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Testing the relationship between marine transgression and evolving island palaeogeography using 3D GIS: an example from the Late Triassic of SW England

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Abstract: The Rhaetian transgression marked a major change in landscape. The Permian and Triassic had been a time of terrestrial conditions across Europe, including much of mainland UK, as well as the North Sea and Irish Sea, represented by red bed clastic successions. Seas flooded across Europe at 205.7 Ma and the shift from terrestrial to marine environments is marked in the UK by the switch from the red beds of the Mercia Mudstone Group to the black mudstones and shelly limestones and sandstones of the Penarth Group. The area around Bristol was marked by a complex landscape in which an archipelago of islands of Carboniferous limestone was formed in the new shallow seas. The application of new methods in geographical information systems allows a detailed exploration of a number of conformable surfaces, the unconformity between the underlying Paleozoic rocks and the overlying Mesozoic strata, as well as levels within the latest Triassic sediments, marking the advance of the sea and interactions with the coeval tectonics, which caused some islands to rise and some basins to descend. The new geographical information system models show a sequence of palaeogeographical reconstructions of the archipelago and relate this to the island tetrapod faunas, which show strong evidence of the species–area effect.

Supplementary material: Supplementary tables S1-S6 and 2D island map GIS files are available at https://doi.org/10.6084/m9.figshare.c.5273256

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The transition from the Triassic to the Jurassic was a time of major global environmental change, with evidence for massive volcanism, accelerated rates of extinction, high-magnitude changes in sea-level and extraterrestrial impacts. The overarching event was the break-up of the Pangaean supercontinent and the onset of eruptions from the Central Atlantic Magmatic Province, which drove a rapid fall and subsequent rise in sea-level, resulting in a sustained marine transgression across much of western Europe, transforming Permo-Triassic continental environments into epicontinental seas. The Late Triassic and Early Jurassic stratigraphy of SW Britain has played a globally significant part in unravelling the sequence of events around this Rhaetian transgression and is the focus of this paper.

Although most previous work has focused on well-exposed outcrop sections, here we take a broader approach using geographical information system (GIS) models and 3D visualization. We analyse a large amount of published and unpublished data on stratigraphic thicknesses from boreholes, quarries, railway and road cuttings, and natural exposures across the Bristol–Bath–Mendips area in an attempt to gain new insights into the impact of the Rhaetian transgression on the palaeogeography and palaeobiogeography of SW England.

A key aspect of the palaeogeography of this area is the Bristol–Severn palaeoarchipelago (Whiteside *et al.* 2016). This was an array of structural highs in the Late Triassic and Early Jurassic, formed largely from Carboniferous limestone, the area and connectivity of which must have changed throughout the Rhaetian transgression (Fig. 1). These palaeoislands are noted for their populations of small tetrapods, including some of the first dinosaurs and mammals, as well as lizard-like sphenodontians, gliding kuehneosaurids, broad-toothed procolophonids and trilophosaurids (Robinson 1957), and slender crocodyliforms. The age of the fissures has been debated, with suggestions that they are either Carnian or Norian, and so predate the Rhaetian transgression (Robinson 1957), or Rhaetian and so more or less coeval with the transgression (Whiteside *et al.* 2016). Key questions concern the impact of the Rhaetian transgression and evolving palaeogeography on the fauna and flora. For example, it is understood from studies of modern organisms on islands that species numbers match island size, and that some groups may show dwarfing as a means of survival in small spaces. Moreover, the age and origin of the palaeokarstic systems in which many of the fossils were preserved have been the subject of much debate.

Our aim here is to test whether we can use GIS methods to produce a 3D model of a focused area in the British Isles, consisting of multiple stratigraphic marker horizons reconstructed as surfaces. We then explore how the tectonics preceding the Triassic, as well as contemporary Earth movements through the Late Triassic and Jurassic, affected the nature of the Carboniferous–Mesozoic unconformity as well as basin-deepening and island-swamping by the rising sea-levels of the latest Triassic. We explore whether these new methods enable us to produce a more accurate map of the archipelago (cf. the maps in Fig. 1), date the karst fissures on the islands and estimate their sizes, and relate these geographical features to contemporary island life.

Geological setting of the Bristol–Mendip Massif

Paleozoic basement

The study area is triangular and is bounded by the Bristol Channel to the west, the Mendip Hills to the south and the Cotswolds

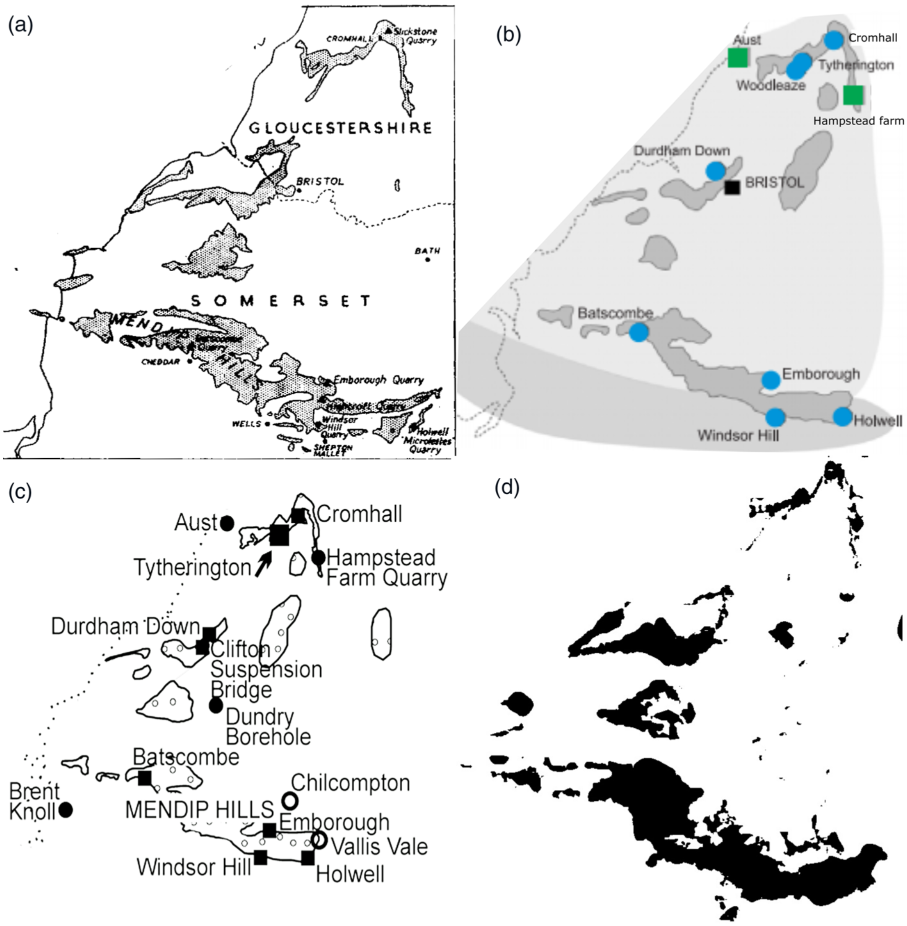

Fig. 1. Comparison between old and new maps of the Bristol archipelago. (**a**) Robinson (1957), (**b**) Whiteside *et al.* (2016), (**c**) Whiteside and Marshall (2008), and (**d**) our new map. Note that the map of Robinson (1957) represents Paleozoic rock outcrops and the fissure localities only because this author did not envisage a palaeoarchipelago at the time of sauropsid fissure filling.

escarpment to the east (Fig. 2). In this area, the Jurassic and younger rocks that make up the Cotswolds and regions to the east have been deeply eroded to reveal underlying folded and faulted Paleozoic 'basement' rocks of Devonian and Carboniferous age. Older rocks are exposed in some areas, such as the Silurian sediments of the Tortworth inlier (Reed and Reynolds 1908).

Areas of high elevation in the district are largely Carboniferous limestone, except for the Devonian sandstones and Silurian igneous rocks exposed in the core of the large periclines that make up the Mendip Hills (Fig. 2). These Paleozoic rocks were deformed by compression during the Variscan Orogeny in the Late Carboniferous (Williams and Chapman 1986). The Carboniferous limestones form a series of curved ridges that represent the often steeply dipping limbs of major fold structures, including the west–east-trending periclines of the Mendip Hills and the north–south-trending Coalpit Heath Syncline between Bristol and Cromhall, which has a core of Carboniferous Coal Measures.

Stratigraphy of the Late Triassic–Early Jurassic cover

The Carboniferous and older basement rocks have a partial, unconformable cover of essentially flat-lying or gently dipping Late Triassic and Early Jurassic strata of the Mercia Mudstone and Penarth groups, and the overlying Lias (Fig. 2). These units formed prior to and during the Rhaetian transgression and show an onlapping relationship with respect to the underlying Variscan basement rocks.

The oldest Mesozoic cover consists of the red, largely continental, mudstones with evaporites of the Mercia Mudstone Group (MMG). Much of the MMG has been interpreted as palaeosols and playa lake sediments (Milroy *et al.* 2019). Older deposits are absent, indicating a prolonged phase of subaerial exposure and erosion of the 'Mendip Massif' during the Permian and Early to Late Triassic, when the adjacent Wessex Basin and Worcester Graben formed major depocentres. Adjacent to the steeply dipping fold limbs of Carboniferous limestone, the MMG is represented by coarse scree and alluvial fan deposits of the 'Dolomitic Conglomerate', now termed the MMG (marginal facies), which infills gullies developed on the flanks of the fold structures and dramatically highlights the exhumed Late Triassic palaeotopography that is still present today. These parts of the MMG are mainly assigned to the Branscombe Mudstone Formation.

The upper part of the MMG, the Blue Anchor Formation (BAF), overlies the Branscombe Mudstone Formation and is identified by a change from red beds to mudstones and fine-grained, green–grey sandstones. The BAF contains marine trace fossils and bivalves and it records the initial Late Triassic marine transgression in SW Britain (Mayall 1981). Landon *et al.* (2017) recorded echinoid and ophiuroid echinoderms as well as cephalopod arm hooks in the BAF at Stoke Gifford, Bristol, confirming the marine conditions. The BAF is 20–40 m thick in the Central Somerset Basin, but thins rapidly towards the Mendips and locally includes altered evaporite deposits (Green 1992). Traditionally, the Norian–Rhaetian boundary was placed between the uppermost part of the BAF (the Williton Member of Mayall (1981) is generally considered Rhaetian) and the Penarth Group, but uncertainties over palynological dating and some local diachroneity mean that the Branscombe Mudstone Formation and BAF are dated as 'Norian to Rhaetian' (British Geological Survey (BGS) Lexicon).

The overlying Penarth Group consists of the Westbury and Lilstock formations. The Westbury Formation reaches a thickness of 14 m in the Central Somerset Basin and consists of dark grey to black shales with thin beds of limestone and sandstone (Kellaway *et al.* 1993). The contact with the BAF is an erosion surface overlain by a marine conglomerate containing abundant phosphatized vertebrate remains (primarily teeth and fish scales) and rip-up

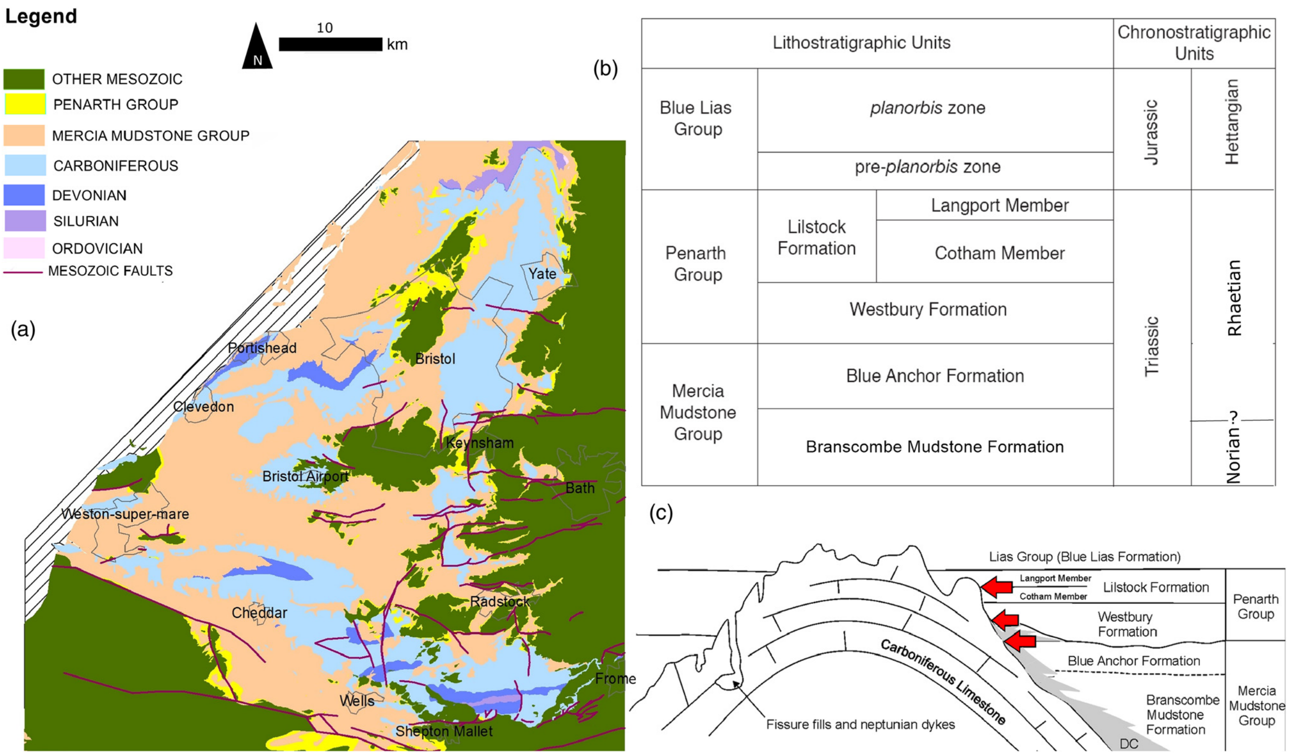

Fig. 2. Geology of the study area. (**a**) Simplified geological map of the study area with Triassic strata shown in detail. Based on British Geological Survey map data. The diagonal lines show which parts of the study area are not mapped by the onshore geology map used for the study. (**b**) Late Triassic to earliest Jurassic stratigraphy of the Bristol area based on the British Geological Survey stratigraphic framework. (**c**) Simplified diagram showing the unconformable relationship between Mesozoic and Paleozoic strata in the study area. The red arrows indicate successive sea levels, from low to high from the top of the Blue Anchor Formation, through Westbury Formation times and into the early Lilstock Formation. DC = Dolomitic Conglomerate, marginal facies of the MMG.

