The large-clast breccias that contain the bones of *Thecodontosaurus* at Tytherington and Durdham Down include dolomitised and ochreous rocks, and dolomite metasomatism of the host limestone may have played a part in the collapse of the breccia into a cavern. The low pyrite content found inside the *Thecodontosaurus* bones by Wings (2004), and the fact that the bones are frequently coloured white, suggests an aerated environment at deposition. The *Thecodontosaurus* breccias at Tytherington have therefore been interpreted as resulting from final gravitational collapse caused by oxygenated meteoric waters flowing around the loosened roof rocks into caverns developed at the edge of a freshwater lens (Whiteside and Marshall 2008). The breccias contain a wide range of tetrapod species and include bones of the largest and smallest terrestrial vertebrates known from the fissures (Van den Berg *et al.* 2012): *Diphydontosaurus* (0.1 m long) is found alongside *Thecodontosaurus* (approximately 2.0 m long).

Most of the fissure bones are disarticulated, suggesting considerable transport, although articulated complete and/or partial skeletons have been found at Cromhall (Fig. 5B), Emborough, Batscombe, Durdham Down, Twyn-yr-Odyn, and Pant-y-ffynnon. These articulated specimens occur in red or green marls, but there are exceptions, such as the articulated forearm of *Diphydontosaurus* in a conglomerate from Durdham Down (BRSMG Cb4715). There are associated bones of *Clevosaurus* from Woodleaze (Klein *et al.* 2015), a

very few co-ossified or sutured bones of *Oligokyphus* from Windsor Hill (Kühne 1956), a partial skull with articulated lower jaws of *Morganucodon* from Pontalun (Parrington 1978), and a *Morganucodon* articular complex from Ewenny (Kermack *et al.* 1973), as well as occasional associated elements from Tytherington, and of *Gephyrosaurus* (a coronoid and dentary; Evans 1980) from St. Brides quarries. However, partially articulated or complete skeletons are very rare or absent from the St. Brides quarries, Tytherington, Ruthin, Windsor Hill and Holwell.

The size ranges of bones also suggest transport, with for example bones from Tytherington similar in size to the reworked Carboniferous Limestone clasts, and presumably possessing similar hydrodynamic properties. On the other hand, other localities yield mixtures of small bones and teeth of larger animals and larger bones of small reptiles. In some small-clast conglomerates, the bones can be well preserved, with fine details intact, such as the rock that yielded *Diphydontosaurus* at Tytherington (Whiteside 1986). Similarly exquisite white-coloured fossils of *Planocephalosaurus* (Fraser 1982) from Cromhall are found in recrystallised limestones containing remanié fossils such as crinoid ossicles and chondrichthyan teeth derived from the Carboniferous Limestone; recrystallised limestones also preserve bones of *Clevosaurus* and *Diphydontosaurus* in fissure 8 at Tytherington.

Red and yellow marly clays yielded most of the isolated bones and teeth collected from Holwell by Moore (1867), and some of the St. Brides fossil material derives from soft red, yellow, green and grey clays as well as harder marls. Many of the red marls from the St. Brides fissures contain abundant haematitic ooids or pisoliths (Kermack *et al.* 1973; Gill *et al.* 2006). Dark grey and black siltstones yielded palynomorphs with terrestrial and marine vertebrates at Tytherington to Whiteside and Marshall (2008) who additionally found palynomorphs in finely laminated greyish limestones at the same locality. Dark grey shales at Cnap Twt and other quarries on St. Brides palaeo-island also contain palynomorphs (Harris 1957; Lewarne and Pallot 1957).

The tetrapod bones in red matrix are generally preserved in light colours such as white or yellow, whereas bones in green and yellow rocks can be coloured from white to brown or black. Bones in black rocks are often black, but fragments can be white and those in a grey matrix range from white to black.

THE FAUNAS

As noted, the standard assumption, proposed by Robinson (1957, 1971) and Shubin and Sues (1991), is that the faunas from the fissures can be separated into two groups: (1) a biota dominated by terrestrial reptile genera and, with the exception of Emborough where Fraser *et al.* (1985) recorded two *Kuehneotherium* teeth, no mammaliamorphs; and (2) a terrestrial tetrapod biota that includes a significant proportion of mammaliamorphs.

The pattern, however, is more complex (Table 2). In the group 1, "sauropsid" fissures, there are, in addition to the reptiles, non-marine fishes of either *Pholidophorus* or *Legnonotus* type in the fissures at Cromhall and Tytherington, and in great numbers at Twyn-yr-Odyn (Howgate 1976), from which no tetrapods have been reported. Teeth of Rhaetian marine fishes have also been found with the reptiles in the Cromhall "slot fissures" and the capping sequence over these (Fraser 1994; Whiteside and Marshall 2008), Tytherington (Whiteside 1983; Whiteside and Marshall 2008), and Durdham Down (Foffa *et al.* 2014). Despite extensive work at the site, Robinson (1957) did not report fish fossils at Cromhall, a key example of a "sauropsid" fissure locality, but she may have missed them because many of the coeval fish teeth are recovered only by sieving the acid-digested sediment through very fine mesh sizes (*e.g.*, Van den Berg *et al.* 2012; Foffa *et al.* 2014). In more recent studies, actinopterygian elements, comprising *Gyrolepis* scales and aff. *Gyrolepis* teeth (Fig. 2K), were found by Mike Curtis at Cromhall (site 4 of Fraser 1994) in rock that contained *Planocephalosaurus* (Whiteside and Marshall 2008; BRSMG CC 6087). This finding contradicts the report of Behan *et al.* (2012) that all fish teeth found in the Cromhall terrestrial deposits were derived from the Carboniferous; those authors only considered chondrichthyan teeth and all are above 0.5 mm and mostly much larger, possibly indicating a sieving sample bias. The narrowest dimension of aff. *Gyrolepis* teeth is *c.* 0.4 mm or shorter, and reworked Carboniferous chondrichthyan fossils are widely recognised (*e.g.*, Whiteside 1983; Whiteside and Marshall 2008; Van den Berg *et al.* 2012), having a different preservation from the terrestrial reptiles and coeval fish fossils.

The group 2, "mammaliamorph" fissures deposits at Holwell, Windsor Hill and in the St. Brides quarries show a range of faunal compositions, from single species to richer faunas with a wide variety

Table 2. Summary of the key localities and faunal compositions, for Triassic and Jurassic ("St. Brides") fissure faunas. Holwell also has the aquatic reptiles *Pachystropheus* and *Psephoderma* and a number of marine fish genera not found in any other locality. Data based on Robinson (1957), Kermack *et al.* (1973), Howgate (1976), Evans and Kermack (1994), Fraser (1994), Säilä (2005), Edwards and Evans (2006), Gill *et al.* (2006), Whiteside and Marshall (2008), Van den Berg *et al.* (2012), Foffa *et al.* (2014), Dalla Vecchia and Cau (2015), and Klein *et al.* (2015), as well as personal observations by the authors and Fraser (personal communication). Abbreviations: C, Cromhall; Ty, Tytherington; D, Durdham Down; W, Woodleaze; P, Pant-y-ffyn-non; R, Ruthin; E, Emborough; B, Batscombe; T, Twyn-yr-Odyn; H, Holwell; M, St. Brides *Morganucodon* fauna; MS, St. Brides *Morganucodon*-sphenodont fauna; Wh, Windsor Hill; ×, taxon present, ?, taxon possibly present; blank, absent or no data. *Lissodus* can also be euryhaline.

	Taxon quarry	Sauropsid type fissures										Mammaliamorph type fissures		
		C	Ty	D	W	P	R	E	B	T	H	M	MS	Wh
Terrestrial reptiles	*Gephyrosaurus*											×	×	
	Clevosaurus convallis												×	
	Clevosaurus hudsoni/minor/sectumsemper	×	×	×	×	×	?	×			×			
	Diphydontosaurus	×	×	×	×	×	×				×			
	Planocephalosaurus	×	×	?			×							
	Pelecymala	×	×											
	Sigmala	×	×											
	other/unidentified lepidosaurs		×		?						×		×	
	kuehneosaur	×				×	?	×	×					
	Thecodontosaurus/Pantydraco		×	×		×	×				×			
	coelophysoid/"theropod"	×	×	×		×							×	
	sphenosuchiid/aff. *Terrestrisuchus*	×	×			×	×						×	
	"thecodont"/suchian/scleromochlid/*Agnosphitys*	×	×			×	×							
	"*Palaeosaurus*"/phytosaur aff. *Nicrosaurus*/*Angistorhinopsis*		×	×							×			
	aetosaur	×												
	drepanosaur	×	×											
	pterosaur	?	?									×	×	
	Tricuspisaurus/aff. *Tricuspisaurus*	×	×				×	×						
	procolophonid	×					×							
Cynodont	*Oligokyphus*												×	×
	other tritylodont										×			
	Pseudotriconodon										×			
Mammalia-formes	*Morganucodon* and *Eozostrodon*										×	×	×	
	Kuehneotherium							×				×	×	
	Bridetherium and *Paceyodon*												×	
	haramiyid											×	×	
Non-marine fish	*Pholidophorus/Legnonotus/Semionotus*	×	×							×	×			
Marine fish	*Gyrolepis*	×	×								×			
	Severnichthys	×	×								×			×
	*Lissodus**	×	?	×							×			×
Fish unknown	unidentified osteichthyan teeth		×	×	×									
Coeval invertebrates	gastropods	?	×								×	×		
	Euestheria	×	×			×								
	terrestrial arthropods	×										×		
Remanié	reworked Carboniferous fossils	×	×	×	×							×	×	
Tetrapod assemblage comparisons	nos. of identified tetrapod genera/types	13	13	5	2	7	7	4	1	0	9	3	11	1
	% of fauna in common with Tytherington	77	100	100	100	86	86	50	0	0	44	0	18	0
	% in common with *Morganucodon*-sphenodont fauna	15	15	20	0	29	14	25	0	0	22	100	100	100

of small tetrapods. The deposits at Duchy, Ewenny, Pontalun and Pant fissures 1–3 have a relatively impoverished fauna (Fraser 1989), comprising the lepidosaur *Gephyrosaurus bridensis* (60% of the fossils, Evans and Kermack 1994), together with *Morganucodon watsoni* and to a lesser extent, and not present at Ewenny, *Kuehneotherium praecursoris* (see Kermack *et al.* 1968). Yet, there are several species of both *Kuehneotherium* and *Morganucodon* in the St. Brides fissures (PGG, personal observation), and any one fissure usually has a single species of either genus, possibly representing time differences between the fissures. Furthermore, Pant fissures discovered later, including Pant 4 and 5, have a more diverse biota, including *Gephyrosaurus*, *Kuehneotherium* and *Morganucodon*, but also possible pterosaurs as well as sphenodontians, sphenosuchian crocodylomorphs, theropods, tritylodonts and haramiyids (Evans and Kermack 1994; Gill *et al.* 2006). Bones and teeth of *Clevosaurus convallis* constitute 65–70% of the tetrapod fossils (Säilä 2005; Gill *et al.* 2006) and there is also a greater diversity of morganucodontans in these Pant deposits, including *Bridetherium* and a large form known from one tooth, *Paceyodon* (Clemens 2011). These slot fissures and their tetrapods were termed the "*Hirmeriella* association" by Kermack *et al.* (1973), based on the relative abundance of the conifer *Hirmeriella*, but they are better described as two distinct biotas, the "*Morganucodon*" and *Morganucodon*-sphenodont" faunas of Gill *et al.* (2006), as both are found with *Hirmeriella*, being abundant in dark clay at Pant 5 and occasionally in red sediments of Pant 4.

Tritylodonts also occur at Windsor Hill, where *Oligokyphus* is represented by more than 2000 bones (Kühne 1956), and at Holwell, represented by a single partial right maxilla (Savage and Waldman 1966; Savage 1971) whose affinities are not yet established. Tritylodonts therefore had a more restricted occurrence than mammaliaforms in the fissures. Holwell and Windsor Hill are neptunian dyke fissures and also include numerous fish teeth and marine invertebrates. Therefore these fissures starkly contrast with the St. Brides mammaliamorph-bearing fissures where no fishes have been reported and the invertebrate fauna is restricted to the gastropod "*Natica*" (= *Naticopsina*) *oppelii* (Kermack *et al.* 1973). However the beetle *Metacupes harrisi* has been recorded (Gardiner 1961) with lepidosaurs at Cnap Twt.

