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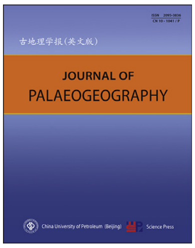

Biopalaeogeography and palaeoecology

Palaeogeographic variation in the Permian—Triassic boundary microbialites: A discussion of microbial and ocean processes after the end-Permian mass extinction

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Abstract Shallow marine carbonate sediments that formed after the end-Permian mass extinction are rich in a thin (maximum *ca.* 15 m) deposit of microbialites. Microbial communities that constructed the microbialites have geographic variability of composition, broadly divisible into two groups: 1) eastern Tethys sites are calcimicrobe-dominated (appearing as thrombolites in the field), with rare occurrence of sediment-constructed microbialites and uncommon cements either within microbial structure or as inorganic precipitates, 2) other Tethys sites are sediment-dominated structures forming stromatolites and thrombolites, composed of micrites and cements, with some inorganic precipitates. These other Tethys locations include western and central Tethys sites but their palaeogeographic positions depend on the accuracy of continental reconstructions, of which there are several opinions. In contrast to geographic variation of microbialites, the conodont *Hindeodus parvus*, which appeared after the extinction and defines the base of the Triassic, is widespread, indicating easy lateral migration throughout Tethys. Conodont animals were active nekton, although being small animals were presumably at least partly carried by water currents, implying active Tethyan surface water circulation after the extinction event. Post-extinction ammonoid taxa, presumed active swimmers, show poor evidence of a wide distribution in the Griesbachian beds immediately after the extinction, but are more cosmopolitan higher up, in the Dienerian strata in Tethys. Other shelly fossils also have poorly defined distributions after the extinction, but ostracods show some wider distribution suggesting migration was possible after the extinction. Therefore there is a contrast between the geographic differences of microbialites and some shelly fossils.

Determining the cause of geographic variation of post-extinction microbialites is problematic and may include one or more of the following possibilities: 1) because calcifying microbial organisms that create calcimicrobes were benthic, they may have lacked planktonic stages that would have allowed migration, 2) eastern Tethyan seas were possibly more saturated with respect to calcium carbonates and microbes, so microbes there were possibly more able to calcify, 3) significant reduction of Tethyan ocean circulation, perhaps by large-scale upwelling disrupting ocean surface circulation, may have limited lateral migration of benthic microbial communities but did not prevent migration of other organisms, and 4) microbes may have been subject to local environmental controls, the mechanisms of which have not yet been recognized in the

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facies. The difficulty of distinguishing between these possibilities (and maybe others not identified) demonstrates that there is a lot still to learn about the post-extinction microbialites and their controls.

Keywords Stromatolite, Thrombolite, Microbialite, Permian—Triassic boundary, Conodonts, Tethys, Mass extinction

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1. Introduction and aim

Permian—Triassic Boundary Microbialites (PTBMs) that formed directly after the end-Permian mass extinction in the latest Permian and earliest Triassic strata occur principally in the low to middle latitudes of Tethys Ocean (Flügel, 2002). Published work by many authors has established a well-developed pattern of microbialite palaeogeographic distribution that has significant geographic variation, principally between western and eastern Tethys, synthesized by Kershaw *et al.* (2012) and outlined later in this paper. However, the key biostratigraphic indicator of the base of the Triassic, the conodont *Hindeodus parvus*, is used as a correlation tool because it was rapidly widespread in a very short time period after the extinction (with possible diachroneity of occurrence, see Zhang *et al.*, 2014). *H. parvus* fossils are the teeth elements of small nektonic chordate-like animals (*e.g.*, Briggs *et al.*, 1983), which although they were mobile, were small and so were presumably also carried by ocean currents. The distribution of *H. parvus* was presumably assisted by active surface ocean circulation. Models indicate a mixed upper ocean across Tethys (*e.g.*, Kidder and Worsley, 2004), with development of gyres in Tethys. Mixed ocean surface waters occur because of wind blow across the ocean surface, which is the principal control on formation of surface ocean circulation. If such circulation patterns really existed then this raises the question of why microbialites are so different between eastern and western Tethys, given that they were most likely composed of bacteria and cyanobacteria. Therefore the aims of this paper are to assess the forces governing these differences and to contribute the knowledge of processes and events in the aftermath of the Earth's largest mass extinction at the end of the Permian period.

This paper is a discussion based on published information. No new data are presented here, and the arguments use the range of current published knowledge of the Permian—Triassic transition facies and biotas. This paper considers key observations of major features of microbia, followed by discussion of the implications for the Permian—Triassic boundary biology and oceanography.