clasts of Carboniferous limestone and the BAF (Sykes 1977). Where the Westbury Formation onlaps Paleozoic basement around the Mendips, a littoral facies composed of bored hardgrounds and well-rounded pebbles of Carboniferous limestone may be developed locally (Green 1992; Ronan *et al.* 2020). The depositional environment of the Westbury Formation has been debated because it combines features suggesting shallow and deep-water deposition, but geochemical (Allington-Jones *et al.* 2010; Fischer *et al.* 2012), trace fossil (Allington-Jones *et al.* 2010) and biomarker (Jaraula *et al.* 2013) evidence suggest that it was deposited in a shallow restricted marine environment with brackish water and periodic photic zone euxinia (Jaraula *et al.* 2013). This restricted marine environment was part of the wider Rhaetian sea that covered most of NW Europe after the Rhaetian transgression (Fig. 3).

The bone beds, primarily at the base of the Westbury Formation, but including later bone beds near the top of the Westbury Formation and in the lower parts of the overlying Cotham Member, are ascribed to storm activity (MacQuaker 1994), which scoured bones, coprolites and semi-lithified sediment from the sea bed, and sometimes included terrestrially derived components (Nordén *et al.* 2015). The storm surge ebb current transported and variably

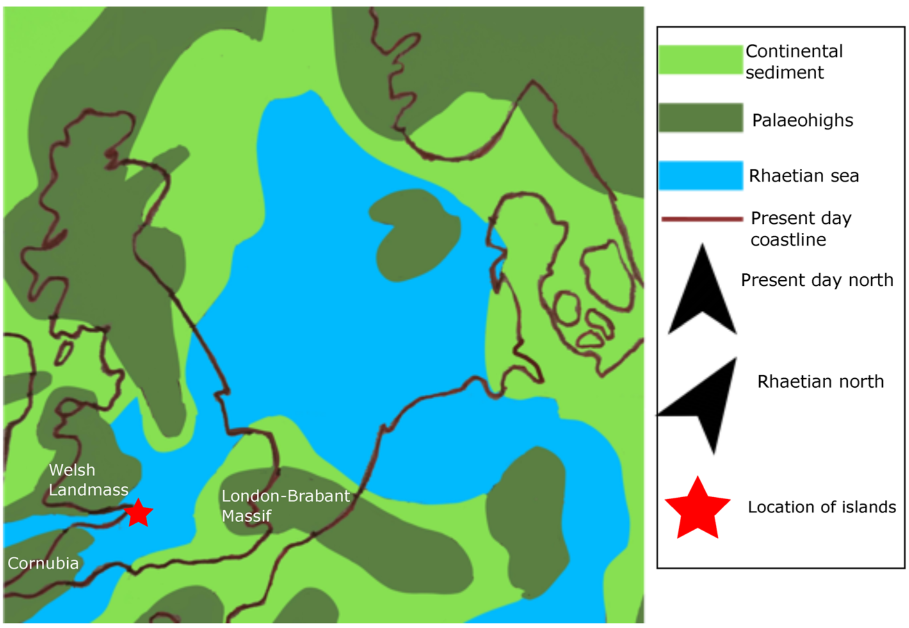

Fig. 3. Extent of the Rhaetian sea in northern Europe and the location of the Bristol island archipelago within this sea. The three regional land masses around the Bristol area are named. Based on Fischer *et al.* (2012, their fig. 1).

abraded these components, winnowing them as they came to rest as a concentrate of phosphatic debris.

The overlying Lilstock Formation consists of the Cotham and Langport members (Gallois 2009). The Cotham Member (formerly the Cotham Beds) consists of greenish grey mudstones with interbedded limestones and ripple-marked sandstones, the base of which is marked by an erosional surface (Kellaway *et al.* 1993; Gallois 2009). Many portions show intense soft sediment deformation attributed to seismic shocks (Simms 2007). The upper parts of the member include tubestone carbonate microbialites formed by stromatolite mounds in extremely shallow water conditions (Ibarra *et al.* 2014) and deep sand-filled cracks of probable desiccation origin (Hesselbo *et al.* 2004). The Cotham Member thus represents a fall in sea-level, followed by a rise towards the end of its deposition (Hesselbo *et al.* 2004) and a transgression event confirmed by biomarkers in the succeeding Langport Member (Fox *et al.* 2020).

The Langport Member includes the White Lias and Watchet mudstones, which consist of porcellaneous or rubbly limestones and bedded calcareous mud and siltstones, respectively (Gallois 2009). These beds indicate the beginning of fully marine conditions in the area (Swift 1995). The sea-level continued to rise during the Early Jurassic, slowly submerging the palaeoislands of the Bristol area, as evidenced by the successive Mesozoic overstepping of the Mendips (Farrant *et al.* 2014; Ronan *et al.* 2020).

Post-Variscan tectonic history of the Bristol–Mendip Massif

The Bristol–Mendip area was a tectonic high throughout the Mesozoic and Cenozoic, bounded to the south by the Central Somerset Basin and to the east by the Pewsey Basin and the southern part of the Worcester Graben, all of these being parts of the Wessex Basin that extended from Somerset and the Vale of Pewsey in Wiltshire to Hampshire and the Isle of Wight. Compared with these rapidly subsiding basins, the preserved Triassic and Jurassic succession is thin and includes multiple gaps in the succession (Green 1992). Strata younger than the Lower Jurassic are now largely absent, due, in part, to erosive episodes in the Early Cretaceous (Late Cimmerian Unconformity) and Miocene coeval with Alpine–Pyrenean compression and basin inversion (Green 1992).

There was continuing NE–SW extension in the Wessex Basin from the Rhaetian to Bajocian, a span of 45 myr, with pulses of tectonic activity causing faults, joints and injection-filled fissures coinciding with marine transgressions (Wall and Jenkyns 2004). These synsedimentary tectonics are expressed over the Bristol region by east-west trending neptunian dykes in certain locations on the coastal regions of the Mendip Palaeoisland, such as at Holwell, where sediment containing fossils was injected underwater into faults and joints. These east–west-trending faults and joints affected both shorelines and basins, especially around the large Mendip island in the south of our study area. Times of intense fissuring seem to correlate with times of high sea-level (Wall and Jenkyns 2004).

Understanding the distribution and magnitude of later deformation is important, but the scaling is subtle and can be best detected through a GIS study. The gently undulating form of what would originally have been an essentially flat plane at the time of deposition is seen, with an increase in the amplitude of folding (to *c.* 200 m) parallel to the anticlinal axis of the eastern Mendips. The Triassic–Jurassic horizons are locally offset by normal faulting, which in the Bristol–Mendip Massif has both a west–east trend inherited from Variscan structures and a north–south trend representing the southern extension of the Malvern Fault Zone.

Triassic–Jurassic 'fissures' in Carboniferous limestone basement

Origin of fissures

The Carboniferous limestone of the Bristol–Mendip Massif is famed for its many fissures infilled with sediments and fossil remains of Late Triassic and Early Jurassic age. The fissures are distributed across most of the exposed limestone ridges from Holwell in the southern Mendips to Cromhall on the plunging nose of the Coalpit Heath Syncline in the north. They appear to fall into two types. Some, particularly those in the Mendips, are linear features with planar walls and appear to be related to tectonic extension and the opening of seafloor fractures (neptunian dykes) as a result of syndepositional Late Triassic (Robinson 1957) or Early Jurassic faulting (Wall and Jenkyns 2004). Other fissures, such as those at Cromhall and Tytherington, show clear evidence of limestone dissolution. These fissures are the result of karstic processes through either the infiltration of freshwater from the vadose zone into the phreatic zone, or freshwater–saline water mixing as the Rhaetian transgression progressively drowned the limestone ridges (Whiteside 1983; Simms 1990; Whiteside and Marshall 2008; Whiteside *et al.* 2016).

Fissure faunas

The Late Triassic and Early Jurassic fissures of SW Britain have produced probably the most globally important terrestrial reptile and mammal microvertebrate faunas around the Triassic–Jurassic boundary (Whiteside *et al.* 2016). A summary of the fissure taxa is given by Whiteside *et al.* (2016). The less well-known locality of Highcroft Quarry has yielded possible *Clevosaurus* fossils (Fraser 1994; Herrera-Flores *et al.* 2018), but that fauna is essentially undescribed. Whiteside and Duffin (2017) updated the Holwell reptile fauna. There are two age ranges of fissures (Robinson 1957), the so-called 'sauropsid' fissures of Late Triassic age, containing mainly reptile fossils, and the 'mammal' fissures with mammal fossils as well as reptiles, which are dated as younger, possibly Latest Triassic or Early Jurassic.

Timing and duration of Triassic fissure formation

The dating of Triassic fissure fills and their fauna has been the subject of much debate and two contrasting views have emerged. First is the 'long-duration view', in which the fissures formed over a time span >30 myr, extending from the late Carnian to the Rhaetian. Second is the 'short-duration view', in which the fissures are all broadly coeval and formed during the Rhaetian.

The long-duration view was initiated by Robinson (1957, 1971), who considered that the Cromhall, Emborough and Batscombe 'sauropsid' fissures were filled in Norian 'uplands' based on projected extensions of mapped Westbury Formation strata, which she considered would overlie the Emborough fissure. Robinson (1957) commented that 'except that at Highcroft Quarry, marine Rhaetic can be shown to have covered the site of the fissures', so, in this view, the fissure deposits date from before the Rhaetian transgression and therefore before the archipelago. Fraser *et al.* (1985) used this dating to argue that two *Kuehneotherium* specimens from Emborough Quarry represented the earliest therian mammal. Fraser and Walkden (1983), Benton (1994), Benton and Spencer (1995) and Lucas (1999) regarded the key Cromhall fissure fills as Norian, whereas Walkden and Fraser (1993) dated the range of those deposits from the Carnian to the Rhaetian, a view supported by Simms *et al.* (1994). Robinson (1957) recognized that the '*Microlestes*' fissure at Holwell was a neptunian dyke as the fauna was largely marine and she regarded these fossils as 'almost certainly derived fossils of Rhaetic age redeposited in the fissure in Inferior Oolite times'.

The short-duration view was proposed by Marshall and Whiteside (1980) and Whiteside (1983, 1986), who demonstrated that a new fissure locality, Tytherington Quarry, which yielded *Thecodontosaurus* and *Clevosaurus*, also included sediments with early Rhaetian palynomorphs and a large component of marine dinocysts. They concluded that the main fissure was infilled at the marine margins of a Rhaetian palaeoisland. Whiteside (1983) and Whiteside and Marshall (2008) noted that the terrestrial reptiles from the 'sauropsid' fissures had many features (e.g. the small size of individuals, but in large numbers combined with low diversity) characteristic of island faunas. The *Kuehneotherium* from Emborough was therefore Rhaetian in age and not the world's oldest mammal (Whiteside and Marshall 1985). Whiteside *et al.* (2016) used comparisons of the elevation of the fissure entrances to the nearest basal Penarth Group to show that all the fissures were filled after the onset of the Rhaetian transgression. Whiteside *et al.* (2016, their fig. 7) hypothesized that the Woodleaze and Durdham Down fissures might have been filled during the earliest early Rhaetian, with Tytherington and Emborough filling later, but before Cromhall and Batscombe; Windsor Hill is the youngest fissure fill (possibly as late as Pliensbachian).

Additional evidence for Rhaetian filling of the red sediments bearing *Clevosaurus hudsoni* of Cromhall is the presence of the conchostracan *Euestheria brodieana* (Morton *et al.* 2017), demonstrating that they are late Rhaetian (= Cotham Member, Lilstock Formation) in age. Whiteside *et al.* (2016) also concluded that, based on the marine fish fauna, the '*Microlestes*' neptunian dyke of Holwell was probably also Rhaetian in age. This is confirmed by finds of terrestrially derived reptile bones in some coastally located marine Westbury Formation bone beds (Nordén *et al.* 2015) and Westbury Formation age marine fish teeth in terrestrial assemblages found in fissures located near the Triassic coastline (Skinner *et al.* 2020).

Methods and data

Our overall approach (summarized in Fig. 4) was to create continuous structure contour surfaces on several key stratigraphic horizons across the Triassic–Jurassic boundary – that is, at different stages of the Rhaetian transgression. Surfaces were constructed on the top of the BAF (= top MMG), the base of the Westbury Formation and the top of the Cotham Member. The surfaces were constructed by interpolating the following three main sources of input data.