In contrast to the neptunian dyke fissures, contemporaneous invertebrates are rare at the other localities. Most commonly found is the predominantly freshwater branchiopod crustacean *Euestheria*, which is known from Cromhall, Tytherington, and Pant-y-ffynnon (Robinson 1957; Whiteside 1983; Whiteside and Marshall 2008) but has been given little attention. A millipede from Cromhall was depicted by Fraser (1988b) and annelids from that locality noted by Walkden and Fraser (1993). Robinson (1957) remarked on the absence of marine invertebrates in the sauropsid fissures. However, gastropod steinkerns, resembling *Hydrobia*-type specimens from Westbury Formation littoral deposits, were reported in the Tytherington deposits, particularly fissure 2, together with other marine and terrestrial components (Whiteside and Marshall 2008).

The faunal composition of each fissure at a particular locality often varies considerably. At Cromhall, Fraser (1994) showed that *Diphydontosaurus* is ubiquitous at the eight sites, but *Planocephalosaurus* and *Clevosaurus hudsoni* do not occur together in any deposit. Further, at *Planocephalosaurus* sites there is a greater overall diversity of tetrapods, and genus *Clevosaurus* is represented by a different species, *C. minor*. Whiteside and Marshall (2008) and Klein *et al.* (2015) also noted that deposits containing abundant *Planocephalosaurus* fossils at Tytherington are indicative of a diverse tetrapod biota. Unfortunately, similar faunal lists at particular sites in other sauropsid localities do not exist. There is evidence that a high proportion of *Gephyrosaurus* in the slot fissures is associated with a low overall diversity of tetrapods, from the description of the St. Brides faunas by Gill *et al.* (2006).

Some fissure localities are so dominated by one tetrapod that they are either monospecific or nearly so. The putatively gliding genera *Kuehneosaurus* and *Kuehneosuchus* predominate, respectively, at Emborough and Batscombe. At Windsor Hill, only *Oligokyphus* has been reported, despite the recovery of about 2000 bones (Evans and Kermack 1994), and at the more recently discovered locality of Woodleaze quarry, nearly all specimens are attributable to a single species, *Clevosaurus sectumsemper* (see Klein *et al.* 2015). It is likely that at least some of the lack of diversity is a result of the small land area available on tiny palaeo-islands (*e.g.*, Kühne 1956).

The notion that the tetrapods lived on islands is vital when considering differences between localities. Although the earliest faunas presumably arose from species that lived in the same area before the Rhaetian transgression, these would have become isolated on emergent islands, and would have evolved their own unique species with time, a pattern that in turn would have been complicated by repeated pulses of sea level rise and fall through the Rhaetian (*e.g.*, Hamilton 1962). Floras on these islands may have been richer than in the preceding Norian arid, sabkha environments thanks to the freshwater lens on these islands postulated

in the model of Whiteside and Robinson (1983) and Whiteside and Marshall (2008). Moreover, although it is likely that the fissures, which presumably represented natural pitfall traps, give a representative sample of the vertebrates living on the limestone surface (Fraser and Walkden 1983; Whiteside 1983), they may have received remains from only a small local area. Whiteside and Marshall (2008) and Klein *et al.* (2015) have suggested that there may be a relationship between the regional differences (*e.g.*, sandstone versus limestone surfaces) on an island and the fauna recovered in the fissures. These differences are hard to differentiate from the expected changes in the faunal composition even over just a few thousand years. Nevertheless it is likely that contemporaneous islands nearest to each other should have had a greater similarity in faunal composition than those further away, in both time and space.

Several biogeographic and temporal associations may be seen among the fissures. For example, Woodleaze and Durdham Down are most similar to Tytherington (Table 2). However Pant-y-ffynnon, Ruthin, and Cromhall all have over 75% and Emborough about 50%, of their tetrapods in common with Tytherington. Batscombe has a recorded *Kuehneosuchus* biota only, a reptile not yet found at Tytherington, although kuehneosaurs are present at Cromhall and Pant-y-ffynnon, as well as Emborough, suggesting that they are part of the same association. In the mammaliamorph-bearing localities, Windsor Hill and the "*Morganucodon*" biota have their limited genera in common with the much more diverse "*Morganucodon*-sphenodont" fauna. Holwell has genera such as *Thecodontosaurus* and *Diphydontosaurus* shared with the Tytherington group but also haramiyids and a morganucodontid, otherwise only jointly present in the "*Morganucodon*-sphenodont" biota of St. Brides. Twyn-yr-Odyn has the fish *Legnonotus*, a taxon not recorded elsewhere in the fissures, but may be closest to the Tytherington group or Cromhall, which includes significant deposits containing actinopterygians such as *Pholidophorus* with abundant terrestrial reptiles fossils. The repeated finding of the associated remains of actinopterygian fossils in terrestrial deposits indicates that the fishes are non-marine. Howgate (1976) regarded the Twyn-yr-Odyn *Legnonotus* as either a fresh- or brackish-water species based on his reconstruction of the enclosing fissure as a cavern collapse.

There are other possible associations between genera, such as the presence of *Diphydontosaurus* and *Clevosaurus* with *Thecodontosaurus* (or the closely related *Pantydraco*) at Durdham Down (Foffa *et al.* 2014), Tytherington fissure 2 (Van den Berg *et al.* 2012) and Pant-y-ffynnon (DIW, personal observation). It is also notable that Tytherington fissure 14 is faunally very similar to the Cromhall deposits (Whiteside 1983; Whiteside and Marshall 2008), as *Planocephalosaurus* is found in high proportions, and *Sigmala, Pelecymala* and *Tricuspisaurus* are present at both localities, yet both seem to lack *Thecodontosaurus* (N.C. Fraser, personal communication about Cromhall). *Diphydontosaurus, Clevosaurus* (Fraser 1994), and *Thecodontosaurus* (Moore 1881) are also all recorded from fissure deposits at Holwell, but it is not known if they are from the same fissure site.

DATING THE FISSURES

BACKGROUND

Assigning a date to the fissure faunas has proved problematic. Put simply, the fissure fill at any locality has to be younger than the host Carboniferous Limestone but older than any capping strata. A wide range of dates has been suggested for the fissures (Fig. 6). Robinson (1957), aiming to date the sauropsid fissures, described field relationships around the Emborough fissure, and projected beds of the nearest "Rhaetic", suggesting that they would have covered the deposit. Whiteside and Marshall (2008) gave counter-arguments and noted that the mapping model failed to demonstrate that the fissure deposit was demonstrably below the base of the Penarth Group and was more likely to date from after the onset of the transgression.

Dating the neptunian dyke fissures has also proved problematic, although embedded marine fossils enable a direct comparison with normal bedded sequences. Moore (1867) dated the Holwell "*Microlestes*" quarry, which yielded teeth of the haramiyid *Thomasia moorei*, as "Rhaetic" based on the associated marine fauna, but Kühne (1947) emphasised the lack of precision in this dating as the invertebrate faunal list published by Moore (1867) included fossils from several different fissures at Holwell, plus material from other localities such as the nearby Marston Road Quarry, which exposed unequivocal bedded Rhaetian (Westbury Formation) deposits (Nordén *et al.* 2015).

	Mid-Triassic	Late Triassic			Early Jurassic			Mid Jurassic
		Carnian Norian	E. Rhaetian	L. Rhaetian	Hettangian	Sinemurian	Pliensbachian Toarcian	

Cromhall
Tytherington
Durdham Down
Pant-y-ffynnon
Ruthin
Emborough
Holwell "*Microlestes*" fissure
Holwell, other fissures and Windsor Hill
St. Brides island
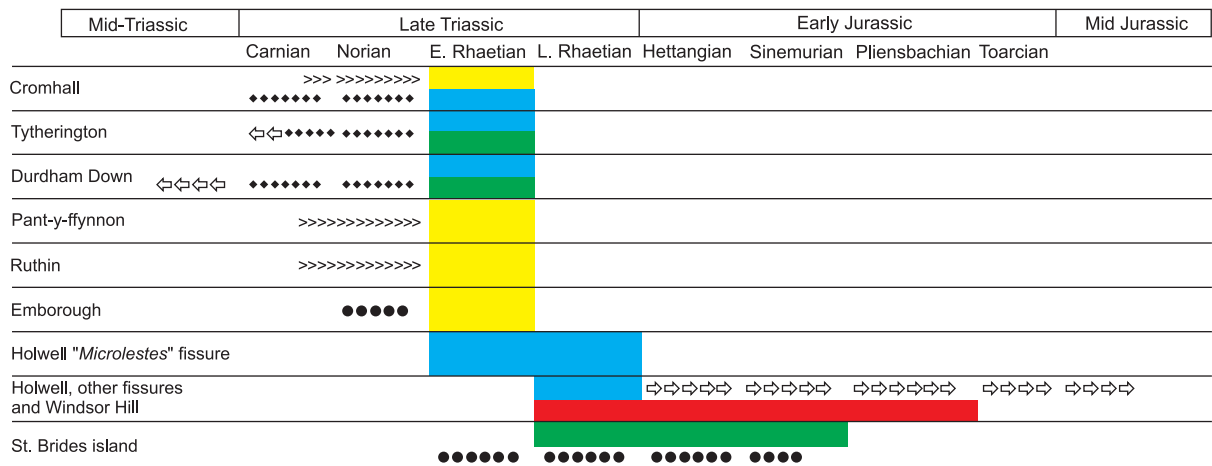
KEY for main evidence

From palynological dating: St. Brides (Kermack *et al.* 1973), Tytherington (Marshall and Whiteside 1980; Whiteside 1983),Tytherington and Durdham Down (Whiteside and Marshall 2008)

From associated marine fish: Holwell (Moore 1867), Tytherington (Whiteside 1983; Whiteside and Marshall 2008; Van den Berg *et al.* 2012), Cromhall (Fraser 1994), Durdham Down (Foffa *et al.* 2014)

From associated marine invertebrates: Holwell (Moore 1867), Windsor Hill (Kühne 1956)

From close similarity of terrestrial faunal assemblages: various (Whiteside 1983, 1986; Whiteside and Marshall 2008)

>>>>>>> From suggested lithological similarities to nearby horizontal beds: various (Robinson 1957), Cromhall (Halstead and Nicoll 1971; Fraser and Walkden 1983)

●●●●● From geological map and palaeogeographical reconstructions: Robinson (1957, 1971).

◆◆◆◆◆◆ From other suggested comparisons, *e.g.*, faunal, sedimentological, and geomorphological: Durdham Down (Moore 1881), various (Benton and Spencer 1995), Tytherington (Simms and Ruffell 1990), Cromhall (Walkden and Fraser 1993), various (Simms *et al.* 1994)

⇦⇦⇨⇨ Possible range from some authors, *e.g.*, Durdham Down (Moore 1881), Holwell (Kühne 1947; Savage and Waldman 1966), Windsor Hill (Savage 1977), Tytherington (Simms *et al.* 1994)

Fig. 6. Suggested dating of the fissures showing different approaches and conclusions by various authors. The principal historical means of dating the fissures is using faunal comparisons, palaeogeographical reconstructions and presumed lithological similarities with normally bedded strata in the UK. Comparisons with global faunas have also been used since the time of Charles Moore. Palynological evidence has been used to give an age assignment for St. Brides fissures initially by Harris (1957) and Lewarne and Pallott (1957), and in a precedent for sauropsid fissures by Marshall and Whiteside (1980).