2. Key observations of microbialite construction and distribution

In both eastern and western Tethys, microbialites occur directly after the extinction event and form layered in-place structures that are most appropriately called biostromes. These microbialite biostromes are very thin, maximum *ca.* 15 m thick, and disappear from the rock record as sharply as they appear after the extinction, interpreted by Kershaw *et al.* (2012) to be facies limited, in shallow waters only, and disappeared when water deepened during the post-extinction transgression. Controls on individual microbialite deposits are much debated in the literature, but the palaeogeographic aspects have been given less attention.

The post-extinction microbialite pattern compiled by Kershaw *et al.* (2012) shows that eastern Tethyan PTBMs are most abundant on the South China Block, across the Yangtze Platform, and are largely represented by microbialites which in the field look like thrombolites, commonly with a dendritic macrofabric. However, although these are substantially recrystallized, there is sufficient preservation to demonstrate that the most common well-preserved component is a *Renalcis*-like calcimicrobe (Fig. 1), occurring throughout the Yangtze Platform so that in many places the microbialite can be demonstrated to be a frame-built calcimicrobial biostromal deposit. Sediment-constructed stromatolites occur in some localities (Yang *et al.*, 2011) and a subordinate small shelly fauna, principally of ostracods and gastropods is widespread. In some sites, microbiotas are also proved (Yang *et al.*, 2015). Some of the microbialites are regarded as comprised of clotted fabrics by Zheng *et al.* (2016),

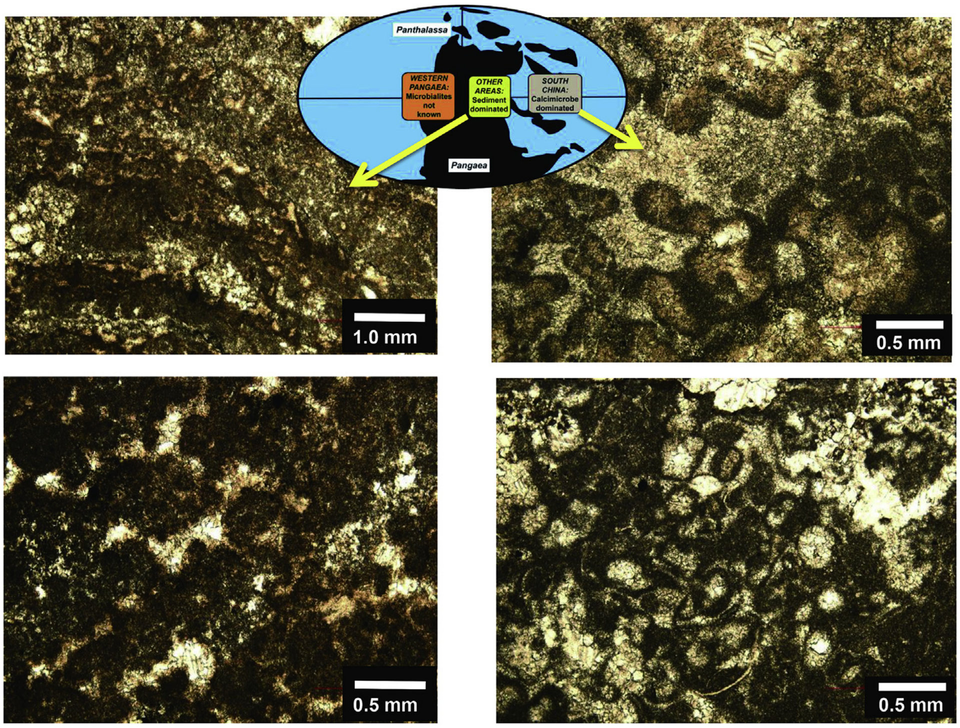

Fig. 1 Thin section photomicrographs of the construction of microbialites directly after the end-Permian mass extinction. The left-hand photographs show stromatolite and thrombolite from Turkey, typical of the western Tethyan microbialites, composed of microbial carbonate sediment. The right-hand photographs show the *Renalcis*-type calcimicrobes that are common in eastern Tethyan sites, of South China. Calcimicrobes are almost completely absent from western Tethyan sites, and in contrast, sedimentary stromatolites and thrombolites are rare in South China. The inset map shows a summary palaeogeography with location of each broad type of microbial material. Note that post-extinction microbialites have not yet been demonstrated in western Pangaea in locations where they may be expected, given their abundance in Tethys; thus the microbialites are essentially a Tethyan phenomenon. Readers are referred to papers in the reference list for a detailed description of the Permian—Triassic boundary microbialites.