(1) Literature sources of outcrop sections (both temporary and permanent), which were georeferenced and compiled into a GIS from descriptions and maps and assigned an elevation using a high-resolution digital terrain model.

(2) Borehole records from the BGS archive to show stratigraphic contacts concealed by younger strata. The elevation of the horizon is determined by subtracting the downhole measured depth from the surface elevation of the borehole top.

(3) BGS 1 : 50 000 scale geological map linework to assign elevations to stratigraphic contacts using a digital terrain model. Such contacts may be conformable on a younger (top) or older (base) stratigraphic unit or may be unconformities, where the unit onlaps older basement rocks.

The aim was to transform and connect numerous disconnected geological observations on the elevation of a particular geological horizon into a continuous surface. This surface could then be intersected with the present basement elevation to determine which parts of that basement would have been areas of non-deposition (above sea-level) at that geological horizon. Using this process, the form of the island archipelago can be partially reconstructed.

This approach relies on the reasonable assumptions that: (1) the stratigraphic units are thin and reasonably isochronous across the relatively small area of interest; (2) exhumation of the Bristol–Mendip Massif is a relatively recent phenomenon and the preserved Triassic–Jurassic palaeotopography of major basement blocks is still present; and (3) post-depositional flexure and faulting of the Triassic–Jurassic surfaces is relatively gentle and has had a corresponding effect on both basement and cover, such that the relative elevation of basement onlaps is unchanged.

Literature sources

Key literature sources include early reports, such as Buckland and Conybeare (1824), De la Beche (1846) and Moore (1867, 1881). These reports used less formal terminology than today, but the stratigraphic units of interest are so distinctive in colour and lithology that it is easy to distinguish them (see Supplementary Material, Table S1). There was then a phase of extensive and systematic fieldwork by geologists such as Richardson (1904, 1911) and Reynolds (1938), who used more standardized locality information, unit terminology and measurements, providing detailed logs through 36 sections. Richardson (1911) was especially useful as he provides detailed descriptions of many Rhaetian sections and also standardizes the stratigraphic terminology of earlier researchers, clearly defining the Westbury, Cotham and Langport beds. Although these are informal terms, their lower and upper limits are identical to our current understanding following formalization as formations and members by Warrington *et al.* (1980).

There is a risk of confusion about the locations of described sections in the older papers because the authors did not use a system of Ordnance Survey map references until after 1945. This proved especially problematic for localities in Bristol where the boundaries of various suburbs have shifted. For example, Short and Reynolds (1904) described the Redland section, but an earlier description revealed that it was located in the area known today as Bishopston.

Boreholes

Borehole information was collated from the BGS Single Onshore Boreholes Index (www.bgs.ac.uk/products/onshore/sobi.html). Boreholes were selected based on three criteria: (1) boreholes were drilled distant from outcrops of Penarth Group or Paleozoic strata to maximize their usefulness; (2) boreholes captured at least

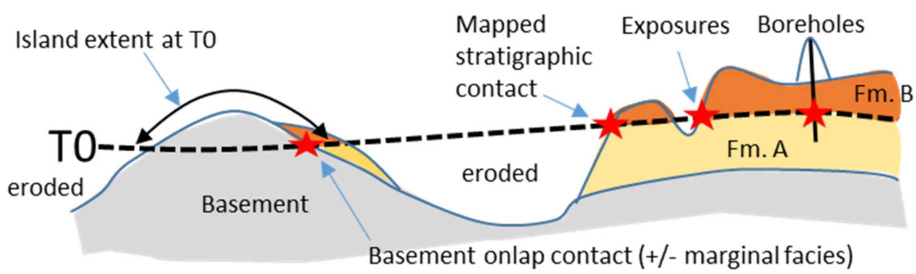

Fig. 4. Geographical information system workflow to generate a palaeosurface. Method of combining the three primary data sources (boreholes, surface exposures and mapped stratigraphic contacts) to generate structure contour surfaces. T0, time zero. Dotted line shows sediment deposited at time zero.

one of the contacts used to generate the surfaces; and (3) the geological descriptions in the borehole records were of sufficient quality to identify particular horizons. Fortunately, the lithologies of the Westbury and Lilstock formations are sufficiently distinct that they do not require specialist knowledge to identify them. A total of 32 boreholes were selected based on these criteria. A further four boreholes were taken from Whittard (1948) (Supplementary Material, Table S2).

Geological map linework

The third source of data for the surfaces was mapped geological contacts. These were processed from BGS 1 : 50 000 scale digital geological maps (DiGMapGB-50). All the contacts within the Paleozoic were used to capture the complex topography of the Paleozoic basement rocks. Several contacts make up the base of the Westbury Formation because it can rest conformably on the MMG or unconformably on Paleozoic basement rocks. This is also true for the top of the Cotham Member, which is either overlain conformably by the Langport Member or unconformably by Jurassic rocks. For the MMG, we excluded the diachronous marginal facies ('Dolomitic Conglomerate') because this unit was deposited as debris flows above the level of the main bedded facies and therefore tends to pull the surfaces generated by the spline-with-barriers function up into sharp spikes. The NEXTmap digital terrain model was used to add Z or height information to each point along the mapped polylines.

Fissure fill, Cotham Marble and bone bed locations

Two locality datasets (one for the fissure fills and one for the bone bed localities) were created to reconstruct the Late Triassic island archipelago. Although the Westbury Formation bone beds are extremely laterally continuous, we added several described localities. These include conventional cliff and quarry localities as well as bone beds described from boreholes along the M4 and M5 motorways and around Bristol Parkway rail station. The Cotham Marble is also laterally continuous and a similar selection of described localities was mapped. The fissure fills were those in the Bristol region as defined by Whiteside *et al.* (2016). The datasets contain the name of each locality and map coordinates. The final dataset includes nine fissure fill localities, 24 Cotham Marble localities and 27 bone bed localities.

Creating the structure contour surfaces

Data from the published literature, boreholes and geological maps were compiled into a GIS. Where an elevation was not available for a particular feature (e.g. a stratigraphic contact), this was generated using the high-resolution NEXTMap British Digital Terrain Model Dataset (www.intermap.com/nextmap). The rugosity of the landscape in the Bristol–Mendip region means that the elevation-assigned BGS mapped geological linework generally provided a high density of control points for creating the surfaces, with an even distribution across the area, particularly for the Mesozoic units. The concealed top of the Paleozoic was least certain because of the small number of boreholes that prove it at depth. For this surface, the published structure contours of Kellaway *et al.* (1993) were used as an additional data source.

Surfaces were constructed using the spline-with-barriers function in ArcGIS 10 (ESRI 2013), which creates a minimum curvature surface that passes through every point in the dataset. Mesozoic faults were set as barriers during the interpolation. Fault data were obtained from BGS geological maps, memoirs and other publications (e.g. Atkinson and Davison 2002). Each Triassic–Jurassic surface was examined against the surface representing the top of the Paleozoic basement in a 3D viewer (ESRI ArcScene) before grid subtraction was applied to determine which areas of Paleozoic basement would have been below and above the interpolated stratigraphic surface. Areas of Paleozoic basement above the Triassic stratigraphic surface are assumed to have formed islands (or areas of positive relief in the case of the MMG) at that time. An iterative process of error checking was used to remove obvious artefacts in the surfaces, such as those produced by later erosion of the Paleozoic basement either by natural (e.g. gorge erosion) or anthropogenic (e.g. large-scale quarrying) causes.

Results

The surfaces produced by these methods are shown in Figures 5–8. The Paleozoic top surface (Fig. 5) reconstructs the topography of the major unconformity in the Bristol area, between the Paleozoic and Mesozoic, showing the elongate topographic high of the Mendip Hills, as well as smaller uplands to the north. The MMG (BAF) top surface (Fig. 6) shows the first phase of basin filling, as different units of Triassic red beds generally fill the deepest parts of the Paleozoic top surface, leaving the topographic highs standing up as

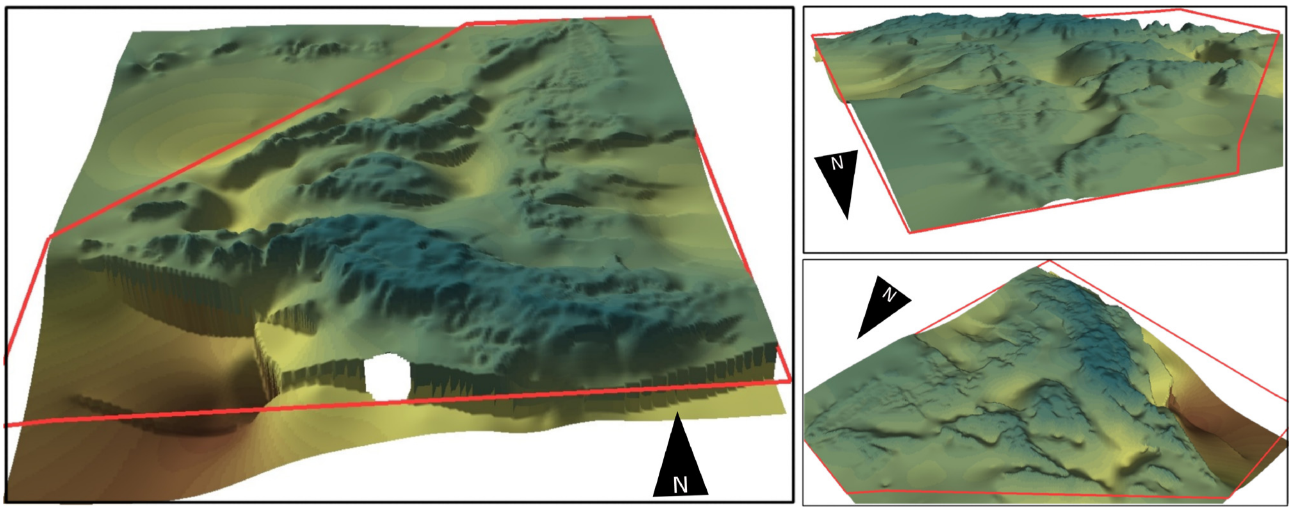

Fig. 5. Paleozoic top surface. A selection of 3D views of the Paleozoic structure contour surface generated by this study. The red outlines represent the barriers used during surface generation and include an outline of the study area and Mesozoic faults. The 3D surfaces were visualized using the Arcscene software package.

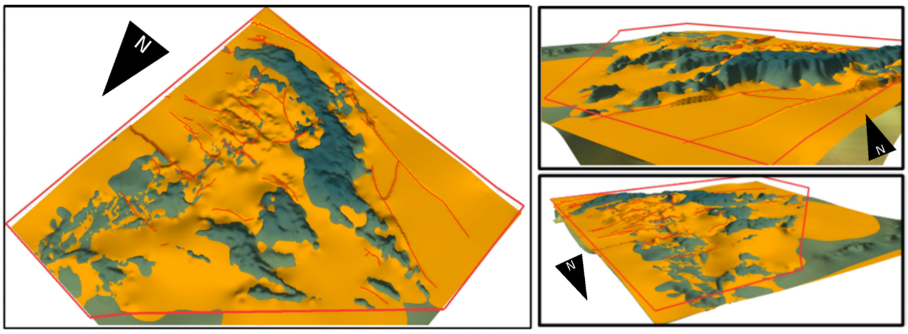

Fig. 6. Mercia Mudstone Group top surface. A selection of 3D views of the Mercia Mudstone Group (orange) and Paleozoic (green) structure contour surfaces generated by this study. The red outlines represent the barriers used during surface generation and include an outline of the study area. Mesozoic faults are also shown by red lines within the outline. The 3D surfaces were visualized using the Arcscene software package.

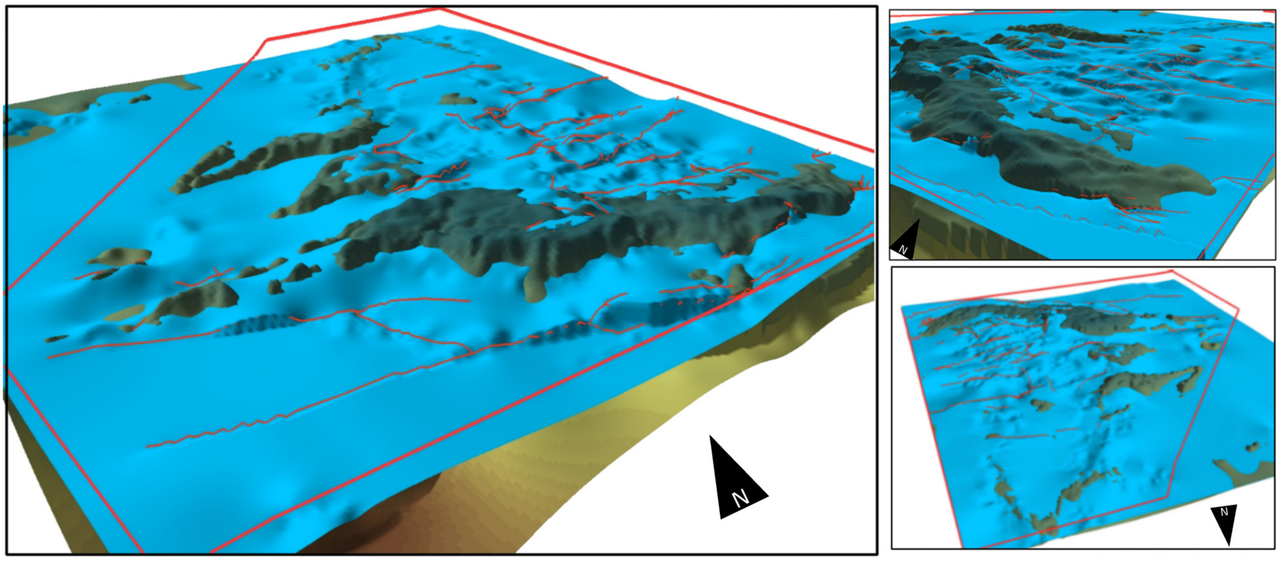

Fig. 7. Westbury Formation base surface. A selection of 3D views of the Westbury (blue) and Paleozoic (green) structure contour surfaces generated by this study. The red outlines represent the barriers used during surface generation and include an outline of the study area. Mesozoic faults are also shown by red lines within the outline. The 3D surfaces were visualized using the Arcscene software package.