Although not recording any invertebrate remains from the "*Microlestes*" fissure, it is clear from Moore's earlier papers (Moore 1859a, b, 1861, 1863) that the three tons of "coarse friable sand" which he had collected from a single fissure and had removed by horse and cart from the quarry to sort at his home in Bath yielded not only *Thomasia*, but the full complement of marine and terrestrial faunal components discussed below for the fissure. The composition of the broader vertebrate fauna of the Holwell "*Microlestes*" fissure thus fully supports a Rhaetian age. Likewise the fauna of Marston Road Quarry includes all the typical Westbury Formation fishes and reptiles (including *Pachystropheus* and a placodont), as well as a small lepidosaur, probably a sphenodontian, a terrestrial wash-in (Nordén *et al.* 2015). Kühne (1947) made a further collection of haramiyid teeth at Holwell and assigned these to the "Rhaetic" based on the associated marine fishes. Kühne (1956) examined the range of marine invertebrates and vertebrate fossils in the Windsor Hill neptunian dyke fissure and determined that the deposit, containing *Oligokyphus*, could be assigned a Pliensbachian age based on the youngest invertebrates such as the belemnite *Pseudohastites* and the brachiopod *Squamirhynchia* (= *Cirpo*) *fronto*. Savage (1977) counter-argued for a younger "Inferior Oolite" (Aalenian–Bathonian) age, as he interpreted the fissure as a swallet that filled subaerially with reworked "Lias" sediments along with contemporaneous mammaliamorph bones.

Although Robinson (1957) discounted Durdham Down as an "underground water-course" fissure, later authors (*e.g.*, Halstead and Nicoll 1971; Whiteside 1983) recognised that the deposit was a fill in a cavern. Moore (1867) claimed that the *Thecodontosaurus* fossils from Durdham Down were "Rhaetic" based on his recognition of similar dinosaur teeth from Holwell and the nearby presence of bone-bed fossils, but later (Moore 1881), suggested that the teeth were older and of "Keuper" age. Foffa *et al.* (2014) reported a few marine fish teeth, considered the palaeogeography, and confirmed Moore's original suggestion of a Rhaetian date. In fact, Holwell and the associated Marston Road site provide unique insights into mixing of terrestrial vertebrates and Rhaetian marine fossils.

HOLWELL

The fauna from the fissure in Moore's "*Microlestes*" Quarry at Holwell is unique in that the terrestrial tetrapod remains (mammaliamorphs, *Thecodontosaurus*, *Diphydontosaurus* and *Clevosaurus*) are far outnumbered by specimens of aquatic reptiles and fishes (see Fig. 2 for examples). Amongst the latter, teeth of *Rhomphaiodon* (*Hybodus*) *minor* have been reported from Ladinian to Rhaetian rocks (see discussion in Duffin and Delsate 1993), although the pre-Rhaetian records are unverified. It is a common taxon in the marine Rhaetian throughout northwest Europe and is well known from the classic basal Rhaetian bone bed and other Westbury Formation deposits of Aust, Westbury Garden Cliff, and Barnstone, for example (Sykes *et al.* 1970). Moore claimed to have up to 50,000 teeth of *Lissodus minimus*, formerly assigned to *Acrodus* (Duffin 1985, 2001; Fischer 2008) from Holwell; *Lissodus* is a long-ranging euryhaline genus, although *L. minimus*, like *R. minor*, is recorded from Ladinian to Rhaetian deposits. Once again, these records require verification, but in the British area, *L. minimus* is an extremely common shark mostly confined to the Westbury Formation; for example it is recorded in abundance from the basal Westbury Formation with rarer occurrences in the top of the Westbury strata and basal Cotham Member, Lilstock Formation in Manor Farm Quarry (Allard *et al.* 2015). The preservation and time range of *Lissodus* fossils demonstrate that the fossils are coeval with the Westbury strata and not derived. The largest hybodont shark teeth from Holwell belong to *Hybodus cloacinus*, which are often highly abraded and fragmented components of Rhaetian Bone Bed faunas; the species may range into the Sinemurian (Duffin 1993). *Palaeobates* is represented by a small number of teeth belonging to *P. reticulatus*, a taxon that is currently unique to the Holwell fauna (Duffin 1998a). Teeth originally ascribed to *Polyacrodus holwellensis* Duffin, 1998b have since been assigned to the monotypic genus *Duffinselache* (Andreev and Cuny 2012), which has been recorded from the Westbury Formation at several British localities (*e.g.*, Korneisel *et al.* 2015; Nordén *et al.* 2015) as well as equivalents in France and Belgium (Andreev and Cuny 2012). The taxonomic relations of *Pseudocetorhinus*, originally described from Holwell, but since recorded from the Rhaetian of Belgium, Luxembourg, and France (Delsate 1995, 2000; Cuny *et al.* 2000), are the subject of some discussion (Cappetta 2012), but the thorn-like teeth and possible associated gill rakers were originally described as belonging to a filter-feeding neoselachian shark (Duffin 1998a). The neoselachian sharks are further represented at Holwell by teeth, fin spines and probable scales of *Synechodus rhaeticus* which, although not common in the Rhaetian fauna, has been recorded from the Westbury Formation and other Rhaetian deposits in continental Europe (Duffin 1982, 1998b; Cuny *et al.* 2000; Korneisel *et al.* 2015; Nordén *et al.* 2015). The chondrichthyan complement of the fauna is completed by the crushing toothplates of the myriacanthid holocephalan *Agkistracanthus mitgelensis*, which has also been recorded from the Cotham Member of the Lilstock Formation at St. Audries Bay, as well as from the Rhaetian and Hettangian of Switzerland and Austria (Duffin and Furrer 1981).

Bony fishes are represented at Holwell by a series of genera that are all typical of the bedded marine deposits of the British Penarth Group — *Gyrolepis albertii*, *Severnichthys acuminata*, and *Sargodon tomicus*. Although the last has also been reported from the Ladinian and Carnian of Germany and the Norian of Italy (see discussion in Duffin and Delsate 1993), the fish specimens in Moore's collection from Holwell all testify to a Rhaetian age (Duffin 1999) for the deposit.

Amongst the reptile remains from Holwell, vertebrae of the putative choristodere or thalattosaur *Pachystropheus rhaeticus* are also well known from the British marine Rhaetian, especially from Blue Anchor, Aust, and Westbury Garden Cliff (Storrs and Gower 1993; Storrs 1994; Renesto 2005), as well as from the Rhaetian of Gaisbrunnen and Olgahain in southern Germany (Huene 1933). Placodont reptiles, represented by teeth and osteoderms of *Psephoderma alpinum* Meyer, 1858 (originally described as *P. anglicum* Meyer, 1867), although poorly represented in marine deposits outside the area of the Mendips (Storrs 1994), have been recorded from the nearby Rhaetian section at Marston Road (Nordén *et al.* 2015).

Moore described collecting material from a number of fissures at Holwell, and it is true that his collection, now housed in the BATGM, does not discriminate between the specimens obtained from different fissures. His faunal lists for the "*Microlestes*" fissure (Moore 1859a, b, 1861, 1863), which clearly formed numerically the greatest part of his collection and involved a huge investment of time and effort to obtain, indicate beyond reasonable doubt that *Thomasia, Thecodontosaurus, Pachystropheus, Psephoderma*, lepidosaurs and the wide range of Rhaetian fishes discussed above were all obtained from the same fissure infill.

It has been suggested that all the bones in the Rhaetian basal bonebed of the Westbury Formation might be derived from older horizons (Martill 1999). This cannot be demonstrated, however, by considering the strati-

graphic ranges elsewhere of bonebed taxa, which, as noted above, all range either below or above that horizon. Further, in a rare earth element (REE) study, Trueman and Benton (1997) showed that the provenance of bone and sediment could be compared; sites with heavily abraded, massive bone lumps, such as Aust Cliff, showed differentiation of bones and source sediments, and hence evidence that each had been derived from separate sources, whereas sites such as Westbury Garden Cliff, where the fish and reptile bones and teeth are small and show no signs of physical abrasion, also show perfect matching of REE signatures between fossils and sediment, hence indicating derivation of both from the same source. Further, the widespread occurrence of such bone beds across Europe at the base of the Rhaetian, all containing the same fauna, makes it hard to understand how older bone-bearing horizons could have been reworked uniformly over such a wide area and leave no remnant of the original horizon(s). More likely the bones and teeth came from fishes and reptiles that were parts of the contemporaneous fauna, and the energy of the transgressive movements of water and sediments churned and winnowed the phosphatic components on the seabed. Contemporaneity of erosion and bonebed deposition at the base of the Westbury Formation is confirmed by *Thalassinoides* burrows formed by callianassid shrimps extending into the top of the underlying Blue Anchor Formation, and infilled with basal Rhaetian bonebed that accompanied the influx of waters as the first act of the Rhaetian transgression (Korneisel *et al.* 2015).

DATING BY PALYNOLOGY

Establishing the ages of the fissure faunas has been controversial, but we propose two approaches that can be applied in a reasonably objective manner: palynology and mapping-scale topographic comparison. Both methods point to the somewhat radical suggestion that all the "sauropsid", green, yellow or red-bed fissures are Rhaetian, and most of the mammaliamorph-bearing fissures are younger, of Hettangian–Sinemurian age.

The first precise age assignment for a sauropsid fissure deposit was made by Marshall and Whiteside (1980), who recovered an assemblage of early Rhaetian palynomorphs and marine phytoplankton associated with *Thecodontosaurus* and *Clevosaurus* bones in fissure 2 at Tytherington. Further palynomorph assemblages were discovered at ten sites in six fissures at Tytherington, and one fissure near the Clifton Suspension Bridge by Whiteside and Marshall (2008). They were able to compare the palynological assemblages at Tytherington with the normally bedded Penarth Group sequence lying unconformably on Carboniferous Limestone at nearby Hampstead Farm Quarry, Chipping Sodbury. These assemblages confirmed the age as early Rhaetian, equivalent to the Westbury Formation. Recent investigations on archival collection material have produced another productive palynological, assemblage from Tytherington. Importantly this is from dark-coloured mudstone clasts embedded in a matrix that also contains bones of *Thecodontosaurus*. The palynological assemblage (Table 3) is dominated by *Rhaetogonyaulax rhaetica* (but only rare *Cymatiosphaera*

Table 3. Palynological analysis of the fissure 2 breccia, bearing the principal *Thecodontosaurus* bones found in Tytherington quarry. Palynomorphs are distinguished into terrestrial and marine forms.

	Taxon	Count	Percentage
Terrestrial 71.7%	*Classopollis classoides*	35	16.0
	Ovalipollis pseudoalatus	35	16.0
	Ricciisporites tuberculatus	29	13.2
	simple spores	19	8.7
	indeterminate	12	5.5
	Vesicaspora fuscus	11	5.0
	Rhaetipollis germanicus	5	2.3
	Classopollis spp.	4	1.8
	Vitreisporites pallidus	4	1.8
	?*Krauselisporites reissingeri*	1	0.5
	apiculate spore	1	0.5
	Alisporites thomasii	1	0.5
Marine 28.3%	*Rhaetogonyaulax rhaetica*	58	26.5
	Dapcodinium priscum	2	0.9
	Cymatiosphaera polypartita	1	0.5
	indeterminate cyst	1	0.5
Total	16 taxa	219	100.2

polypartita), *Classopollis classoides*, *Ricciisporites tuberculatus*, *Ovalipollis pseudoalatus*, and *Vesicaspora fuscus*. The content of *Rhaetipollis germanicus* is low. The taxa and their relative proportions are similar to those from the normally bedded Rhaetian Penarth Group section at Hampstead Farm Quarry near Chipping Sodbury recorded by Whiteside and Marshall (2008), The Hampstead Farm Rhaetian strata are located on the same palaeo-island as the Tytherington fissure deposits, confirming the new palynological assemblage age as equivalent to the lower part of the Westbury Formation (lower and middle Bed 5 using the bed number in Whiteside and Marshall [2008], based on the work of Curtis and Curtis in Donovan *et al*. [1989]). The high relative abundance of *Ovalipollis pseudoalatus*, *Ricciisporites tuberculatus* and *Rhaetogonyaulax rhaetica* shown in Table 3 also agrees with this age assignment (*cf.* Whiteside and Marshall 2008, fig. 15). This new discovery of *Thecodontosaurus* with fragments of lower Westbury Formation provides unequivocal evidence for the Rhaetian age of this reptile and its associated fauna. The assemblage includes a mixture of terrestrial and marine palynomorphs demonstrating the marginal location of the deposit near the Rhaetian sea.