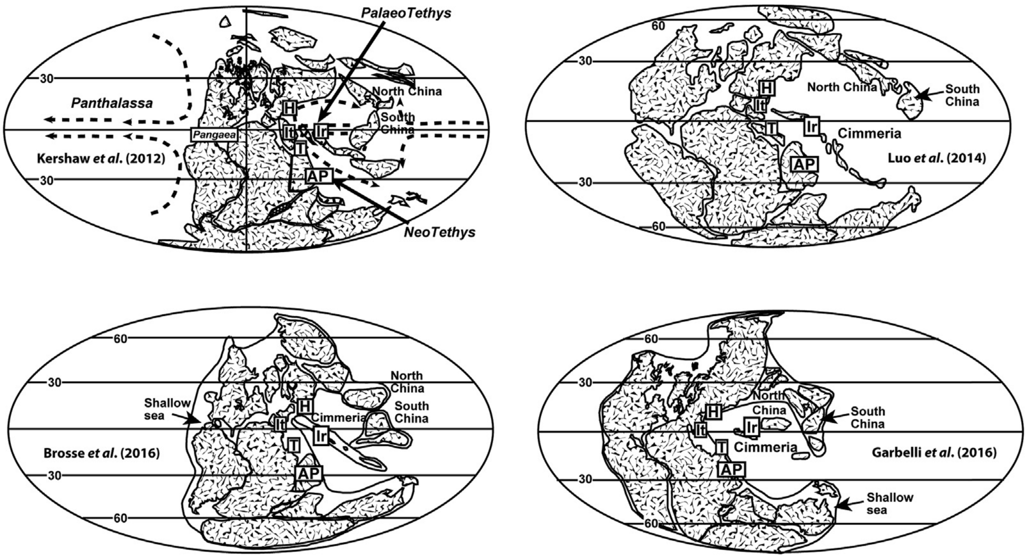

Fig. 2 Four selected recently-published palaeogeographic maps of the Permian—Triassic boundary time (Brosse *et al.*, 2016; Garbelli *et al.*, 2016; Kershaw *et al.*, 2012; Luo *et al.*, 2014), showing variations in opinion of the positioning of continents, with particular relevance to Tethyan sites, where post-extinction microbialites occur. The variations in positioning of continents may have impacts on interpretations of geographic distribution and migrations of organisms after the extinction, as discussed in the text. Abbreviations: AP = Arabian Plate; H = Hungary (especially the Bükk Mountains of the northern Hungary); Ir = northern Iran; It = northern Italy; T = southern Turkey.

although it is not yet possible to verify whether or not these are recrystallized fabrics from a prior structure no longer preserved.

In contrast to eastern Tethyan sites of the South China Block, age-equivalent microbialites in western Tethys (represented by key sites in Turkey and Iran and others) almost completely lack calcimicrobes (Fig. 1), instead the microbialites are dominated by thrombolites of clotted sediment, stromatolites of layered sediment and some thin (a few mm thick) layers of in-place calcite crystals. In some cases the latter have a stromatolitic appearance in the field and polished samples, so that some cements are inorganic whereas others may be organically mediated. Thus some are hybrid microbialites (Riding, 2008) comprising mixtures of inorganic cements and microbial micrite on a millimeter scale. All these fabrics are well displayed in the key sites in Turkey (Baud *et al.*, 2005), forming repetitive units interpreted by Kershaw *et al.* (2011) to be the result of changes in water depth and therefore minor sea-level fluctuations.

The impact of palaeogeographic reconstruction plays a potentially important role in the debate on controls on microbialite distribution. The accuracy of palaeocontinental reconstructions depends on data quality and there are numerous interpretations of the relative positions of the continents at the Permian—-Triassic boundary. Fig. 2 shows a selection of recently published reconstructions, presented in papers that use prior reconstructions referenced in those papers. It is inevitable that reconstruction accuracy will vary with opinions, in rocks formed before the oldest widespread ocean crust (Early Jurassic). Palaeogeographic locations of the principal PTBM-bearing sites depend on these reconstructions. All reconstructions show agreement that South China lay in eastern Tethys but the interpreted locations of other areas vary from positions close to South China to positions much farther away. If the true relative positions were relatively near each other, this increases the problem of explaining geographic differences between microbialite deposits that have a different composition.