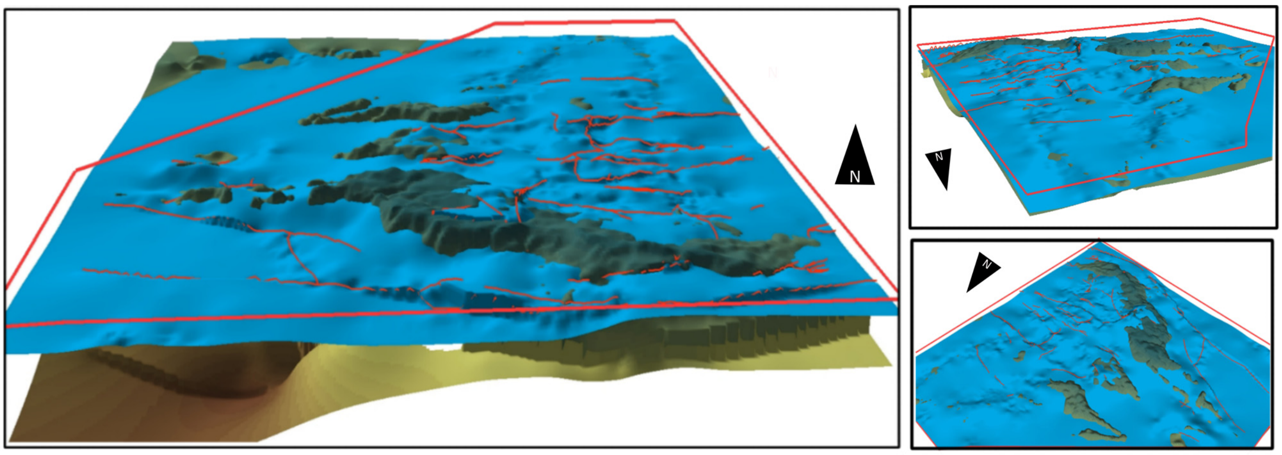

Fig. 8. Cotham Member top surface. A selection of 3D views of the Cotham (blue) and Paleozoic (green) structure contour surfaces generated by this study. The red outlines represent barriers used during surface generation and include an outline of the study area. Mesozoic faults are also shown by red lines within the outline. The 3D surfaces were visualized using the Arcscene software package.

mountain belts, associated with linear, largely east–west contemporary faulting.

Two models of Rhaetian-age sedimentation (Figs 7 and 8) represent the base of the Westbury Formation and top of the Cotham Member, respectively. The base Westbury Formation map (Fig. 7) matches the top MMG map (Fig. 6) in terms of implied age, but was calculated independently and acts as a check on the results. It can be interpreted as representing the first major phase of flooding and defines the highs as islands in the Bristol archipelago. The top Cotham Member model (Fig. 8) shows further basin filling coupled with further activation of the fault systems. The island shapes remain roughly the same, with just the loss of some lower parts beneath the Mesozoic sediment level.

The environmental maps (Fig. 9) show more detail, highlighting where the MMG and the ‘Dolomitic Conglomerate’ in particular were deposited (Fig. 9a), the latter filling low-lying coastal areas and extending up valleys inland on the larger uplands. The detail of the palaeoislands can be seen at the base of Penarth Group sedimentation, marking a known point of the early transgression (Fig. 9b) and, *c.* 4–5 myr later, at the top of the Cotham Member (Fig. 9c). The island shapes have changed, with reductions around the coastlines of nearly all the islands. The current geology (Fig. 9d) reflects this phase, with the Paleozoic hills that were palaeoislands still visible.

Further detail is provided in Figures 10–13, which are 2D maps derived from the 3D surface models. The upland–island shapes are exactly derived from the topographic models and so show greater detail and precision than previous work based simply on field mapping. At the start of the sequence, the MMG is widespread around all the structural highs formed by the Paleozoic basement (Fig. 10), with ‘Dolomitic Conglomerate’ covering some coastal areas and defining numerous valleys and gullies, where it accumulated during catastrophic erosive events. The two Rhaetian maps, marking more or less the beginning of marine deposition (Fig. 11) and its end (Fig. 12), show the shapes of the palaeoisland as well as some individual sampling points, namely bone bed and fissure localities. The comparison of earliest and late Penarth Group deposition (Fig. 13) highlights the substantial changes in island shape and area during the 4–5 myr separating these two snapshots, as confirmed by estimates of changing island areas (Table 1). This level of detail and clarity has never before been possible. All the islands reduce in size (pale green) and some smaller palaeoislands are simply overwhelmed by the accumulation of sediment as the

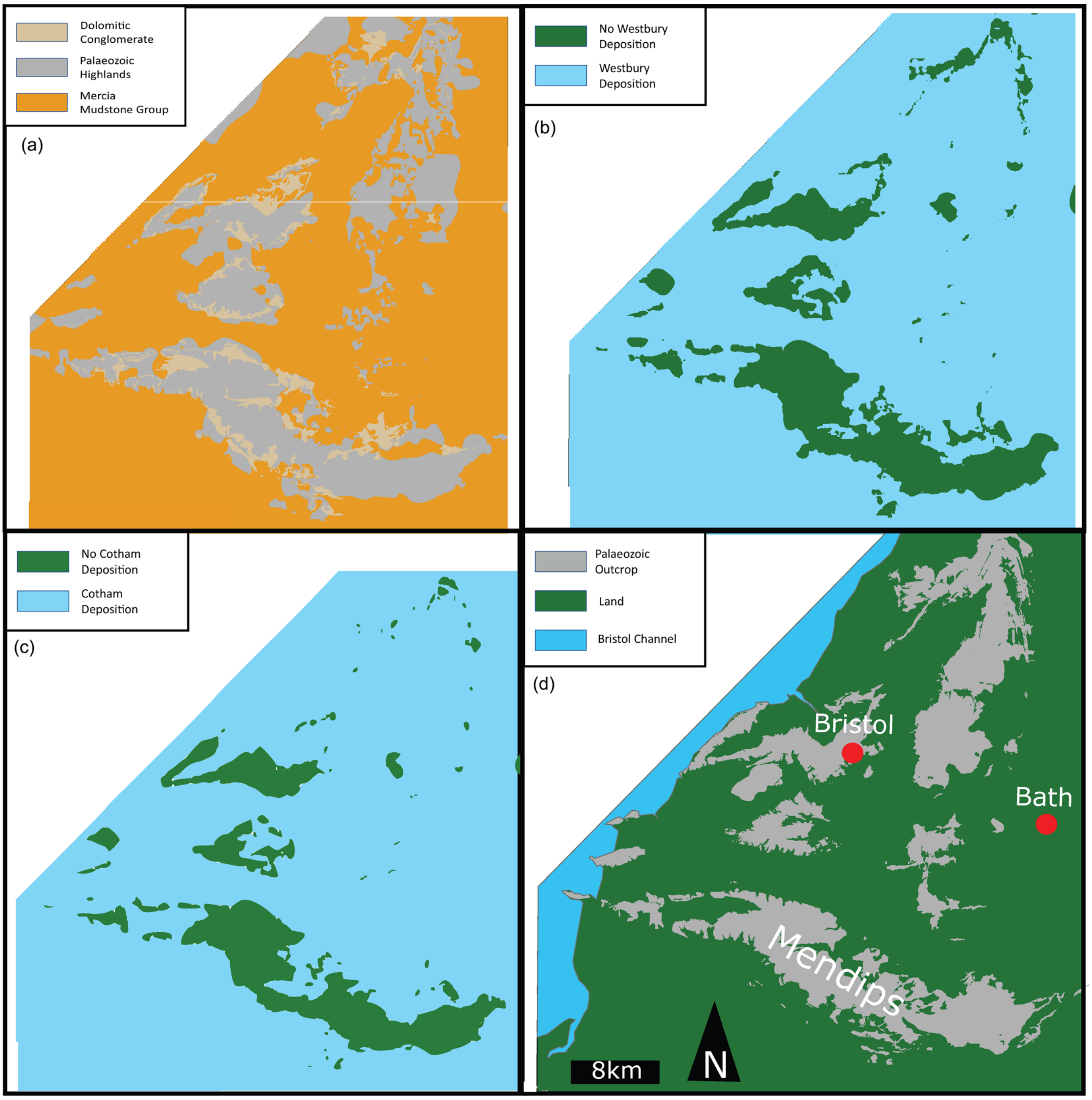

Fig. 9. Environmental succession. Four 2D maps showing three snapshots of the changing environment during the (**a–c**) Late Triassic compared with (**d**) the Paleozoic outcrops of the present day. The three Triassic snapshots are (**a**) deposition of the uppermost Mercia Mudstone Group, (**b**) deposition of the lowest Westbury Formation and (**c**) deposition of the uppermost Cotham Member. Areas labelled with a formation/group name represent areas where that group was deposited.

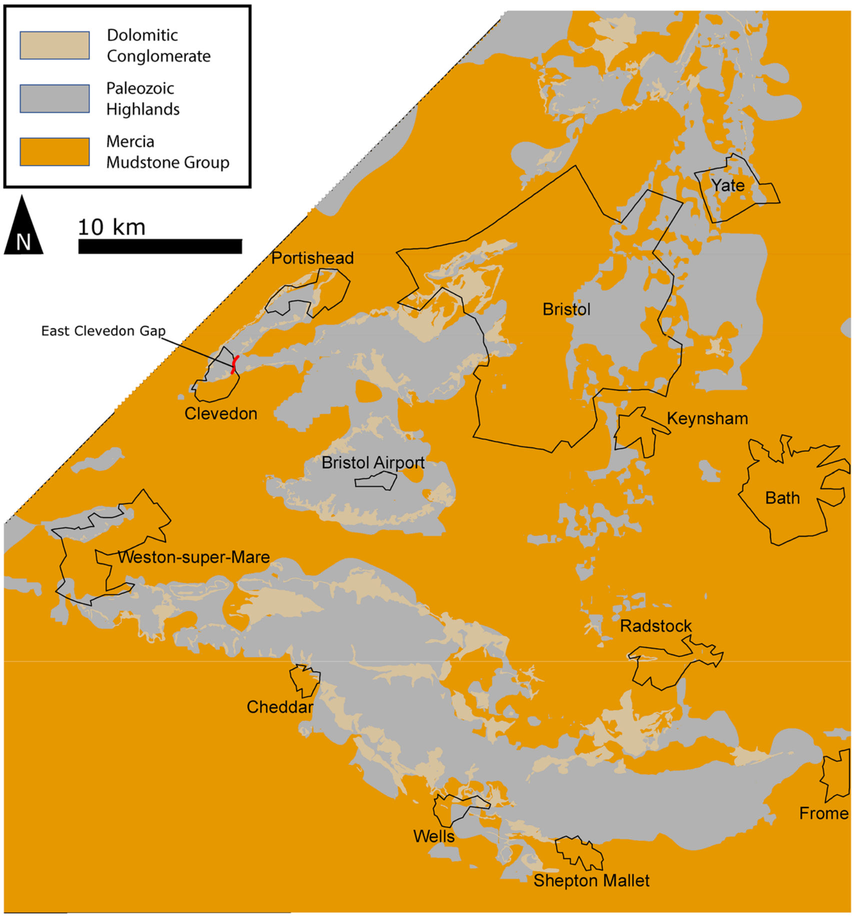

Fig. 10. Arid uplands of the Mercia Mudstone Group. The map shows the locations of the Paleozoic uplands at the time of deposition of the top of the Mercia Mudstone Group. The conglomeratic marginal facies of the Mercia Mudstone Group (the 'Dolomitic Conglomerate') is also mapped. Built-up areas are outlined in black.