Unfortunately, despite extensive sampling, palynomorphs have not yet been found in the other major Triassic fissure fills, but comparisons of the vertebrate faunas have been used to extend the argument. Based on the tetrapod similarities of Tytherington to Cromhall, Durdham Down, Pant-y-ffynnon and Ruthin, Whiteside and Marshall (2008) concluded that those fissures were infilled during the Rhaetian. The new, distinctive clevosaur, *Clevosaurus sectumsemper* at Woodleaze (Fig. 2G) has similar features to a species from fissure 2 (Fig. 2H) at Tytherington (Klein *et al*. 2015) and Pant-y-ffynnon (DIW, personal observation), suggesting that the deposits are coeval. Whiteside and Marshall (1985, 2008) additionally suggest that the presence of *Kuehneotherium* at Emborough indicates a Rhaetian age for that deposit and the co-occurrence of abundant kuehneosaur fossils also indicates a Rhaetian date for Batscombe. Whiteside and Marshall (2008) argued that no tetrapod-bearing fissure has been dated as older than earliest Rhaetian, or in particular pre-transgression, and that has not been contradicted.

The dates of the younger, *Hirmeriella* faunas are founded on established palynological evidence. Macrophytic fossils of the conifer *Hirmeriella muensteri* had been collected at Cnap Twt (Harris 1957), and more were discovered in many other St. Brides quarries by the University College London team led by K.A. Kermack. *Hirmeriella muensteri* is found with the tetrapods in St. Brides fissure fills, particularly at Ewenny, and Kermack *et al*. (1973) referred to the overall assemblage as the "*Hirmeriella* association". Evans and Kermack (1994) noted that the plant and palynomorph evidence used to date the St. Brides fauna included *Hirmeriella*, and *H. muensteri* is also found in southern German Lower Lias beds equating to the *Thaumatopteris* Zone of East Greenland, southern Germany, Poland, and Sweden. They identified the significant presence (6%) of *Krauselisporites* (*Heliosporites*) at Cnap Twt, which related to the late or "latest" Rhaetian *Heliosporites* Zone of Orbell (1973) and probably extended into the early Hettangian. They also emphasized the absence in St. Brides deposits of *Ovalipollis*, *Rhaetipollis* and *Ricciisporites*, palynomorphs that are typical of the Penarth Group (mainly Rhaetian), but absent from the base of the Jurassic and higher units. These studies indicated to Evans and Kermack (1994) a latest Rhaetian or Early Jurassic date for the Cnap Twt deposit, a typical *Hirmeriella* locality. Robinson (1971) considered the Early Jurassic palaeogeography of the area and suggested that St. Brides island was finally submerged in the early Sinemurian; Evans and Kermack (1994) concurred, stating that "the *Hirmeriella* association cannot be younger than that". Some later authors (Gill 2004, in Clemens 2007) considered that the depauparate *Morganucodon* fauna, possibly extant at a time when the island was smallest, might be younger than the more diverse *Morganucodon*-sphenodont fauna.

These conclusions are generally confirmed by comparison with the geochronologically dated Newark Supergroup in eastern North America. There, the palynomorph assemblages document a "fern spike" at the top of the Triassic (latest Rhaetian; J. Whiteside *et al*. 2010), indicating significant ecological change (Fowell *et al*. 1994). Although the palynoflora below the fern spike is diverse, the overwhelmingly dominant palynomorph that follows is *Classopollis*, and the collapse in diversity is attributed to the ETE environmental crisis. Hounslow *et al*. (2004) report a high proportion of *Classopollis* just above the Langport Beds in the Wilmcote Limestone Member (formerly the Pre-planorbis Beds and Planorbis Beds; Rhaetian–Hettangian) of the Blue Lias Formation. In their reassessment of the palynomorphs from Ewenny quarry, Whiteside and Marshall (2009) noted the absence of any marine taxa, as seen in the older, Rhaetian, assemblages, and the remarkable dominance by *Classopollis*, comprising over 95% of all palynomorphs. *Classopollis* is the pollen of *Hirmeriella* and related cheirolepidacean conifers, and indicates a very monotonous conifer-dominated vegetation. They also noted that trilete spores are very rare, being represented by only two specimens, *Carnisporites megaspiniger* and *Krauselisporites reissingeri*, which range into the Early Jurassic.

Further work on the assemblage has confirmed the absence of typical UK Rhaetian palynomorphs including *Rhaetipollis germanicus* and *Ovalipollis pseudoalatus*; the last occurrence of these at St. Audries Bay (for location see Fig. 4) is at the top of the Cotham Member, Lilstock Formation (Hildebrandt *et al.* 2013) and therefore before the Triassic–Jurassic boundary. Warrington *et al.* (2008, fig. 14) also show the last appearance datums (LADs) of *Rhaetipollis germanicus* and *Ricciisporites tuberculatus* at just below their proposed Triassic–Jurassic boundary for the St. Audrie's-Doniford Bay section. The horizon with an abundance of *Classopollis* in the basal Wilmcote Limestone Member at St. Audries Bay that correlates with the GSSP base of the Jurassic System at Kuhjoch (Austria; shown by Hildebrandt *et al.* [2013, fig. 27]) indicates that it is at the base of the Hettangian. Our sample from Ewenny is nearly all *Classopollis classoides* (= *C. torosus*), as opposed to *C. meyeriana*, and it is perhaps noteworthy that this species has a similar dominance in the mid–upper *Planorbis* Zone, as shown by Warrington *et al.* (2008, fig. 10) at St. Audries Bay. Specifically, the St. Brides palynomorph assemblage therefore demonstrates equivalence to the basal Blue Lias Formation and a dating of at least early Hettangian for the *Morganucodon* fauna from Ewenny quarry.

DATING BY TOPOGRAPHY

The second approach to establishing the relative ages of the different vertebrate-bearing units is to explore their field relationships and topographic levels. We have considered the height of the host Carboniferous Limestone surface overlying the fissures, or where that is imprecisely known, or where there are many tetrapod-bearing fissures, the maximum height of the pre-quarrying Carboniferous Limestone within 50 m of the quarry. The height of the base of the nearest outcrops of the Penarth Group strata from the appropriate BGS digimap© is then compared and the difference plotted in a simple bar chart (Fig. 7). This approach produces a pattern which shows that, where specific palynological or coeval fish dating of the sauropsid fissures is known, the limestone surface at the entrance to the fissures stands at 2–9 m above the base of the Penarth Group.

There are reservations to this approach. For example the Carboniferous Limestone at the mouth of the fissures may have undergone some erosion since its exhumation from younger Mesozoic strata, reducing its height relative to the Penarth Group base. Also, the base of the Penarth Group may not be chronologically equivalent everywhere. Furthermore, we know that there were cycles of sea level rise and fall in the Rhaetian, indicated for example by cycles in the Westbury Formation, and therefore all fissures in one quarry need not be contemporaneous. However, even with these provisos, we suggest that there is a pattern that provides evidence to indicate, in general, the relative ages of the fissure localities. The rationale is that final infilling would have occurred as the rising Rhaetian sea lapped up around the top of the fissure. Caverns on the palaeo-islands presumably formed phreatically in a freshwater lens maintained by a high sea level similar to those described by Mylroie (2013) on modern Bahamian islands. The top of the freshwater lens on islands such as the Bahamas is at most only 1–2 m above sea level (J. Mylroie, personal communication). In particular,
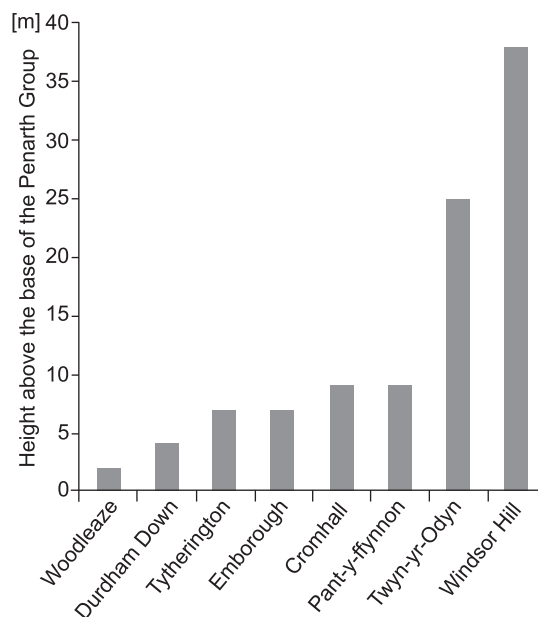
Fig. 7. Heights of Carboniferous Limestone in sauropsid fissure localities above the base of nearest Penarth Group. The height of the limestone surface in the near vicinity of a terrestrial vertebrate-bearing fissure is plotted with respect to the base of the nearest occurrence of bedded Penarth Group. The field relationships of the fissures and the Penarth Group are most reliable for Cromhall, Tytherington, Woodleaze, Durdham Down, Emborough and Windsor Hill. There is some uncertainty in the plots of Pant-y-ffynnon (where a mid-range figure is given) and Twyn-yr-Odyn due to some faulting in the vicinity; however, the fissure entrances are above the Penarth Group base. Holwell and Ruthin are not plotted, as the former is a neptunian dyke, and the geology around the latter is heavily faulted and sufficiently complex that some nearby Penarth Group strata are below the fissure entrance, whereas other sites are above. Batscombe fissure was not specifically located and was presumably quarried away, but the limestone surface in that vicinity is substantially higher (more than 12 m) than the nearest White Lias and therefore the Penarth Group base. Based on BGS digimap© geological maps, quarry maps where available, Ordnance survey digimap© and Google Earth© images of the area.

the presence of non-reworked fish teeth suggests a nearby sea and the presence of palynomorphs signifies a position below the vadose zone, as oxygenated water is destructive to pollen and spores. Furthermore, amorphous organic material in the palynological assemblages (Marshall and Whiteside 1980; Whiteside and Marshall 2008) indicates anoxic depositional environments that are likely to have been below, at, or near to sea level. Indeed, fissures just a few metres above sea level may still have been eroding, particularly at freshwater/saline water mixing zones (Whiteside and Marshall 2008). Vertical solution-formed voids such as "banana holes" and pit caves (Harris *et al.* 1995) are known to continue to widen and deepen a few metres above sea level (J. Mylroie, personal communication). Landlocked karstic water-filled voids in these locations with a connection to the sea are termed anchialine.

Comparison of the main sauropsid sites shows that putative Rhaetian fissures, such as Emborough, Pant-y-ffynnon and Twyn-yr-Odyn are also significantly above the base of the Penarth Group. From this analysis, it appears that Emborough has a similar field relationship as Tytherington to the Penarth Group and that Twyn-yr-Odyn may have been infilled later in the Rhaetian. However, it is worth noting that the base of the White and Blue Lias that lies within 500 m of Emborough is just 1 m below the top of the fissure, so all three localities may well be younger than those at Tytherington. We have not plotted Holwell, as the fissure is a neptunian dyke, nor the Ruthin fissure deposit, as the geology near the quarry is complex, with significant faulting, and calculations show some nearby basal Penarth Group sediments below the limestone surface whereas others are higher. The geology around Pant-y-ffynnon is also more complex than the other fissures plotted in Fig. 7 due to a greater degree of nearby faulting, so a middle figure has been plotted.

Windsor Hill, interpreted as a Pliensbachian neptunian dyke by Kühne (1956), but as an "Inferior Oolite" (Aalenian–Bathonian) "swallet" (*i.e.,* doline) by Savage (1977), shows, as predicted, the top of the fissure high above (nearly 40 m) the base of the Penarth Group.