3. Discussion

3.1. *Contrasts between post-extinction conodonts and microbialites*

Lai *et al.* (2001) considered the animal containing *H. parvus* conodont elements to have lived in shallow ocean waters and unaffected by deep ocean anoxia, thus forming a globally-accepted biostratigraphic scheme based on rapid and unrestricted conodont migration. Furthermore, although the earliest Triassic post-extinction conodonts are normally found in low abundance, Brosse *et al.* (2015) found rich faunas in a site in South China, indicating a well-developed conodont animal biota in at least that one place. However, the regional restriction of calcimicrobial-dominated deposits to South China and the rarity of sediment-constructed microbialites in South China are a surprising contrast to other areas. The constructors of the range of microbial carbonates may be expected to be benthic microbia, but being microbes were likely subject to circulation in the ocean, particularly in Tethys where the PTBMs mostly occur. It has been suggested that the first appearance of *H. parvus* is diachronous (*e.g.*, Zhang *et al.*, 2014); if this is correct, it may be due either to real variations in the timing of arrival of the conodont animal in different locations, or to continuing sampling issues in sections that have low fossil abundance. Nevertheless diachronous first appearance does not prevent the conclusion that conodonts after the extinction were able to move laterally throughout the Tethys Ocean. Yang *et al.* (2015) demonstrated that the PTBMs at the Dajiang section, Guizhou Province, South China, contained a higher diversity of marine fossils than has been previously recognized, emphasizing the oxygenated state of environments in which the microbialites formed, and thus a mixed shallow water in contact with the atmosphere. Thus, if there was an active ocean-surface circulation in the post-extinction times, such a circulation clearly did not distribute microbial components throughout the Tethys Ocean, reducing the likelihood that microbialite regional differences are due to ocean circulation processes.

3.2. *Planktic and benthic fossils in the Permian—Triassic transition*

Prior to the end-Permian extinction, a cosmopolitan radiolarian (microscopic zooplankton) fauna was abundant (Feng and Algeo, 2014), indicating ability of these planktic forms to be distributed throughout Tethys; however, radiolarian taxa demonstrate preferred water depth ranges, and so maintained an ecological preference, despite being presumably transported by ocean currents through Tethys. Feng and Algeo (2014) recorded greater survival of Palaeozoic-type radiolarian taxa in higher latitudes across the end-Permian extinction, and interpreted this to indicate higher levels of anoxia in the lower latitudes; presumably there is an effect of depth here, since shallower waters are likely to have been well-oxygenated. Vachard (2014), in a work-in-progress report, described the distribution of Late Permian nodosariate foraminifera, which became extinct a few meters below the first occurrence of *H. parvus*. Vachard (2014) provided a map of the latest Permian distribution of the genus *Collianella* and demonstrated its widespread occurrence immediately prior to the end-Permian extinction, and noted that this genus developed this wide distribution in the late Changhsingian, geologically a relatively short time before the extinction occurred. However, *Collianella* is not abundant everywhere; it is absent or poorly represented in some sites where PTBMs, after the extinction, became common (*e.g.*, the Zagros area of Iran, the Taurus area of southern Turkey, and Hungary). A key issue is the interpretation of the lifestyles of these extinct organisms. *Collianella* was probably benthic (Vachard, 2014) so its occurrence throughout Tethys may be presumed to indicate efficiency of ocean currents to transport it around the complex Tethyan ocean continental geography, with its numerous large microcontinents scattered through Tethys. Thus a complex pattern of current circulation must be presumed, reaching at least all the parts where *Collianella* is found. Nevertheless, Vachard (2014, p. 20) indicated that although *Collianella* is restricted to Tethys, some large-scale palaeogeographic variation of occurrence is recognised, with differences between East Tethys and West Tethys, suggesting the existence of processes (as-yet undetermined) that affected Tethyan environments both before and after the extinction. The restriction of *Collianella* to Tethys has a parallel with the occurrence of the earliest Triassic post-extinction microbialites within Tethys because PTBMs were absent in the western Americas (eastern Panthalassa), as indicated by Kershaw *et al.* (2012). Clearly there is more to learn about controls on distribution of foraminifera in the latest Permian.