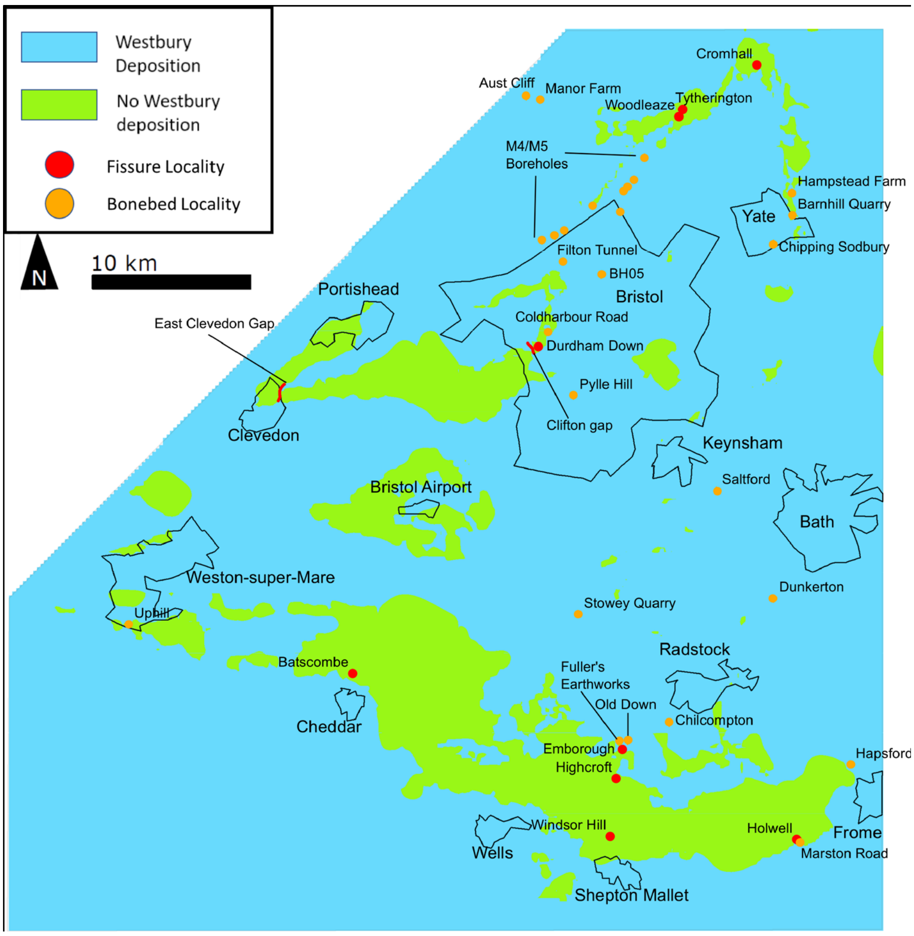

Fig. 11. Bristol archipelago map (base of the Westbury Formation). The map shows the location of the palaeoislands of the Bristol archipelago at the time of deposition of the lowest Westbury Formation. The shallow seas between the islands are represented by areas with deposition of the Westbury beds. Fissure fill localities and described basal bone beds are marked with red and orange dots, respectively, and built-up areas are outlined in black.

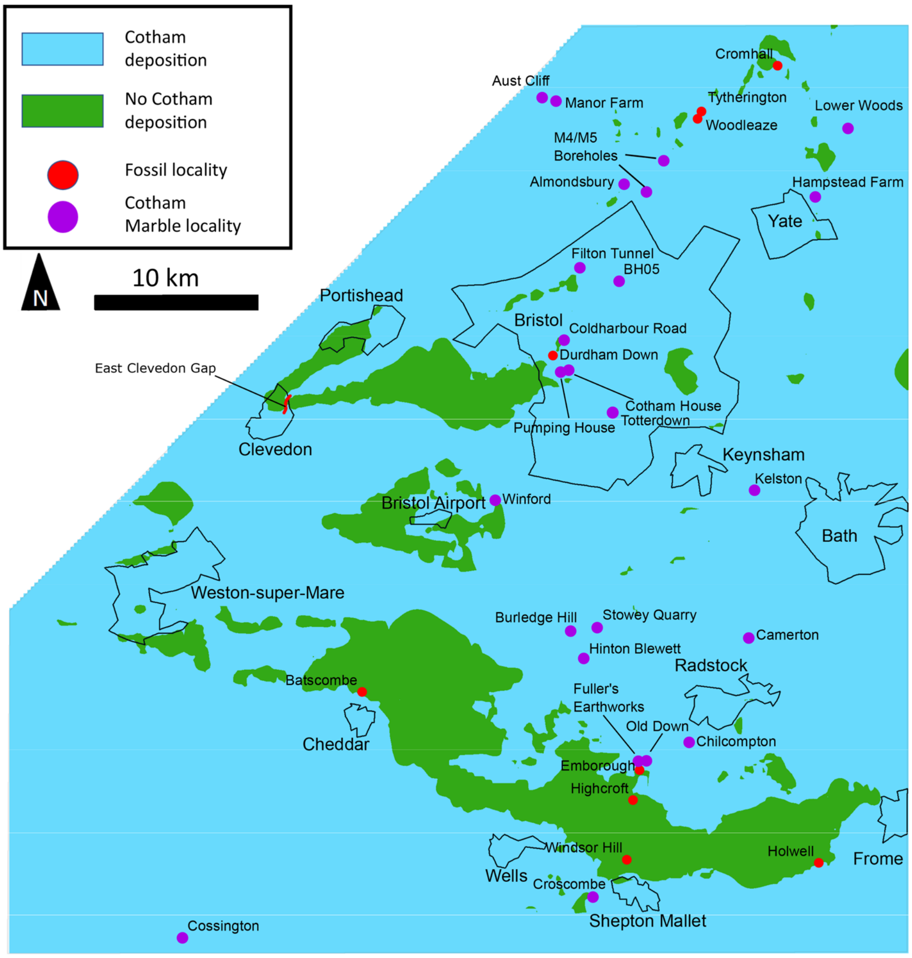

Fig. 12. Bristol archipelago map (top of the Cotham Member). The map shows the location of the palaeoislands of the Bristol archipelago at the time of deposition of the uppermost Cotham Member. The shallow seas between the islands are represented by areas with deposition of the Cotham Member. Fissure fill localities and described Cotham Marble localities are marked with red and purple dots, respectively, and built-up areas are outlined in black.

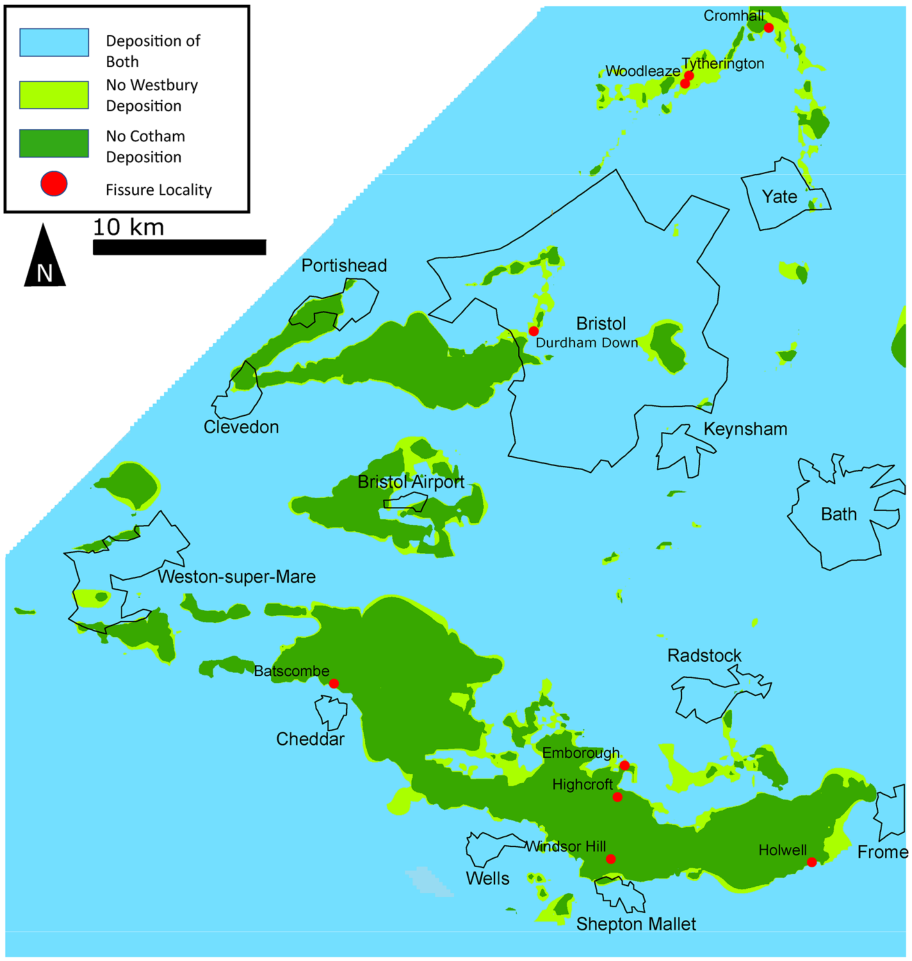

Fig. 13. Bristol archipelago map (comparison map). The map shows the palaeoislands during the time of deposition of the lowest Westbury Formation and uppermost Cotham Member. The shallow seas between the islands are represented by areas with deposition of Westbury Formation or Cotham Member. Fissure fill localities are marked with red dots, and built-up areas are outlined in black.

Table 1. *Palaeoisland areas derived from the geographical information system analysis of the Bristol archipelago*

	Mendip Palaeoisland	Broadfield Palaeoisland	Cromhall Palaeoisland	Tytherington Palaeoisland	Durdham–Failand Palaeoisland (conservative)
Base of Westbury Formation	146.35	11.46	4.77	6.89	26.14
Top of Cotham Member	103.61	9.55	0.72	NA	13.43

NA, not applicable.
Areas are in km^2 and are minima calculated for the times of deposition of the basal Westbury Formation and the uppermost Cotham Member, Lilstock Formation. ‘Conservative’ refers to the island area of Durdham–Failand Palaeoisland assuming that the Clevedon Gap exists, but the Clifton Gap does not (see Fig. 11). The size of Tytherington Palaeoisland is calculated for the basal Westbury Formation and the Cromhall Palaeoisland for the basal Westbury Formation and the uppermost Cotham Member. For a joint Cromhall–Tytherington Palaeoisland area estimate without the Sodam stream gap, see Supplementary Material.

sea-level rises. Further detail of these changes is provided for the Mendip Palaeoisland (Fig. 14) and the Cromhall–Tytherington Palaeoisland systems (Fig. 15), shown against the detail of modern maps. We also illustrate the nine major palaeoislands and suggest names for them (Fig. 16).

Discussion

The GIS approach used in this study presents the most complete picture yet of the palaeogeography and evolution of the island archipelago that developed across the Bristol–Mendip Massif during the Rhaetian transgression (Figs 9–15). By cross-plotting other datasets against the surfaces, we can also improve our broader understanding of: (1) the age of the fissures; (2) the distribution of the bone beds; and (3) the island palaeogeography. Each of these is considered in the following sections.

Distribution and bedrock geology of the islands

The shape of the islands is clearly controlled by the folded and thrusted structure of the Paleozoic basement, which forms a series of elevated, sinuous fold limbs and anticlinal crests. As previous researchers have noted, the islands are mainly Carboniferous limestone, partly as a consequence of the relatively slow denudation rate of carbonates under the arid climate of the Permian and Early Triassic (Simms 2004). Late Devonian sandstone and Silurian igneous rocks (in the eastern Mendips) would have formed smaller components of the island bedrock.

A naming scheme for the islands of the Bristol–Severn archipelago is introduced here (Fig. 16), partly based on the terms used previously for the fossiliferous islands by earlier researchers, but largely new. The three palaeoislands with fossiliferous fissure fills are the Mendip Palaeoisland (MPI), the Cromhall–Tytherington

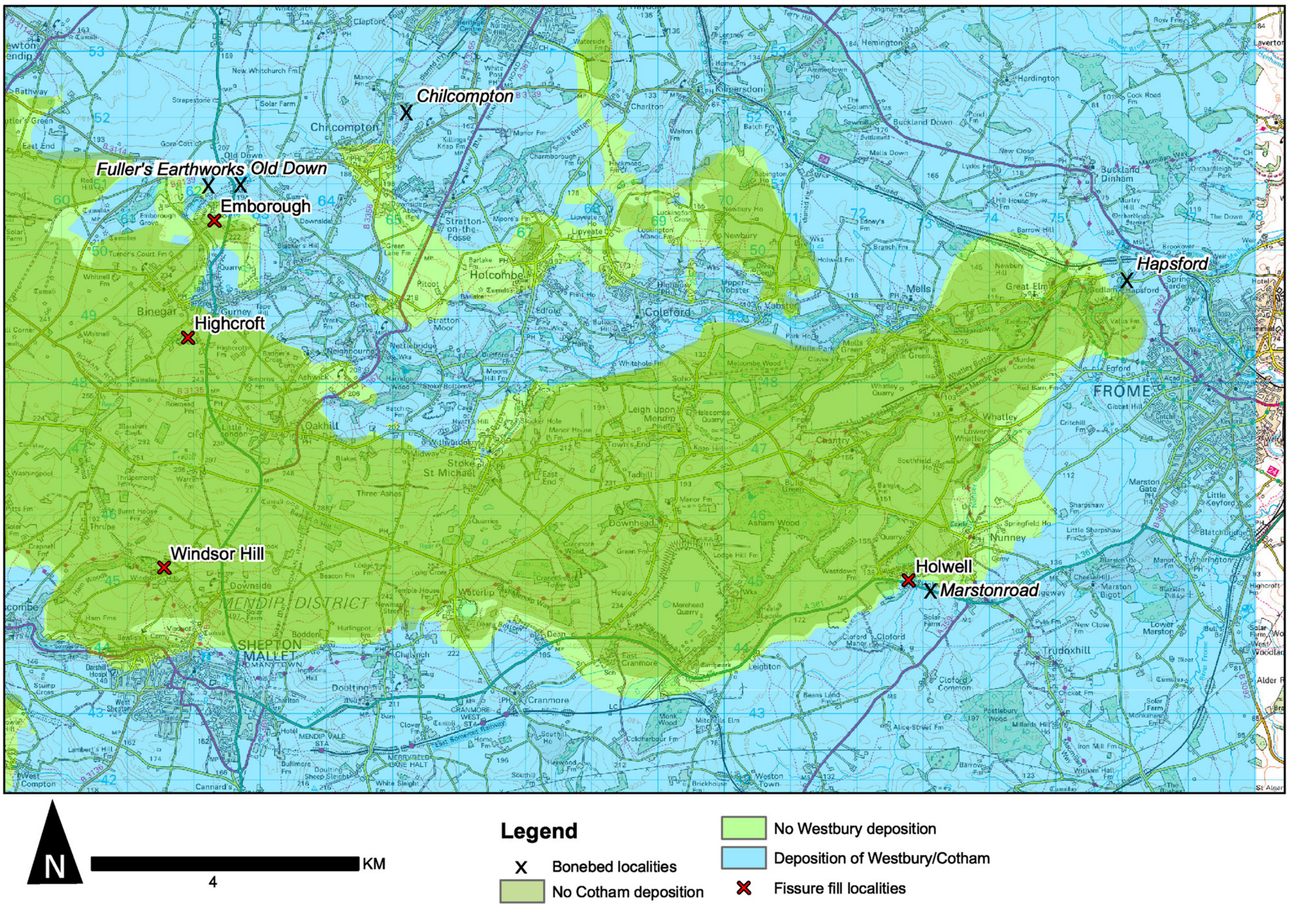

Fig. 14. Transparent map of the eastern Mendip Palaeoisland. Transparent overlay of Figure 13 over an Ordnance Survey map giving a more detailed view of the fissure fill localities on the Mendip Palaeoisland and their position relative to the palaeoisland shoreline. Fissure fill localities are marked with a red cross and bone bed localities are marked with a black cross. Contains Ordnance Survey Data © Crown Copyright and database rights 2021. Ordnance Survey Licence No. 100021290 EUL.