The same technique can be extended to consider the field relations of the St. Brides palaeo-island fissures to local normally bedded strata. However, in these cases, the base of the Penarth Group lies at or below present-day sea level in the vicinity of the Carboniferous Limestone hill that encompasses the quarries. Using the regional geological model (Fig. 8A) of Wilson *et al.* (1990), and giving the threshold as the nearest mapped base of the Porthkerry Member, Blue Lias Formation, (the unit succeeding the Lavernock Shales Member), that lies just in the *Alsatites liasicus* Zone of the (mid) Hettangian, the relative position of the St. Brides fissures can be inferred (Fig. 8B). This analysis indicates that Ewenny contains the oldest deposits, of early–mid Hettangian age; Pant 2, Pontalun and Duchy form a second, later Hettangian group; and Pant 4 and 5 have the youngest deposits, perhaps of latest Hettangian or early Sinemurian age. This pattern fits with the three observed faunal groups: Ewenny has *Morganucodon* and *Gephyrosaurus* only (Kermack *et al.* 1973; PGG, personal observation); Pant 2, Pontalun and Duchy have *Kuehneotherium* in addition to those genera; while Pant 4 and 5 have a fauna where *Clevosaurus convallis* numerically dominates and *Gephyrosaurus* is very rare. Pant 4 and 5 also yield haramiyids, *Kuehneotherium*, and *Oligokyphus*, as well as the greatest diversity of morganucodontans, which are present in significant numbers (Gill *et al.* 2006; Clemens 2011). This pattern also accords with the palynological data from Ewenny, which indicate an age of at least early Hettangian, and the initial low tetrapod diversity concurs with an assignment just into the Early Jurassic following the ETE. As an indicator of the time for the proposed faunal succession, the Hettangian is between 1.5–2.5 Myr long, and the minimum duration of the Sinemurian *Arietites bucklandi* Zone is given as 342 ka by Weedon *et al.* (1999).

A criticism of this method could be that Pleistocene ice sheets and subsequent flooding (Crampton 1966) have variously depressed and eroded the Carboniferous Limestone around the Severn estuary, and so the match of topography to fissure age could be compromised. Such periglacial effects, for example, could have deepened the Triassic landscape of the Pant, St. Brides, and Afon Alun valleys, where the lower boundaries of the quarries lie. However, all the South Wales fissures are likely to have been affected to the same extent, and so the relative ages estimated for the fissures may still be accurate. It might also be argued that the greater diversity in Pant 4 and 5 was caused by the animals occupying different topographic levels, namely on the surface of the High Tor limestone rather than the Gully Oolite of the other localities. However, the area is so small (*c.* 20 km^2) that it is unlikely to have hosted substantially different habitats that would then be associated with different vertebrate diversities.

We can use these analyses to suggest a faunal succession of the fissures of the Bristol and South Wales region (Fig. 9). The faunas of Tytherington have a palynologically dated early Rhaetian age for
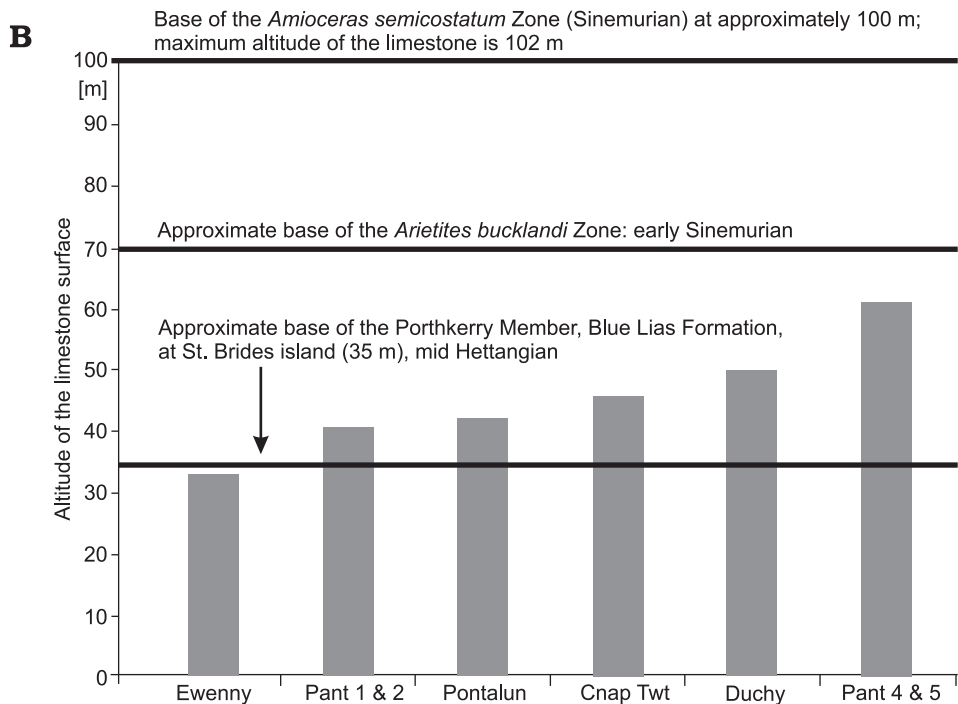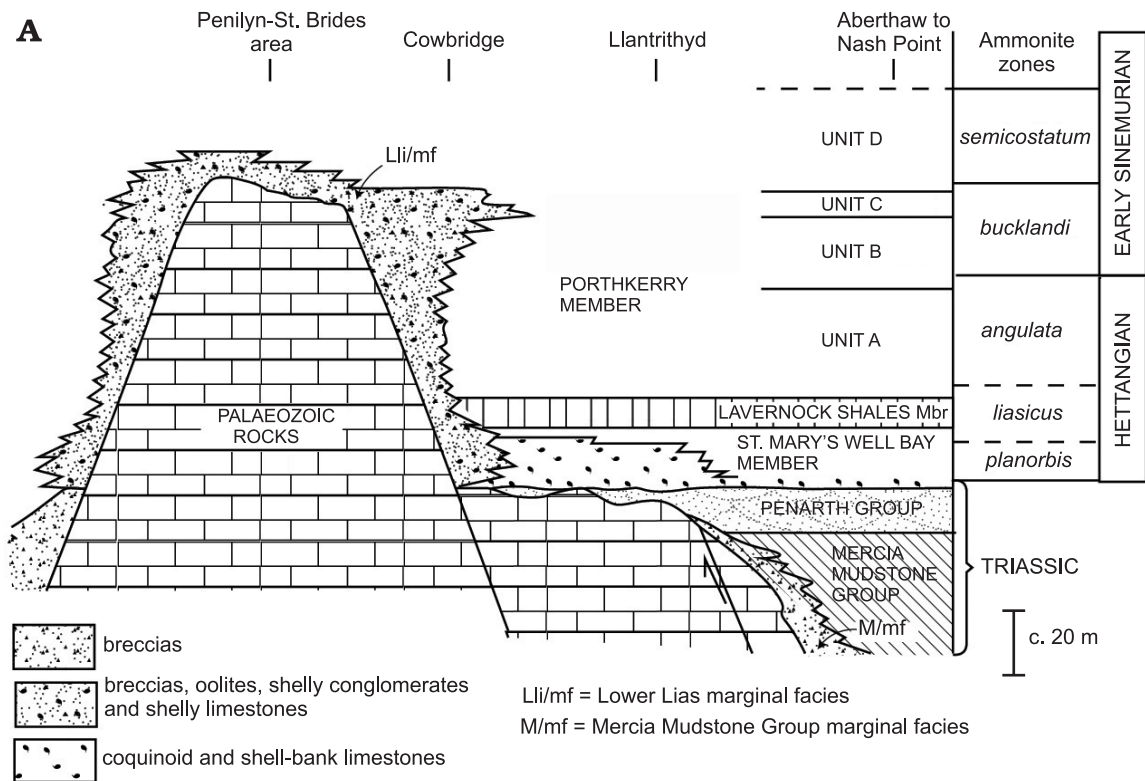
Fig. 8. Model of St. Brides area during the Early Jurassic transgression and altitude plot of the St. Brides fissures. **A**. Geological model in the Bridgend area as the Liassic transgression progressed. Simplified modern restatement of basement/cover relationships in South Wales (from BGS Memoir Sheets 261 and 262; Wilson *et al*. 1990). Note that it is not a simple transgressive flooding as relative sea levels throughout the period are likely to have gone down as well as up. **B**. Altitude of Carboniferous Limestone surface above the principal St. Brides fissure localities. The model shows the approximate topographical heights reached by named strata with respect to areas of Palaeozoic rocks in the Bridgend area as the transgression progressed. The base of the Porthkerry Member, Blue Lias Formation, and the Lower Sinemurian is the best estimate from this model, but mapping of the nearest Lavernock Shale Member suggests that the base of the Porthkerry Member may extend down to 20 m. Based on BGS Memoir for sheets 261 and 262 (Wilson *et al.* 1990), BGS geological maps, Ordnance Survey maps, quarry company historical maps, and Google Earth© images of the area.
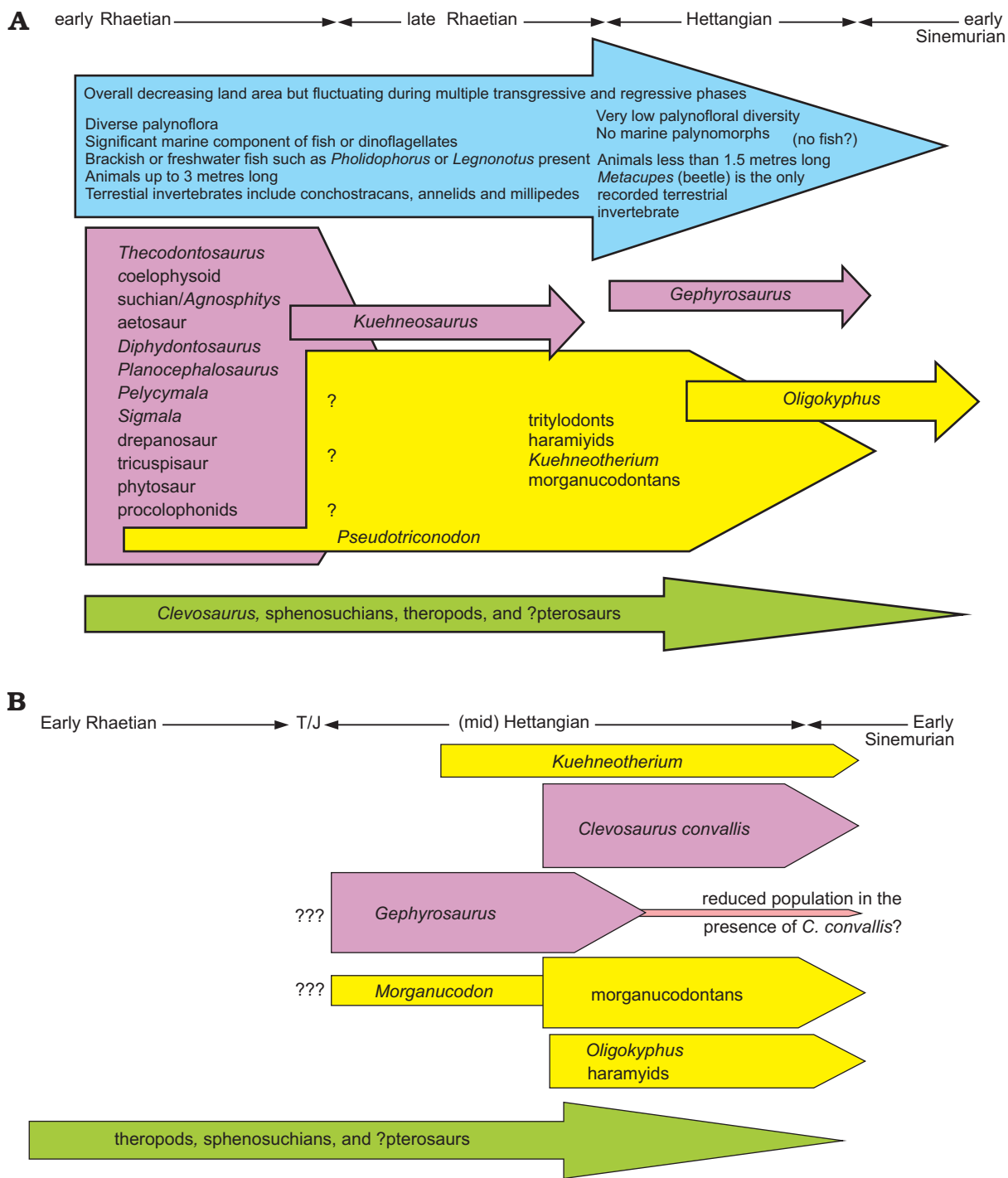
Fig. 9. Changes in the tetrapod biota of the fissures of southwestern UK. **A**. Overall changes in the fissure terrestrial tetrapod assemblages: a summary of the suggested changes in the tetrapod biota from the early Rhaetian to the Pliensbachian based on analyses in this paper. Reptiles and mammaliamorphs are grouped separately, and the lower arrows show reptiles that probably spanned the time range, but evidence for them at some time periods is scant, *e.g.*, pterosaur metacarpals have been recorded at Cromhall but that identification is disputed. All assemblages are dominated by short tetrapods (< 0.5 m). However, the sauropsid assemblages include animals such as phytosaurs, sauropodomorphs, and coelophysoids, that range from 2–3 m in length whereas larger forms are very rare in the St. Brides deposits; the largest tooth recovered in those fissures derives from an archosauromorph 1–1.5 m long. **B**. Changes in the fissure terrestrial tetrapod assemblages of St. Brides palaeo-island. We propose three faunal assemblages for the St. Brides palaeo-island tetrapod community. The earliest assemblage comprises *Morganucodon watsoni* and *Gephyrosaurus bridensis* only, followed by a second younger biota that includes those genera as well as *Kuehneotherium*. The third and youngest fauna includes all three plus *Clevosaurus convallis*, morganucodontans including *Bridetherium* and *Paceyodon*, together with the tritylodont *Oligokyphus*. Pterosaurs were probably present in the second assemblage and also in the youngest biota alongside sphenosuchian crocodylomorphs and theropods.