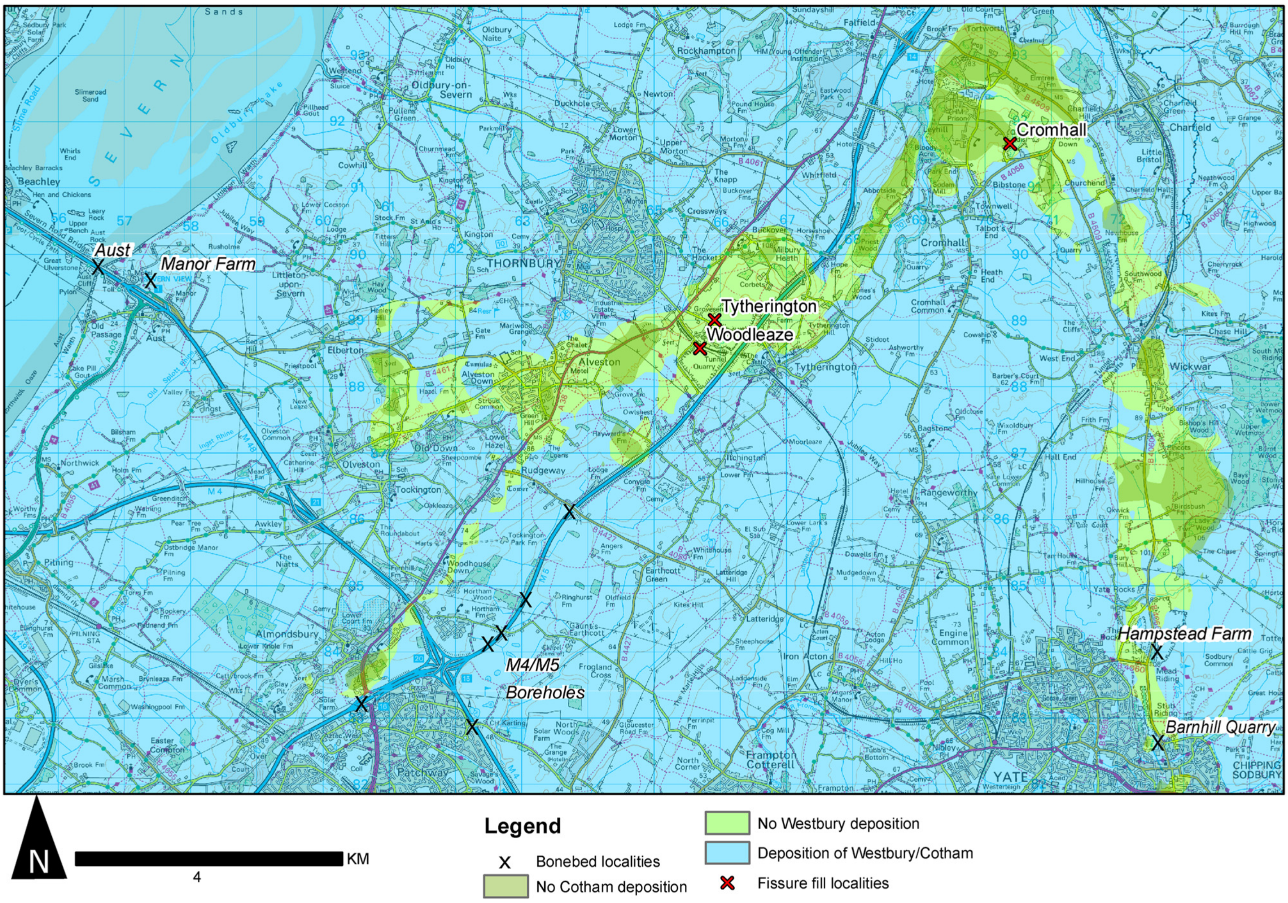

Fig. 15. Transparent map of the Cromhall–Tytherington Palaeoisland. Transparent overlay of Figure 13 over an Ordnance Survey map giving a more detailed view of the fissure fill localities on the Cromhall–Tytherington Palaeoisland and their position relative to the palaeoisland shoreline. Fissure fill localities are marked with a red cross and bone bed localities are marked with a black cross.

Palaeoisland (CTPI) and the Durdham–Failand Palaeoisland (DFPI). Other islands, so far without described fossiliferous fissure fills in the karst, are named here as the Broadfield Palaeoisland (BPI), the Bleadon Hill Palaeoisland (BHPI), the St Thomas Palaeoisland (STPI), the Kingswood Palaeoisland (KPI), the Wick Rocks Palaeoisland (WRPI) and the Paulton Palaeoisland (PPI).

Although we are reasonably confident of the outline of the four major palaeoislands (the MPI, CTPI, DFPI and BPI), there are unresolved questions concerning the outline of the DFPI. This island has an unusually attenuated shape (Figs 12 and 13), featuring a sharp bend at the west end at Clevedon and an outlying small extension at the Clifton end. It is unclear to what extent these points were marked, or not, by marine flooding. The Clevedon Gap (Figs 10–12), identified in earlier work (e.g. Robinson 1957; Whiteside *et al.* 2016), is a narrow break (*c.* 135 m) between the main part of the DFPI and the Clevedon–Portishead Carboniferous limestone outcrop at the time of MMG deposition. Our GIS mapping indicates continuous land across this point (Figs 12 and 13), so it might represent filling by non-marginal MMG (‘Dolomitic Conglomerate’), whereas some studies (e.g. Gilbertson and Hawkins 1978) were unable to locate MMG deposits in this valley and interpreted it as a Quaternary glacial feature. It is equally plausible that we show continuous Paleozoic outcrop across this area because a lack of input subsurface data from around the Clevedon Gap.

The second gap in the DFPI separates the Clifton portion containing the Durdham Down fissure during the deposition of the Westbury Formation (Figs 10–13). This gap is located around the Ladies Mile road, *c.* 300 m to the east of the Avon Gorge, but its cause is uncertain. It might have been created artificially through the extensive quarrying, infilling and landscaping of the area during previous centuries. Further, a deposit in this area mapped by the BGS as interbedded Westbury/Cotham formations pulled the base of the Westbury surface to a higher altitude in our GIS modelling, but may not include the base of the Westbury Formation. When calculating the area of the DFPI, the conservative view is taken that the Clevedon Gap was present during the deposition of the base of the Westbury Formation, but the Clifton Gap was not.

There is little doubt that these land masses became isolated at the beginning of the Rhaetian transgression during deposition of the BAF/early Westbury Formation. There were cycles of transgression and regression throughout the Rhaetian (e.g. Hamilton 1962), but the land area shrank overall through this interval and is much smaller at the top of the Cotham Member than in the basal Westbury Formation (Fig. 13).

Implications for a mixed origin for the ‘Dolomitic Conglomerate’

The ‘Dolomitic Conglomerate’, now termed the MMG (marginal facies), including brecciated and large rounded clast fabrics, borders the limestone–sandstone islands and indicates scree slopes on the steep contours of the land masses. This rock is usually considered to have accumulated in dry valleys, canyons or wadis during the time of deposition of the MMG (Fig. 10). However, similar brecciated rock is found in the fissure deposits of Durdham Down and Tytherington. In Tytherington, fissure 2 (Whiteside and Marshall 2008; Mussini *et al.* 2020), the clasts include unaltered Carboniferous limestone and dolomitized Carboniferous limestone, which can be either white or yellow. These clasts derive from metasomatically changed Carboniferous limestone from other

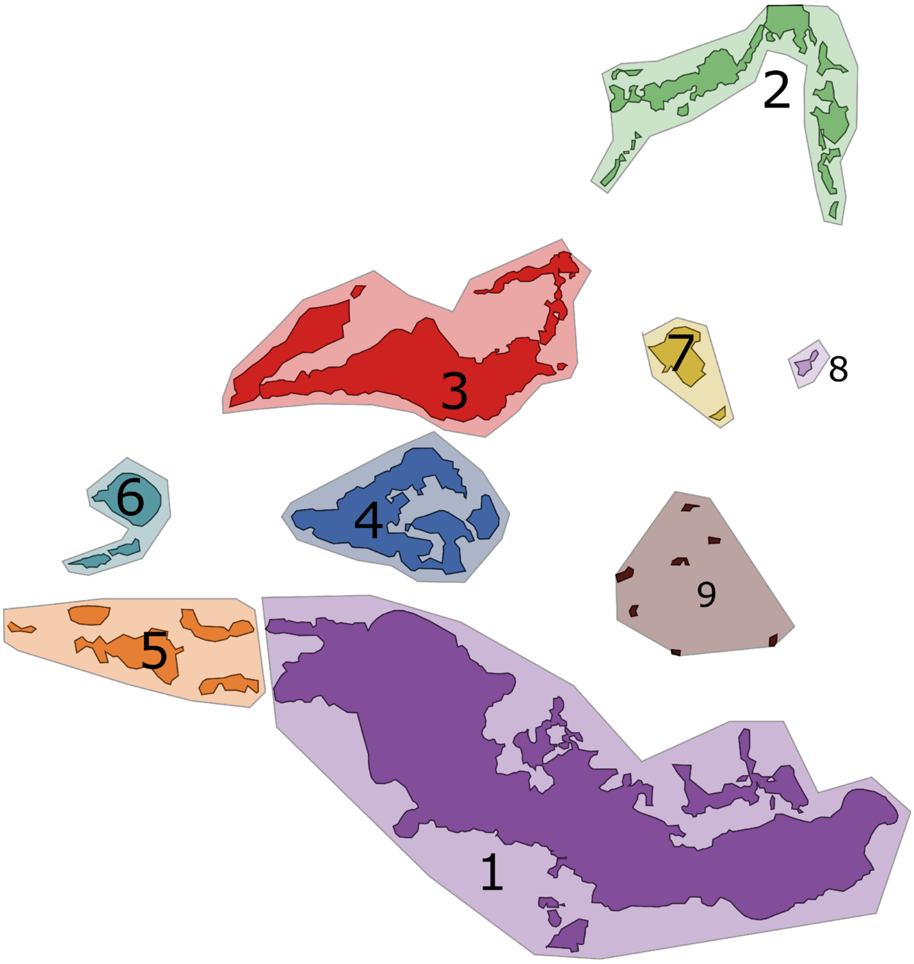

Fig. 16. Map of the main palaeoislands and island chains of the Bristol archipelago. The numbered palaeoislands are: 1, Mendip Palaeoisland; 2, Cromhall–Tytherington Palaeoisland; 3, Durdham–Failand Palaeoisland; 4, Broadfield Palaeoisland; 5, Bleadon Hill Palaeoisland; 6, St Thomas Palaeoisland; 7, Kingswood Palaeoisland; 8, Wick Rocks Palaeoisland; 9, Paulton Palaeoisland.

fissures immediately above; the range of dolomitized Carboniferous rock in the clasts was observed *in situ* in another fissure at Tytherington (Mussini *et al.* 2020). There are also repeated sequences of large rounded clast 'Dolomitic Conglomerate' in the same lower Rhaetian fissure. It is possible that some of the deposits of 'Dolomitic Conglomerate' could have formed by cavern collapse on the island margins, but it is more likely that most of the palaeoislands were sufficiently steep that the breccia accumulated during flash rainstorms with lithification and dolomitization by saline waters *in situ*.

Implications for the Westbury bone beds

North of Bristol, known locations of the basal bone bed of the Westbury Formation occur in what would have been shallow water (10–30 m deep; MacQuaker 1994), along the chain of small islands that lead from the DFPI to the CTPI, as well as at Aust and Manor Farm, although bone bed sites also occur on palaeohighs, such as in Barnhill and Hampstead Farm Quarries (Fig. 13). Recently described basal Westbury Formation bone beds in the southern area also include the offshore location of Stowey Quarry and the marginal Hapsford and Marston Road sites. Marston Road is especially interesting as it occurs very close to the Holwell fissure site and the two share faunal elements. The Marston Road classic marine basal Westbury Formation bone bed yields fossils of terrestrial reptiles (Nordén *et al.* 2015) and the Holwell site neptunian dykes including diverse terrestrial reptiles and mammals, as well as marine fish remains.