Planocephalosaurus, Diphydontosaurus and *Thecodontosaurus*; the presence of at least two of these genera unites the fissures in Tytherington, Cromhall, Ruthin, Holwell, and Durdham Down. The new clevosaur found at Woodleaze by Klein *et al.* (2015) is also present at Pant-y-ffynnon as well as being similar to the species in the palynologically dated fissure 2 at Tytherington; moreover *Terrestrisuchus* is found at Pant-y-ffynnon (Crush 1984), as well as at Tytherington and Cromhall. Assuming that the two teeth are not contaminants from processing other fissures, the *Kuehneotherium* found at Emborough (Fraser *et al.* 1985) suggests at least a Rhaetian age (Whiteside and Marshall 1985) and is found with huge numbers of *Kuehneosaurus* fossils; kuehneosaurs are also present in Batscombe as well as the probable Rhaetian deposits at Cromhall and Pant-y-ffynnon. The suggestion that *Oligokyphus* (Fig. 1F) is present in the youngest of the known St. Brides faunas is also in accord with its presence at Windsor Hill, probably the youngest of the fissure deposits in the Bristol region. The morganucodontids and haramiyids of Holwell may indicate that some fissures there include deposits younger than early Rhaetian. It is worth emphasising that these fissure faunas are from island communities and, as such, immigration, genetic drift and local extinctions could have significantly changed the biota quickly. In addition, there may be species that are only found in certain habitats on an island and therefore it may never be possible to achieve a precise chronology of faunal changes.

COMPARISON WITH GLOBAL FAUNAS

Individual taxa found in the fissures are recorded from pre-basal Rhaetian normally bedded strata from elsewhere in the world. An example is cf. *Diphydontosaurus* from the Ladinian of Germany (Jones *et al.* 2013) and Norian of Italy (Renesto 1995), *Clevosaurus* from the Norian of Brazil (Bonaparte and Sues 2006), and a probable *Planocephalosaurus* from the Carnian of North America (H.-D. Sues, personal communication). Heckert (2004) also ascribed some jaw fragments from the Carnian of Texas to *Planocephalosaurus*. However, none of these genera or other abundant fissure tetrapods, except procolophonids, is reported from tetrapod assemblages in pre-Rhaetian sites in the UK. Moreover, some distinctive reptile genera and species, including *Clevosaurus hudsoni*, *C. sectumsemper*, *Sigmala*, *Pelecymala*, and *Thecodontosaurus*, appear to be unique to the sauropsid fissures, with no direct equivalents reported from elsewhere. The procolophonid genera of the fissure deposits have not yet been established, so they cannot currently be compared directly with UK genera such as specimens from the Anisian Otter Sandstone Formation of Devon. The single aetosaur scute found at Cromhall (Lucas *et al.* 1999) does not convey any clear age evidence (Whiteside and Marshall 2008). In contrast, cf. *Clevosaurus* and *Diphydontosaurus* are recorded from European sites closest to the fissure localities, such as in the Belgian Rhaetian by Duffin (1995). Individual taxa may have long, and currently unknown, stratigraphic ranges and the rarity and incompleteness of small tetrapod skeletons makes it hard to use individual genera in a strictly biostratigraphic manner.

Comparison of the fissure vertebrate assemblages to global biotas is somewhat more informative (Fig. 10), despite the problems with assigning ages to known normally bedded terrestrial strata. In particular, many formations traditionally regarded as Late Triassic were shown some time ago to be of Early Jurassic age (Olsen and Galton 1977). Fine-tuning of this dating continues and there is some uncertainty about the ages of major fossiliferous successions, such as the Newark Supergroup of the USA, the Chinese Lower Lufeng Formation, and units in parts of Europe. For example, the basal part of the McCoy Brook Formation (Newark Supergroup) was regarded as Hettangian by Sues *et al.* (1994) but is now considered "latest" Rhaetian (Fedak *et al.* 2015). The richest comparative European fauna from a normally bedded sequence is the "Grès infraliasiques" Formation at St. Nicolas-de-Port (SNP) near Nancy, France, regarded as post-transgression Rhaetian (Debuysschere *et al.* 2015, p. 2). The collection sites at the locality are from lenticular beds with considerable lateral variation and "for this reason, the precise level from which the mammalian teeth described by Sigogneau-Russell [*e.g., Brachyzostrodon, Delsatia,* and *Morganucodon*] were collected remains uncertain" (Debuysschere *et al.* 2015, p. 2); the original site is lost (E. Chenal, personal communication). Cf. *Diphydontosaurus* has been found at a Rhaetian horizon (the basal lower conglomerate) at Serres, 11 km to the northeast of SNP and *cf. Planocephalosaurus* from Vaubexy 36 km to the south of SNP (M. Debuysschere and E. Chenal, personal communication). E. Chenal (personal communication) has also recovered specimens of cf. *Diphydontosaurus* from SNP. Overall, the tetrapod fauna from SNP and nearby localities is in accord with a dating of the Bristol fissures as Rhaetian. However, *Clevosaurus*, prevalent in the "sauropsid" fissures and the *Morganucodon*-sphenodont fauna from St. Brides palaeo-island, is not

	Ladinian–Carnian	Norian	Rhaetian — SNP. Seres and Vaubexy — French, Belgian, Luxemburg and UK non-fissure sites	late Rhaetian — McCoy Brook Fm. N. America	Hettangian — Lufeng Fm. China	Sinemurian — Kayenta Fm. N. America
	Worldwide	Worldwide				
SAUROPSID TYPE						
"*Palaeosaurus*" aff. phytosaurs	?	present	present			
aff. *Thecodontosaurus*	?	similar	similar	similar		similar
Diphydontosaurus	similar	similar	similar			
aff. *Planocephalosaurus*	similar	?				
Sigmala and/or *Pelycymala*	similar	similar				
aff. *Clevosaurus hudsoni*	similar	similar	similar			
Procolophonid	similar	present		present		
Kuehneosaur	similar	similar	similar			
aff. *Tricuspisaurus*	similar	?				
Aetosaur	similar	similar				
Drepanosaur	similar	similar				
Coelophysoid/theropod			present	similar	similar	similar
aff. *Terrestrisuchus*	?	similar	?			
MAMMALIAMORPH TYPE						
Pterosaur			?	?	?	
Haramiyid sp.			present	?	?	
Pseudotriconodon/cynodont			present		?	
Morganucodon sp.		?	present		present	
Eozostrodon			present			
Kuehneotherium praecursoris		?	present	?	?	?
Paceyodon davidi			present			
Gephyrosaurus			present			
aff. *Clevosaurus convallis*	?	similar	similar	similar		?
aff. *Oligokyphus major*				similar	similar	similar

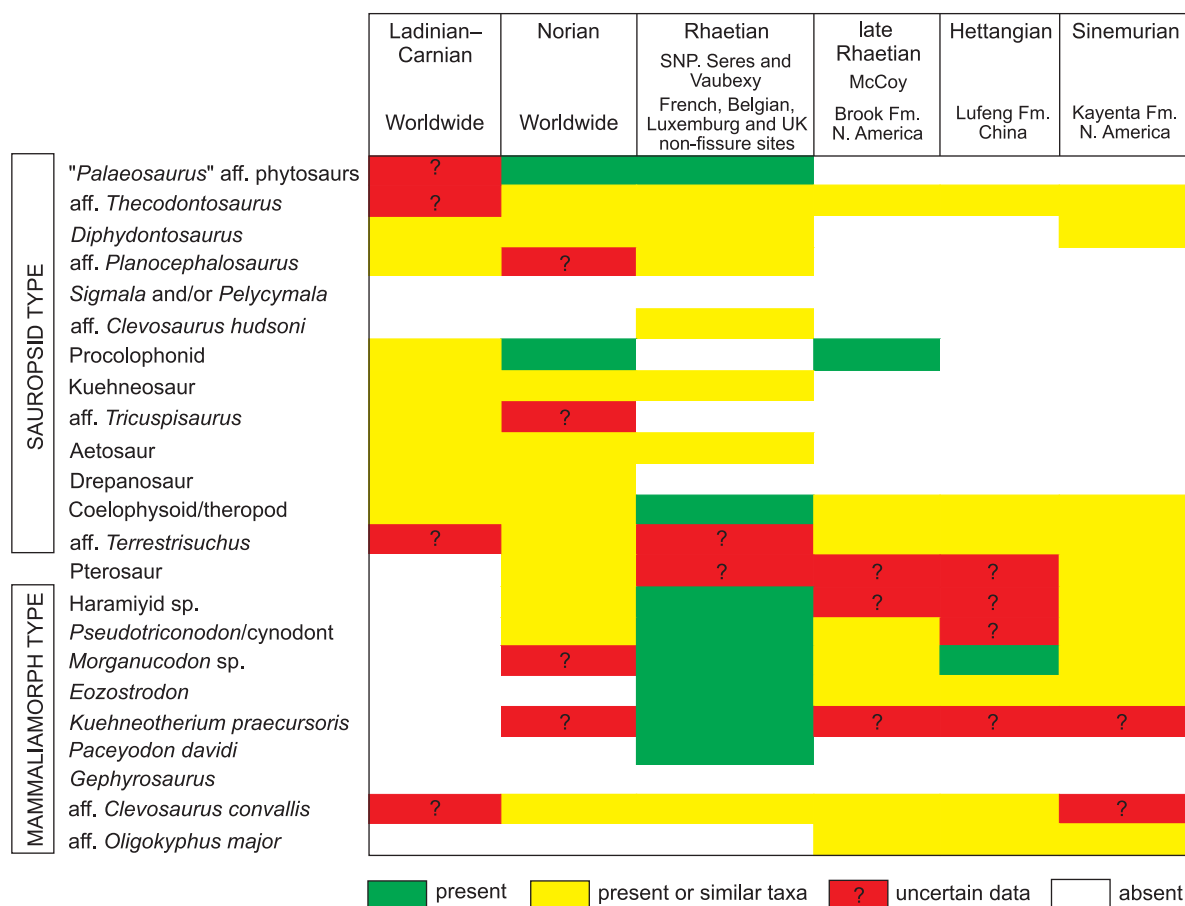Legend: ▮ present ▮ present or similar taxa ▮ ? uncertain data ▯ absent

Fig. 10. Comparison of the fissure tetrapod faunas with global examples. Red is where the deposit has been well sampled, but no evidence of a taxon has been found. Green refers to a taxon or type being present, and yellow is the presence of a closely related or possibly the same taxon. White is where no evidence of the taxon has been found, but further sampling may yield additional information. Some of the fossils found in normally bedded strata are similar but cannot with certainty be referred to a species, such as the cf. *Clevosaurus* and cf. *Diphydontosaurus* specimens of Duffin (1995). Data from Fraser (1994), Luo and Wu (1994). Shubin *et al.* (1994), Sigogneau-Russell and Hahn (1994), Storrs (1994), Cuny (1995), Curtis and Padian (1999), Bonaparte and Sues (2006), Lucas and Tanner (2006), Heckert (2004), Whiteside and Marshall (2008), Irmis *et al.* (2013), Jones *et al.* (2013), Debuysschere *et al.* (2015), and Fedak *et al.* (2015). M. Debuysschere, E. Chenal, and H.-D. Sues all provided written information (personal communication).

recorded from SNP or nearby localities despite over 1000 bones collected there. Also, the deposits of SNP have yielded many genera, including the mammaliamorphs *Megazostrodon*, *Brachyzostrodon*, *Rosierodon*, *Paikasigudodon*, *Woutersia*, *Delsatia*, and *Theroteinus* (Debuysschere *et al.* 2015), that have not been recorded in the Holwell or the St. Brides fissures. Furthermore, there are no records of any tritylodont from SNP, which is a significant additional difference from Pant 4 and 5 as well as from Holwell.

Many taxa characteristic of the sauropsid fauna, such as *Planocephalosaurus*, tricuspisaurs, procolophonids, and kuehneosaurs, are absent from global Early Jurassic deposits. However, comparisons with the Lower Lufeng Formation, China and the McCoy Brook and Kayenta formations in North America suggest some key similarities to the St. Brides and Windsor Hill fissures. The McCoy Brook Formation, of the latest Rhaetian and Early Jurassic, shares faunal similarities with St. Brides palaeo-island, notably *Oligokyphus* found in the latest Rhaetian Scots Bay Member (Fedak *et al.* 2015). *Oligokyphus* of probable Pliensbachian age has also been recorded in the Kayenta Formation (Sues 1985; Fedak *et al.* 2015), which is in accord with the same dating of *O. major* (including *O. minor*) by Kühne (1956) at Windsor Hill. As noted by Fraser (1994), *Clevosaurus convallis* from Pant 4 bears greater similarity to *C. bairdii* from the McCoy Brook Formation and the Chinese clevosaurs than to *Clevosaurus hudsoni* from the sauropsid fissure fills.

Comparing the fissure faunas further with the Chinese Dull Purplish and Dark Red Beds of the Lower Lufeng Formation shows some significant accord. Although Luo and Sun (1994) suggested that the Dark Red Beds are no older than Sinemurian and the Lower Dull Purplish Beds are no older than Hettangian,

Fedak *et al.* (2015) note that the Lower Lufeng Formation has not been precisely dated. What is agreed by both sets of authors is that *Oligokyphus lufengensis* from the Dark Red Beds lacks the accessory cuspules on the anterior margin of the postcanine molariform tooth crown found in *O. major*, *Oligokyphus* sp. from the Kayenta Formation and *Oligokyphus* sp. from the McCoy Formation. *Morganucodon*, ubiquitous in the St. Brides fissures, is found in the Dark Red Beds (possibly Sinemurian) of the Lower Lufeng Formation. It is interesting that the Lower Purplish Beds have a lower diversity than the Upper Red Beds, which matches our suggestions for the St. Brides biotas that the putatively younger Pant 4 and 5 assemblage is much more diverse than the other fissures.

The possible succession in the vertebrate assemblages of the fissures is in accord with the notion that they span the ETE. In this context, the sauropsid fissures contain a diverse, mainly reptile-dominated biota that was extant before the end-Triassic volcanic event, and this was followed by an Early Jurassic recovery with initially a depauparate "*Morganucodon*" fauna succeeded by greater tetrapod diversity exemplified by the *Morganucodon*-sphenodont fauna of Pant 4 and 5. The missing link in this suggestion is a probable late Rhaetian locality (equivalent to the Lilstock Formation), although some of the sauropsid-type fissures may actually be of this age, *e.g.*, Twyn-yr-Odyn, where the fish *Legnonotus* found in the Cotham Member at Aust (Egerton 1854), is abundant. It has also been suggested that the Holwell fissure, where Charles Moore collected a fossil later named *Pseudotriconodon,* may be late Rhaetian (*e.g.*, Cuny 2004).

REINTERPRETING THE PALAEOENVIRONMENT

The sauropsid tetrapods of the Rhaetian-age Bristol fissures were interpreted as members of a unique, higher-ground or upland fauna by Robinson (1957) and Halstead and Nicoll (1971), whereas Marshall and Whiteside (1980), Whiteside (1983) and Whiteside and Marshall (2008) argued that they lived on small, low-lying limestone islands. They noted that the fauna is best perceived as an insular biota, which could explain the small body size of the dinosaurs and some other taxa. Whiteside and Marshall (2008) also suggested that some caverns near the current limestone surface at Tytherington were the result of carbonate dissolution in a mixed freshwater/saline water regime at the edge of a freshwater lens maintained by a high nearby Rhaetian sea level. In a modern analogue, Mylroie (2013) has shown that caverns in Bahamian island limestone form at the top of the freshwater lens as well as near the halocline and at flank margins, with the lens maintained by the sea. It is likely that the cavern at Cromhall shown in Fig. 5A was also formed in a similar manner, indicating a high sea level at that locality, and similarly near the Durdham Down deposits (Foffa *et al.* 2014).

Further evidence of nearby saline waters for the sauropsid localities is suggested by the dolomitisation of the limestone in the Carboniferous host rock, and breccias that infill the fissures; Whiteside and Marshall (2008) reported authigenic dolomite crystals in mixed terrestrial and marine Rhaetian palynomorph-bearing rock. Dolomitic breccias are common at Tytherington and Durdham Down, and dolomitised rocks have been found at Cromhall (Walkden and Fraser 1993). The presence of coeval fish teeth in fissures at Cromhall, Durdham Down and Tytherington is in accord with a high sea level maintaining a freshwater lens a few metres below the surface of a limestone island. Therefore it is likely that fresh water was available for a relatively rich plant life that supported the reptiles and arthropods, which also formed their prey. The crevices and cracks (karren) on the surface and openings to the dolines would, perhaps, have been generally moist areas for the plants. In a more recent analogue, the Sawmill Sink blue hole on the Bahamian Abaco Island yields the wax myrtle as by far the most common pollen in Quaternary samples (Steadman *et al.* 2007), a plant that grows around the edge of sinkholes. This is similar to Tytherington, where the Rhaetian palynological sample from Fissure 16 is dominated by *Ovalipollis pseudoalatus* together with the fresh water alga *Botryococcus*, indicating a monotypic stand of vegetation surrounding a freshwater pool. Similarly, fissure 13 is another freshwater pool with *Botryococcus* and a minor marine component, but dominated by different vegetation, comprising mainly *Ricciisporites*. The *Ricciisporite*s parent plant has now been identified (Mander *et al.* 2012) from ultrastructure as a gymnosperm with some similarity to the bennettitaleans, rather than a liverwort, *e.g.* Balme (1995).

This varied plant life provided a damp leaf litter that could sustain the millipedes, and a seasonal rainfall is indicated by the presence of the conchostracan ("clam shrimp") *Euestheria* at Tytherington, Cromhall and

Pant-y-ffynnon. Modern conchostracans live in the detritus of (mostly) temporary freshwater pools and have a life span of about 2–3 weeks (*e.g.,* Weeks *et al.* 1997). By analogy, the presence of *Euestheria* colonies comprising 50+ individuals of variable sizes and no preferred orientation in small rock hand specimens from the Cromhall collection of BRSUG indicates that deposition and fossilisation of their carapaces occurred *in situ* in the red-coloured sediment of their habitat. Had there been vadose flow, this would have selectively transported, separated and broken the delicate carapaces of these small crustaceans. Therefore, at the time that the animals died, the freshwater in the fissures would have ponded and dried, with a slow drainage denoting a raised water table as a consequence of a nearby high sea level.

The mammaliamorph-bearing fissures of St. Brides suggest a slightly different scenario. In common with the sauropsid fissures, the St. Brides fissure faunas represent a limestone island community, but the palaeogeography and modern topography indicate that the islands would have been higher, certainly 100 m or more, at the end of the Rhaetian. Although the vegetation of St. Brides was dominated by one plant, the conifer *Hirmeriella,* there is evidence for a variety of flora such as club mosses, bennettitaleans and possibly cycads and ferns (Evans and Kermack 1994; Gill *et al.* 2006). The palynological assemblages contain a vast proportion, over 95%, of *Classopollis* (the pollen of *Hirmeriella*) and this suggests a limited food resource for arthropods and their predators, the tetrapods, which may explain the depauparate *Morganucodon* fauna, comprising only insectivorous mammals and no herbivores (as noted by Gill *et al.* 2006). The more diverse *Morganucodon*-sphenodont fauna, consisting of the herbivorous haramiyids and *Oligokyphus* in addition to a wide range of insectivorous and (presumably) carnivorous mammaliaforms and reptiles, may have benefited from greater access to freshwater as the sea level rose, bringing the permanent water of the freshwater lens closer to the limestone surface, and/or it may be a result of recovery after the ETE. The general humidity is supported by reports of large quantities of haematitic pellets or ooids in some fissure deposits at Pontalun and particularly Pant, but not at Ewenny (Kermack *et al.* 1973; Evans and Kermack 1994; Gill *et al.* 2006). Based on the work of McFarlane (1976), these ferruginous ooids or pisoids were interpreted by Gill *et al.* (2006) as forming in a pedogenic laterite where fresh rock was subjected to alternating extreme wetting and drying cycles. In another example, Thorne *et al.* (2014) recorded microorganism-mediated iron pisoids from a modern fluvio-lacustrine wet/dry environment in Western Australia. This indicates a climate with heavy seasonal rains, as suggested by Evans and Kermack (1994), with waters running quickly into slot fissures and blocking them near or at the water table with surface debris including lateritic soils, vertebrate remains and plant material.

The St. Brides fissures may have been generally located further above the water table than the Rhaetian fissures, based on the modern topography of the area, which is higher than nearly all the sauropsid localities, and the greater frequency of narrow slot voids. There are exceptions; for example, the large caverns at Ewenny (Kermack *et al.* 1973), a cave in Cnap Twt (Harris 1957), and also a cave in Pant 4 fissure and one higher in the quarry at the western end (PGG, personal observation). Such large caverns suggest they were close to, or even below, sea level to maintain the phreatic conditions necessary for their formation. Furthermore, fossil charcoal present in abundance in the clay deposits of the slot fissures displays features of waterlogging (Gill *et al.* 2006), indicating a water table maintained for a sufficiently long time and therefore likely to have been near sea level. The presence of pollen and spores in these slot fissures also suggests deposition at the water table rather than under vadose conditions, which are highly oxygenated and destructive to palynomorphs. Although fishes are not recorded from these fissures, we know that modern-day solution pit caves commonly fill with terrestrial deposits and little marine sediments on "even small" Bahamian islands (J. Mylroie, personal communication). The occurrence of *Naticopsina oppelii* (see Kermack *et al.* 1973) in Pant 2 perhaps indicates the proximity of a marine environment at the time of deposition.