The Westbury Formation at Hapsford, at the easternmost end of the MPI, shows evidence of classic littoral facies, with boring of the Carboniferous limestone under shallow seawater by marine invertebrates, then storm activity and the removal of blocks of that limestone. The limestone blocks then became encrusted with Rhaetian-age oysters and were deposited in the jumbled breccia of the basal Westbury Formation bone bed (Ronan *et al.* 2020).

An unusual basal Westbury Formation bone bed locality occurs at Saltford, located between Keynsham and Bath (Fig. 13). Here, the bone bed is nearly 1 m thick and consists of unconsolidated sand with vertebrate remains throughout, rather than a thin, cemented concentrated storm bed as elsewhere. Perhaps it lay in deeper water than any of the other sampled Rhaetian basal Westbury Formation bone beds (Moreau *et al.* 2021).

Implications for the Cotham Marble

The Cotham Marble is a bioherm consisting of microbialites and laminar and thrombolytic stromatolites (Fox *et al.* 2020) that formed over an area of *c.* 2000 km^2, extending from north of Bristol to the Dorset coast (Ibarra *et al.* 2014). The Cotham Marble unit sits at the top of the Cotham Member and is particularly well known and prevalent in areas of Bristol and to the north of the city. There is good development of the stromatolitic rock at localities including Aust (Cross *et al.* 2018), Manor Farm Quarry (Allard *et al.* 2015), sites between Almondsbury and Tytherington (Fig. 11; Slater *et al.* 2016) and at Wetmoor Wood SSSI (NGR ST741877) to the east of Wickwar (and near Hampstead Farm Quarry). Cotham Marble is also found at Stowey Quarry (Fig. 9; Cavicchini *et al.* 2018) and in other localities south of Bristol (Fig. 12).

The Cotham Marble has been traditionally considered as forming in intertidal (Hamilton 1961) or schizohaline waters (Mayall and Wright 1981) that fluctuated between hypersalinity and freshwater. The shallow waters around the archipelago islands would have provided this environment. Recent work by Fox *et al.* (2020) emphasizes that freshwater indicators are prevalent in the Upper Cotham Member. Modern day microbialites are well documented in hypersaline conditions, but others are found in freshwater environments, such as the living thrombolites and stromatolites of Lake Clifton, Western Australia, which remains 'at or below seawater salinity levels throughout much of the year' (Moore and Burne 1994). There salinity varies depending on the seasonal rainfall and evaporation rates, but there is also a highly saturated Ca^{2+} groundwater input (Moore and Burne 1994). Stromatolites today are limited to water depths of 4 m because the cyanobacteria need sufficient light for growth; the thrombolites in Lake Clifton occur in waters 1–3.5 m deep and can be exposed at times. This information provides a reasonable guide to the probable water level in the vicinity of the DFPI and CTPI during the time of the uppermost Cotham Member. However, desiccation cracks within the laminae (Ibarra *et al.* 2014) suggest localized subaerial exposure.

Implications for distribution, age and origin of the fissures

A comparison of the interpolated stratigraphic horizons with fissure localities shows that the fissures are almost invariably located on the marine margins of the palaeoislands. This is true of the three large palaeoislands, including the best-known sauropsid fissures at Batscombe, Cromhall, Durdham Down, Emborough, Tytherington and Woodleaze (Figs 1, 11 and 12). These fissures have produced mixed terrestrial/marine palynomorphs at Tytherington (Marshall and Whiteside 1980; Whiteside and Marshall 2008) and scarce marine fish in the island margin fissures at Tytherington, Cromhall, Durdham Down and Woodleaze (Whiteside *et al.* 2016).

There are other records on the island margins. For example, Fraser (1994) reported a *Planocephalosaurus* maxilla in a Mesozoic fissure in Barnhill Quarry (Fig. 11; part of the CTPI) where no other terrestrial tetrapod is recorded. It is likely that fissures with terrestrial tetrapods are present on the main area of the DFPI, BPI and other land masses to the west of the MPI. Carboniferous limestone quarries in some of these areas (e.g. at Lulsgate, Failand and quarries near Portishead–Clevedon) have been visited a few times by DIW and others, but with very limited success (Rhaetian shark fossils were found in a fissure near the Clifton Suspension Bridge and a fish scale in a Lulsgate Quarry fissure).

The location of the fissures near the saline–freshwater margin of the islands (Figs 14 and 15) is probably a causal factor in cavern and doline formation, as suggested by Whiteside and Marshall (2008) and Whiteside *et al.* (2016). Infilling of the cavities would have occurred when precipitation, rather than dissolution, of calcium carbonate was favoured, presumably as the waters in the vicinity of the voids became more saline or during minor regressions when meteoric waters dumped their sedimentary load. Associated skeletal fossils (e.g. at Emborough, Batscombe and Woodleaze) and rare articulated skeletons (e.g. at Cromhall; Whiteside *et al.* 2016, their fig. 5) probably indicate nearby high marine waters at the time of deposition.

Our terrain models provide evidence in the debate over the age of the Bristol region fissure fauna. All of the fissure fauna localities, with the exception of Holwell, were located on islands at the beginning of deposition of the Westbury Formation, but the Tytherington, Woodleaze and Durdham Down localities were submerged by the time of deposition of the top of the Cotham Member. The fact that the Holwell fissures were filled in a marine rather than terrestrial environment supports its interpretation as a neptunian dyke (Robinson 1957). The BPI is unique among the four major islands in not having yielded any terrestrial fauna, although the island does have fissure fills (Whiteside 1983).

Our GIS study enables us to test the earlier suggestion (Whiteside and Marshall 2008; Whiteside *et al.* 2016) that the fissure heights indicate they were all Rhaetian or younger (Supplementary Material, Table S3). We can confirm that all the sauropsid fissures would probably have been emergent at the start of the Rhaetian transgression, which contradicts the views of Robinson (1957) and Fraser (1985) that Rhaetian beds covered the fissure openings (Fig. 14), so dating the Emborough fissure sediments as Norian. Emborough is the most marginal fissure site, at 2 m above the base of the Westbury Formation, smaller than the 7 m value shown by Whiteside *et al.* (2016, their fig. 7). That previous estimate used the highest point of the limestone within 50 m of the fissure to allow for the reduction in the height of the land surface from cavern collapse, evidenced by conglomerates with large boulders of Carboniferous limestone in the upper part of the fissure fill (Savage 1977). In our GIS-based analysis, we base our measurements on the limestone height at the fissure entrances, with the fissures submerged by *c.* 3 m at the time of the latest Cotham Member.

The assumption by earlier researchers that fissures such as Emborough were flooded by the Rhaetian transgression was based on the fact they were inundated by rising sea-levels by the top of the Cotham Member, even though they were still emergent at the basal Westbury Formation. It is also worthwhile emphasizing that at least the uppermost BAF is considered to be Rhaetian and there are marine fossils known from the stratum (e.g. Landon *et al.* 2017). Savage (1977) recorded 'Rhaetic fossils' in the subsoil, suggesting that, at times during deposition of the Westbury Formation, marine waters intruded onto the land close to the fissures.

The Batscombe fissure fauna was dated by Whiteside and Marshall (2008) as similar in age to those at Emborough because of the occurrence of the gliding reptile *Kuehneosuchus* in the former and the similar *Kuehneosaurus* in the latter. However, the Batscombe fissure is much higher than the Emborough fissure, well above the basal Westbury Formation (*c.* +52 m) and the top of the Cotham Member (*c.* +43 m). *Kuehneosuchus* therefore survived much later on the MPI than *Kuehneosaurus*, possibly into the Early Jurassic, but further study is needed.

Whereas the MPI would have been hilly (>170 m above Rhaetian sea-level) with steep sides, the smaller northern DFPI and CTPI would have been lower lying at the time of initial deposition of the Westbury Formation, perhaps as low as 5 m above its base, with some of the fissure entrances at Cromhall and Tytherington possibly up to 11 m above the Westbury Formation. The limestone or sandstone surface might have been a few metres higher, but the narrow fissure entrances seen above Rhaetian caverns in fissure 13 at Tytherington (Whiteside 1983; Whiteside and Marshall 2008) and the Cromhall fissure shown by Whiteside *et al.* (2016, their fig. 5) suggest that they were near the top of the Late Triassic terrain. In contrast with all other UK Triassic fissure locations, small solution dolines are numerous at Cromhall and Tytherington. This confirms the suggestion that the CTPI was low-lying because dolines tend to be absent on steep slopes. Our analysis suggests that the fissures at Woodleaze (on the CTPI) and Durdham Down, at 5 m above the basal Westbury Formation, filled earlier than some fissures in Tytherington Quarry. The more marine-marginal position of Woodleaze supports the suggestion of Klein *et al.* (2015) that its very limited fauna inhabited limestone terrain subject to some saline intrusion in the lower Westbury Formation.

By contrast, some fissures at Cromhall were probably unfilled until after the end of the Cotham Member (Fig. 15). This is in accord with the finding of the Cotham biostratigraphic indicator, the conchostracan *E. brodieana*, in Cromhall fissure deposits by Morton *et al.* (2017). The terrestrial fauna of Cromhall Quarry is the most taxonomically diverse (Fraser 1994; Whiteside and Marshall 2008) of the sauropsid fissures, which may reflect minor regressions or lowstands of sea-level during the lower Cotham

Member. Warrington in Poole (1978), Hesselbo *et al.* (2004) and Fox *et al.* (2020) provide biomarker evidence of the lowstand and freshwater conditions in the Upper Cotham Member. This sea-level lowstand may also explain the presence of *E. brodieana* in fissure 12 at Tytherington and the higher diversity of fissure 14; parts of the limestone surface close to Tytherington Quarry (Fig. 15) were emergent during the time of deposition of the Cotham Member, supporting these suggestions. Although the CTPI was probably continuous in the Lower Rhaetian (Westbury Formation), it had split into many smaller islands by the end of the Cotham Member. The largest of these islands includes the main fossiliferous fissures of Cromhall Quarry (Fig. 15), which may have been > 3 m above the top of the stratum.

Changing island areas and faunas

Palaeoisland sizes reduced through the Rhaetian (Fig. 13; Table 1) and this was especially true of the CTPI, where a single sickle-shaped land mass reduced to a string of 15–20 small islands through 4–5 myr of flooding. Although the CTPI was split in two by a narrow channel even at the time of deposition of the earliest Westbury Formation (Fig. 11), this channel was extremely narrow and might be an artefact created by the Sodam stream valley, so was probably not a barrier to all but the smallest taxa. This is supported by the similarity of the three CTPI fissure localities (Cromhall, Tytherington and Woodleaze), with the rhynchocephalians *Clevosaurus* and *Diphydontosaurus* in all three and *Planocephalosaurus* and *Terrestrisuchus* also found at both Tytherington and Cromhall. However, there are differences, with the impoverished Woodleaze fauna dominated by *Clevosaurus sectumsemper* and a similar species from Tytherington (Klein *et al.* 2015), but not recorded from Cromhall. The dinosaur *Thecodontosaurus* is absent (or extremely rare) at Cromhall, but abundant at Tytherington. The shrinking and fragmentation of the CTPI (Fig. 13) may have resulted in the extinction of the largest tetrapod, *Thecodontosaurus*, through the Rhaetian.

The separation of the DFPI, very early in the Rhaetian, from the CTPI to the north might explain some differentiation between the *Thecodontosaurus* on these islands, with a more robust morph from Durdham Down, but not Tytherington (Foffa *et al.* 2014; Ballel *et al.* 2020). Our data suggest that the DFPI was separate from the CTPI in the basal Westbury Formation and was inundated by the end of the Cotham Member, but it is possible that it was partially emergent during lowstands of the late Rhaetian sea.

Isolation from other land masses

The main sources from which the terrestrial tetrapods might have migrated onto the islands would have been nearby islands and neighbouring land masses. The large Welsh Landmass lay *c.* 40 km from the CTPI and 60–70 km from the MPI, which is also about the distance from that island to the Cornubia Massif (Fig. 3). These palaeoislands were more remote (>120 km) from the large London–Brabant Massif. The long distance from major faunal reservoirs could be the reason why cynodonts are apparently absent from the CTPI. By contrast, however, cynodonts are found in Holwell and St Brides quarries, which are likely to have been contemporaneous with some fissure fills in the CTPI. It is possible that a greater diversity of niches was present on the higher islands of the MPI and St Brides Palaeoisland, which favoured mammaliamorphs. Alternatively, it could be that cynodonts travelled to the southern islands from the Cornubia or London–Brabant Massifs, or they were unable to reach the north Bristol–Severn archipelago before inundation of the islands. Perhaps cynodonts were absent on the Welsh Landmass in the early Rhaetian. The South Wales Ruthin fissure fauna is probably the earliest of the whole region, possibly Norian–Rhaetian and most likely equivalent to the basal Westbury Formation (Skinner *et al.* 2020). The Ruthin Palaeoisland fauna was a remnant of a continental fauna almost certainly derived from the Welsh land mass and no cynodont is recorded from the fissure (Skinner *et al.* 2020).

As for modern islands, it would be expected that animals that were good dispersers over water would have been best at colonizing the islands. If amphibians had been present, the most likely place would have been the MPI because it had the highest elevation and would have had habitats sufficiently distant from saline waters. However, with the exception of Batscombe, all the fissure localities of the MPI are at the palaeoisland marine margins, so amphibians are unlikely to be found there.

Our palaeogeographical model (Figs 13 and 16) suggests that there was a chain of small islands in a shallow sea running from the DFPI to the CTPI, which would have provided an island-hopping route for terrestrial tetrapods after the initial phase of the Rhaetian transgression. There might have been rapid changes in sea-level in this area and therefore too in island size, where some islands would shrink and others would unite to form larger islands. The effect would have been local extinctions as small populations on very small islands became unviable, or new opportunities for surviving taxa or new immigrant species as the islands expanded. The uniting of small islands could lead to the hybridization of closely related subspecies or to the extinction of new allopatric species.

The relatively rapid changes in land area of the northern archipelago would have favoured opportunistic colonizers that thrived in niches subject to saline intrusion. *Clevosaurus* and *Diphydontosaurus* are found in these palaeoenvironments, just as they are found in great abundance in the fissures with a marine influence at Tytherington and Woodleaze (Mussini *et al.* 2020).

Overall, there are distinct faunal differences between the northern parts of the palaeoarchipelago (the CTPI and DFPI) compared with the southern parts (the MPI). Cynodonts and *Variodens* are only found on the MPI and *Planocephalosaurus*, *Pelycymala*, *Sigmala*, a drepanosaur and a multicuspid procolophonid only on the CTPI. Other taxa, known only from one or very few specimens, including *Gephyrosaurus evansae*, *Penegephyrosaurus* (and other unnamed rhynchocephalians figured by Whiteside and Duffin 2017) are confined to the MPI. What is surprising is that the amphibious *Pachystropheus* has not been recorded from the fissures of the DFPI or CTPI, yet it is found in Rhaetian bone bed deposits on the MPI at Holwell and at Hampstead Farm Quarry and Aust Cliff (Mears *et al.* 2016; Cross *et al.* 2018).

Implications for island biogeography

The terrestrial faunas sampled by the fissures provide evidence that can be interpreted in terms of island biogeography theory (MacArthur and Wilson 1967). Modern small island faunas show relatively small body sizes and a low diversity of taxa, but large numbers of individuals; these are all characteristics of the sauropsid fauna found in the Bristol fissures (Whiteside and Marshall 2008). Modern islands also show the species–area effect (the number of species is roughly proportional to the size of the island), the distance effect (islands further from the nearest mainland show fewer species), the dwarfing of large species, the larger size of some small species and sometimes primitiveness as a result of isolation (Foster 1964; Lomolino 1985; Whittaker and Fernández-Palacios 2007; Losos and Ricklefs 2010).

Whiteside and Marshall (2008) were the first to suggest that the Late Triassic faunas of the Bristol palaeoislands might show some of these characteristics of island faunas based on unpublished work by Whiteside (1983). Skinner *et al.* (2020) made an initial quantitative study counting all species. They found some (but not significant) support for the expectation that the larger islands in the Bristol/South Wales archipelago supported higher species richness than the

Table 2. *Palaeoisland areas derived from the geographical information system analysis of the Bristol archipelago (Fig. 16) with taxa counts from intensively worked single localities where dating is known*

Island	Geographical information system area (km^2)	Old area (km^2)	Minimum number of taxa	Maximum number of taxa
Cromhall Palaeoisland Fissure 1	0.72	NA	5	5
Tytherington Palaeoisland Fissure 2	6.89	NA	8	8
Durdham–Failand Palaeoisland	26.14	22	6	7
Mendip Palaeoisland Holwell *'Microlestes'*	146.35	112	16	18
Pant-y-ffynnon		16	8	8
Ruthin		34	9	12
St Brides Pant 4		15	11	11

Basal Westbury Formation for Mendip Palaeoisland, Durdham–Failand Palaeoisland and Tytherington Palaeoisland. Cotham Member for Cromhall site 1 on Cromhall Palaeoisland. Ruthin is basal Westbury Formation, Pant-y-ffynnon middle Penarth Group and Pant 4 Hettangian Lias. Data from Skinner *et al* (2020) provide the 'old area' calculations partly based on Whiteside *et al.* (2016). Further data on taxa present are from Fraser (1994), Foffa *et al.* (2014), Keeble *et al.* (2018), Morton *et al.* (2017), Mussini *et al.* (2020) and Whiteside and Duffin (2017). Ruthin and Pant 4 are also from single-fissure collections and Pant-y-ffynnon from (probably) one collection of fissure material.

smaller islands, but only when the largest palaeoisland, the MPI, was treated as an anomaly. One problem with such an analysis is that species lists from any locality might derive from many fissure strata of different ages spanning thousands or even hundreds of thousands of years. Perhaps the most obvious issue is that the islands are not necessarily equally sampled; some islands such as the DFPI have a single fissure site, whereas others such as the CTPI and MPI have several (Fig. 16). A small island with many fissure sites could yield a larger fauna than a large island with few fissure sites.

In revising the analysis here (Table 1), we attempt to avoid these problems by selecting one well-sampled fissure per palaeoisland (Supplementary Material, Table S4). We ensure that the selected fissures also yield fossils indicative of Westbury Formation or Cotham Member ages. Further, we provide minimum and maximum estimates of species numbers, the latter including unconfirmed taxa such as *Planocephalosaurus* in the DFPI or, in the case of the MPI, two amphibious reptiles (Table 2). We find statistically significant positive relationships for both minimum and

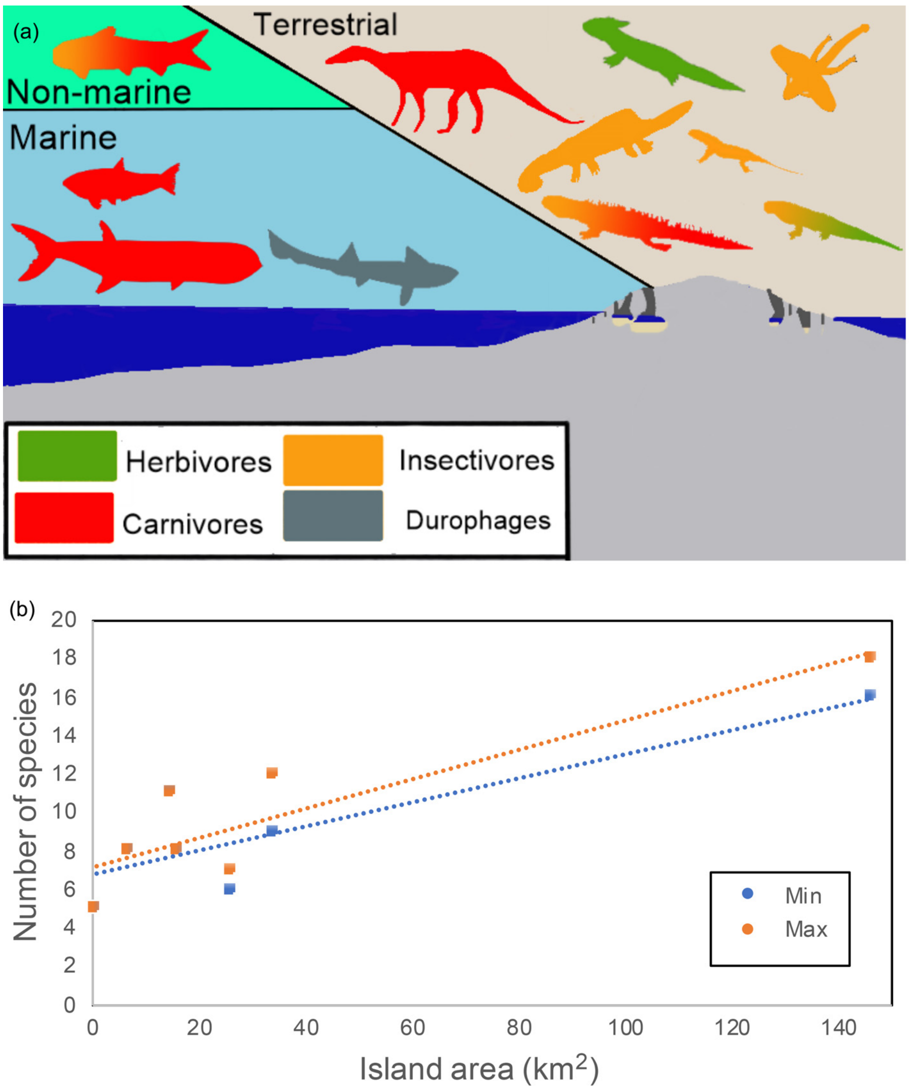

Fig. 17. The species–area effect in the Late Triassic. (**a**) A selection of taxa from the Cromhall fissures shown over a sketched cross-section through the Cromhall–Tytherington Palaeoisland based on the model described in this paper. The silhouettes are divided by environment and coloured based on ecology to show that, despite being mainly known for their terrestrial faunas, the fissures contain a sizeable minority of freshwater and marine taxa. The freshwater fish is *Pholidophorus.* The marine taxa featured are (right to left) *Lissodus*, *Severnichthys* and *Gyrolepis*. The terrestrial taxa featured are (clockwise from top right) a kuehneosaur, *Diphyodontosaurus*, *Planocephalosaurus*, *Clevosaurus hudsoni*, a drepanosaur, *Terristrisuchus*, and a procolophonid. Based on faunal table from Whiteside *et al.* (2016). Taxa not to scale. (**b**) Plot of species counts on each palaeoisland showing highly significant positive slopes for both minimum (blue line, $R = 0.862$, $P = 0.0127$) and maximum (red line, $R = 0.894$, $P = 0.007$) species counts.

maximum counts of species (Fig. 17b), providing good evidence for the species–area effect and support for the hypothesis that these fissure faunas are derived from island communities (Supplementary Material, Tables S5 and S6).

These results are remarkably clear despite the sampling issues noted and more work will be needed to find more comprehensive estimates of species diversity on each island, rather than the one-fissure proxy we used. We cannot control for time-averaging, in other words, the matching of faunas to exact island sizes depending on the exact history of each island as sea level fluctuates. Other evidence that the fissure faunas show island characteristics has been noted before (Skinner *et al.* 2020), including dwarfing of sphenodontians, procolophonids, trilophosaurids and the dinosaur *Thecodontosaurus* compared with mainland relatives (Benton *et al.* 2000). Further, most of these taxa also appear primitive, being most like their Carnian–early Norian relatives, *c.* 20–30 myr older, from mainland deposits in North America and elsewhere.

The land areas of some of the smallest palaeoislands calculated through the GIS (Tables 1 and 2), such as the 72 ha Cromhall Palaeoisland or the 689 ha Tytherington Palaeoisland are sufficient to maintain very sizeable populations of lepidosaurs and other reptiles. Considering modern islands as an analogue, they have a much higher population density of lepidosaurs than the mainland. For example, Buckley and Jetz (2007) recorded average densities of 1920 individuals per hectare on islands compared with a mainland average of 128 individuals per hectare, an order of magnitude greater, and they concluded that the much greater island density is 'a ubiquitous and global phenomenon'. Very small modern day islands can support animals the size of *Theodontosaurus* found at Tytherington Palaeoisland – for example, the Galapagos land iguana, *Conolophis,* an animal similar in size to *Thecodontosaurus* has a large colony on the 13 ha Galapagos island of Sur Plaza (Fisher *et al.* 1969).

Conclusions

The palaeogeography of the Rhaetian Bristol archipelago has been successfully mapped using 3D GIS methods for the first time, demonstrating a new application for these methods. Our mapping demonstrates that land area shrank substantially from the basal Westbury Formation to the top of the Cotham Member. The island masses were flanked by steep screes of the 'Dolomitic Conglomerate,' which is extensively developed around the MPI, BHPI, BPI, DFPI and CTPI. It is much less prominent on the KPI, WRPI and PPI in the area from Yate, through East Bristol and Keynsham, down towards Radstock (Fig. 10). The land areas formed an archipelago of islands in the Rhaetian sea and these islands split into smaller isles and islets as the transgression progressed and sea-levels rose. Our mapping confirms the presence of the Westbury bone beds near the margins of the archipelago and particularly in the vicinity of the chain of palaeoislands between the DFPI and CTPI and towards Yate. The bone bed at Saltford appears to lie in deeper water, which possibly explains its different lithology. The proximity of the Hapsford Bridge and Marston Road bone beds to the margin of the MPI is in accord with their littoral facies and mixed terrestrial marine faunas. In the later Rhaetian, Cotham Marble stromatolitic bioherm localities also flank the small islands of the archipelago, particularly in Bristol and the region immediately north (Fig. 12).

The resolution of the archipelago mapping is high, but further borehole and exposure data would refine the maps further. The East Clevedon Gap and the Clifton area are examples of areas where further data gathering could better resolve the outline of the palaeoislands. We cannot yet, however, refine the maps so that we could establish the land masses in the lowstand of the Cotham Member or regressions within the Westbury Formation. However, we have established the most detailed map of Triassic palaeogeography that we are aware of.

The GIS mapping confirms that the sauropsid fissure fills from Cromhall Quarry and the Mendips region would still have been above water after the start of the Rhaetian transgression and therefore that the fissure fill faunas could post-date this. We also show that some fissure fills, such as at Cromhall Quarry, could have been filled during the deposition of the Cotham Member, whereas others such as Durdham Down and Emborough Quarry are likely to have been inundated during the time of the Westbury Formation. The species richness of the sauropsid fissure faunas shows a strong relationship with island area, in accord with island biogeography theory.

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