A notable feature of all the fissure deposits is the range of colour of the bones and teeth. The colour ranges from white, through yellows, browns, blues, greys, and black. The white bones may indicate deposition in an oxygenated environment and the black bones in anaerobic conditions, similar to the anoxic environment deduced for some Rhaetian Westbury Formation Beds reported by Macquaker (1999). Black terrestrial tetrapod bones have been found at Woodleaze (Fig. 2G), Tytherington, and Windsor Hill, whereas white bones predominate at Cromhall, Emborough, Batscombe, some deposits at Tytherington (Fig. 2H), such as the *Thecodontosaurus* breccia where bones have low pyrite (Wings 2004), and some lithologies such as the red matrix (Kermack *et al.* 1973) in St. Brides fissures. The St. Brides fissures also contain yellow, orange-stained, grey, and brown bones; bones at Ruthin are usually yellow or yellowish-white and Pant-y-ffynnon has a range of white and grey bones. Bones at Holwell range from yellow to dark brown, although some fish teeth are almost black. A variety of colours suggests different environments at deposition; white bones in an oxygenated

or vadose setting, through to black bones, perhaps settling at the halocline or just, below where sulphur-reducing bacteria moderated the formation of metal sulphides. Plant material in the form of charcoal is much more abundant in the grey clay matrix (Ewenny, Pontalun 3 and Pant 5) with brown bones.

The accumulations of bones in the fissures show some evidence for catastrophic killing, but it is most unlikely that they represent predator accumulations. In both the sauropsid fissures at Tytherington and in the St. Brides deposits, fossil charcoal or fusain has been discovered. This led Harris (1958) and Whiteside and Marshall (2008) to suggest that wildfire was a significant factor in the death of the tetrapods, through smoke inhalation or direct baking, and the subsequent decay of the animals' bodies would have provided an abundant supply of bones to be deposited in the fissures. The partial *Clevosaurus hudsoni* skeleton from Cromhall (NHMUK PV R36832; Fig. 5B) demonstrates that some articulated skeletons entered the sauropsid fissures where they started to dissociate; it is likely that this is a key source of disassociated bones in the fissure deposits, but other bones may have been individually washed into the fissures from the surface. The predator bone accumulation hypothesis (Kühne 1956; Kermack *et al.* 1973; Evans and Kermack 1994) as the key origin and constitution of the assemblages is rejected here on the basis of three lines of evidence. First, although some bones show tooth marks (*e.g.*, Evans and Kermack 1994), none of the bones shows any evidence of acid digestion in the gut of a predator (PGG, observation of material not prepared in acetic acid). Second, in most of the assemblages there is scant evidence of predators. In the *Morganucodon* fauna, any of the three genera are unlikely to have been a major predator on the others, as *Morganucodon* and *Kuehneotherium* are tiny and interpreted as insectivorous (Gill *et al.* 2014) whilst *Gephyrosaurus* was also probably insectivorous (Evans 1980). Furthermore, searching for other predatory animals amongst the thousands of specimens from the *Morganucodon* fauna yields only one possible pterosaur fossil (Fraser 1989) and some teeth from small archosaurs (Fraser 1989; Evans and Kermack 1994). Postulating that the *Morganucodon* faunal composition was a result of predator accumulations would require an extreme (and probably unfeasible) selection of prey, hunting the probably nocturnal or crepuscular *Morganucodon* and *Kuehneotherium* but also the possibly diurnal *Gephyrosaurus*. Yet this hypothesised predator was not catching sphenodontians or tritylodonts as none were found in the *Morganucodon* fauna although these animals are abundant in the *Morganucodon*-sphenodont fauna.

Thirdly, although there has been reported evidence of predatory bite marks on bones on the *Oligokyphus* accumulation of Windsor Hill, and despite (Kühne 1956) suggesting otherwise, the possibility of opportunistic cannibalism in times of starvation cannot be eliminated as the cause of bite marks; in that assemblage the putative predator again left no trace of its own teeth or bones.

Potential predators such as small archosaurs are found in greater abundance in the *Morganucodon*-sphenodont fauna accumulations of Pant 4 and 5, residing in the same assemblages as the rhynchocephalians and larger morganucodontans. Considerably bigger carnivorous archosaurs of *c.* 2.5 m long are indicated by isolated teeth or other remains in assemblages of the sauropsid fissures (*e.g.*, Van den Berg 2012; Foffa 2014) but not in the St. Brides deposits where the longest animal was perhaps a maximum of 1.5 m. Overall, however, as emphasised by Whiteside and Marshall (2008), the "washed-in" hypothesis better explains the great range of small and larger exquisitely preserved bones, as well as the occurrence of articulated or nearly articulated skeletons such as shown in Fig. 5B.

The fissure assemblages are similar to void-fills on modern day and Quaternary islands where species diversity is low, but individual species have numerous individuals (Whiteside 1983; Whiteside and Marshall 2008). The terrestrial animals on the small islands are frequently small, and can be found preserved as individual elements in fissure fills on limestone islands such as Aldabra (Arnold 1976) and New Providence in the Bahamas (Etheridge 1966). Furthermore, the differing species, biodiversity and variable proportions of reptile taxa that can be found in closely positioned fissures in localities such as Cromhall and Tytherington is paralleled in the Quaternary deposits such as those from Barbuda reported by Etheridge (1964).

CONCLUSIONS

The fissure deposits of the Bristol region and in South Wales provide a unique window on the Late Triassic and Early Jurassic faunal changes across the ETE. In general terms, our analysis supports the view of Robinson (1957), that the earlier faunas were dominated by reptiles and the later ones by mamma-

liamorphs. However, *contra* Robinson (1957), we have found no evidence of tetrapods in fissures that pre-date the Rhaetian transgression. The oldest faunas, from Durdham Down, Tytherington, Cromhall, Pant-y-ffynnon, and possibly Ruthin, are characterised by clevosaurs with large flanged teeth, *Diphydontosaurus* and, in some localities, *Planocephalosaurus* and *Thecodontosaurus* or *Thecodontosaurus*-like species. Phytosaurs are present in the earliest of these biotas. Sphenosuchian crocodylomorphs, procolophonids and coelophysoids are also found in most of these deposits. Kuehneosaurs are particularly known from Emborough and Batscombe, as well as more rarely from Cromhall and Pant-y-ffynnon. Despite the recovery of thousands of tetrapod bones from all sauropsid fissures, cynodonts and particularly mammaliaforms have not been recorded in sauropsid localities except for the two *Kuehneotherium* teeth at Emborough found by Fraser *et al.* (1985). Either the cynodonts were absent or exceptionally rare owing to the small land areas of fluctuating sizes as the Rhaetian sea transgressed and regressed, or to the relative isolation of the individual palaeo-islands.

The fauna at Holwell is an amalgam of most probably Rhaetian faunas, but as the fissure vertebrates derive from neptunian dykes, and the specific sites where Moore collected his specimens are uncertain, it is not possible to be certain about the precise dating. The presence in the fauna of *Thomasia*, *Eozostrodon*, *Pseudotriconodon* (Cuny 2004), and *Diphydontosaurus* is in accord with the Rhaetian biota of SNP in France. The finding of a probable haramiyid, *Hypsiprymnopsis rhaeticus* Boyd-Dawkins, 1864 (possibly = *Thomasia*) in the Rhaetian grey marls (Williton Member) at Watchet and the report of *Tricuspes*, a possible cynodont from the Westbury Formation of Vallis Vale, near Frome Somerset (Huene 1933; Storrs 1994), is also in accord with a Rhaetian date for the Holwell fauna. The additional presence of *Clevosaurus* and *Thecodontosaurus* agrees with the Rhaetian dating of Tytherington and Durdham Down. However, the presence of tritylodont *incertae sedis*, the affinities of which are not established (Savage 1971), makes further comparisons moot.

We have presented evidence that the St. Brides faunas range in age from Hettangian to possibly early Sinemurian, and that there is an increasing faunal diversity as the entrance to the fissures and the fossiliferous horizons became topographically higher. What remains unclear is whether any of the "sauropsid" or "mammaliamorph-type" fissure localities could be of late Rhaetian age, equivalent to the Lilstock Formation. There is no reliable evidence that any fissure is of that age, although the faunal content of Holwell does include some marine fishes more typical of the late Rhaetian; Cuny (2004) tentatively suggested a later Rhaetian age for Holwell. Holwell also has an intermediate fauna between sauropsid and mammaliamorph type fissures (Table 2). There are examples of animals that are known to be representative of the late Rhaetian such as *Euestheria brodieana* in Tytherington fissure 12 and the fish *Legnonotus* in Twyn-yr-Odyn, also recorded from the Cotham marble (Cotham Member, Lilstock Formation) at Aust Cliff (Egerton 1854). It seems likely that a fissure of confirmed late Rhaetian age may be found in the future.

Overall, the characteristics of all fissure faunas are animals of small to small-medium size, numerous individuals and a range in diversity from low to comparatively diverse depending on locality. Possibly owing to isolation by saline waters, amphibians are unconfirmed and probably absent from all fissures; yet non-marine (possibly brackish water) fishes are present in the older deposits, but fishes in general, appear to be absent in St. Brides infills. Although some of the animals may have derived from neighbouring sandstone areas, in general the tetrapods lived on the karstic landscape of small islands. A diverse reptile biota is found in the older fissures, with sphenodontians abundant, comprising at least seven species in five genera. Procolophonids, aetosaurs, phytosaurs, tricuspisaurs, kuehneosaurs and *Thecodontosaurus* are not recorded from the younger fissure fills of St. Brides. Mammaliamorphs became much more prominent members of the fauna, particularly after the ETE, but, although reptile diversity is much lower, two species of rhynchocephalians from the St. Brides deposits are the most dominant numerically.

It is a curiosity that *Gephyrosaurus*, generally regarded as a basal rhynchocephalian (*e.g.*, Jones *et al*. 2013), is present and common in many of the St. Brides fissures, but does not occur in the older fissures or (apparently) anywhere else in global faunas of the Late Triassic–Early Jurassic. Sphenodontian rhynchocephalians, usually considered to be more derived, dominate the earlier sauropsid fissures. It is likely that the abundance and diversity of acrodont sphenodontians in the sauropsid faunas was favoured by the absence of their probable competitors and possible predators, the cynodonts. Possibly also, the presence of a significant proportion of mammaliamorphs with shearing teeth in the St. Brides fissures favoured a niche suitable for a lizard-like species with a puncturing dentition, or there was a daytime/night-time niche separation, as suggested above.

NOTE: LOST SPECIMENS

It is worth reporting that many specimens from the Bristol fissures have been lost, or at least mislaid. From the vertebrate collections at Holwell made by Charles Moore over a number of years commencing in 1858, three of the mammaliamorph teeth are not accounted for (M. Williams, personal communication). From the sauropsid fissures, the millipede from Cromhall figured by Fraser (1988b) is lost (Fraser, personal communication) and some key fossils of a procolophonid, possibly *Hypsognathus,* from that locality are also missing. The many fish fossils from Twyn-yr-Odyn described by Howgate (1976) cannot currently be found.

From the Duchy deposit, a symmetrodont tooth of *Kuehneon* and dental fragments of a possible amphibian and a dipnoan, all found by Kühne, have been lost (Evans and Kermack 1994). Although not from a fissure deposit, the probable haramiyid *Hypsiprymnopsis rhaeticus* found at Watchet by Boyd-Dawkins (1864) has also been lost. These specimens could all have added greatly to our knowledge of the fissure faunas and their loss is to be greatly regretted.

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ADDENDUM

Since the acceptance of this paper and the arrival of the proofs we have been able to study in greater detail the fossils of small terrestrial reptiles from Moore's "*Microlestes*" quarry at Holwell held at the BATGM. We have recognised the presence of *Gephyrosaurus*, a procolophonid and *Variodens* as well as a number of previously undescribed rhynchocephalians. This has strengthened the view suggested in this paper that Holwell is a link between the sauropsid-type and mammaliamorph-type fissures.

Also a new species of sphenodontian, *Sphenotitan leyisi*, has been described from the Late Triassic of northwestern Argentina by Martinez *et al.* (2013). We have been able to compare the description with some new specimens of *Pelecymala* from Tytherington fissure 14 and, although *Sphenotitan* is much larger, there appear to be strong affinities between the genera. Martinez *et al.* (2013) regard the Quebrada del Barro Formation which has yielded *Sphenotitan* as Norian although Apaldetti *et al.* (2011) considered that it was younger, possibly Early Jurassic. Therefore essentially little modification is required to our Fig. 10 except to indicate that present or similar taxa could be added to the *Sigmala* and/or *Pelycymala* row under the category "Norian, Worldwide".

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