Within the molluscs, post-extinction ammonoids show several taxa with wide distributions, not just within South China but also to the Arctic and the Himalayas (Brüwhiler *et al.*, 2008), which is expected because of their pelagic lifestyle. However, Brüwhiler *et al.* (2008, p. 1156) also noted that the lowermost Triassic ammonoid-bearing rocks, called the “Otoceras” beds, of the earliest Griesbachian time (the first part of the Induan Stage of the lowermost Triassic) in South China, are not as widespread in the Tethyan realm as in the Boreal realm. Although it may be that the ability of these ammonoids to be transported around Tethys was affected by the oceanographic conditions in Tethys after the extinction, the paucity of faunas due to mass extinction may leave a patchy record. Brüwhiler *et al.* (2008, their Fig. 4) showed that later in the Induan Series, the basal part of the Dienerian (the second part of the Triassic Induan stage) shows correlation between Chinese and Canadian ammonoids indicating effective correlation between Tethys and the open ocean in these Early Triassic horizons. The presence of later Early Triassic microbialites in western North America, well described in several papers, is a possible indication of more widespread development of microbialites later in the Early Triassic because microbialites are found in the overlying Smithian unit (lowest part of Olenekian, the second Triassic stage) of western North America. Thus, overall there is poor evidence of widespread correlation of ammonoid taxa immediately after the extinction, when the microbialites were abundant and widespread in Tethys, but the records do not yet permit a clear understanding of the controls. In contrast, good evidence of a wider ammonoid distribution later in the Early Triassic, after the Tethyan earliest Triassic microbialites had disappeared, may be due to greater abundance (or perhaps better preservation) of ammonoids, or may reflect better environmental conditions and more effective ocean circulation. Nevertheless, the abundance of *H. parvus* elements (and therefore the mobile conodont animal) in Tethys immediately after the mass extinction does prove there was no physical or physiological barrier to its migration. Brayard *et al.* (2009) showed how the ammonoids recovered significantly quicker than bivalves and gastropods. Nevertheless, amongst the bivalves, the genus *Claraia* stands out because it is widely distributed in the earliest Triassic deposits in East Tethys and West Tethys (personal observations in South China and Turkey). Gastropods, however, are poorly represented in the earliest Triassic after the extinction (Nützel, 2005). More recent work by Kaim *et al.* (2010) reported taxonomic similarities between gastropods in Russia and South China, and between South China and Oman, a tentative indication of homogeneity of gastropods and therefore an ability to migrate, although data are not yet sufficient to give robust conclusions.

For brachiopods, Clapham *et al.* (2013) interpreted the patchy distribution of rhynchonellid brachiopods after the end-Permian extinction as due to uneven occurrence of anoxia in shallow waters. They noted that the rhynchonellids that survived into the Mesozoic were short-term survivors of families that became extinct at the mass extinction, and that extinction was patchy throughout the Tethys Ocean region. These conclusions do not reveal whether rhynchonellids had the ability to distribute laterally or not through the Tethys Ocean after the extinction occurred, but Clapham *et al.* (2013) noted that their survival after the extinction was likely to be because they were holdovers from large populations. Thus such survivors may not have had the capacity for geographic spreading. In another case of brachiopods, shell shape of the early Induan lingulids in the Mazzin Member, just after the extinction, was interpreted by Posenato *et al.* (2014) to indicate tolerance to increased temperature and to hypoxic conditions after the extinction, which may be relevant in the interpretation of varying shallow ocean anoxia after the extinction.

Hautmann *et al.* (2011) reported unusually rich benthic faunas in the earliest Triassic in South China, and in some cases (Hautmann *et al.*, 2015) they are associated with microbialites, in Guangxi and southern Guizhou, indicating that well-developed post-extinction faunas existed in some places. If this example is indicative of the rapid recovery after mass extinction, then it suggests the recovery was patchy. However, the microbialites are highly widespread across Tethys and occur in most shallow water carbonate platforms. Thus it is reasonable to deduce that the microbial communities took advantage of the extinction process to develop, and were provincial.

Crasquin and Forel (2013, their Fig. 6) provided a useful comparison chart of ostracods, brachiopods, conodonts and ammonoids through the Permian—Triassic transition, showing how all these faunas were in general strongly affected by the extinction event. Crasquin-Soleau *et al.* (2001) demonstrated the similarity between ostracod faunas and palaeofloras on the Arabian Plate and the South China Block, using this as evidence that the two areas were relatively closer together (the Pangaea B model) than other interpreted continental reconstructions (the Pangaea A model) as described by Crasquin-Soleau *et al.* (2001). Regardless of which palaeogeographic interpretation is more accurate, the fact of benthic marine faunas having similarities between eastern and western Tethys indicates lateral faunal migration was possible. Forel *et al.* (2015, pp. 440—441) state that *Bairdiawailiensis* occurs through the Permian—Triassic transition, and occurs in the Permian of Iran, and the earliest Triassic of South China (Guangxi) and Hungary, indicating apparently unrestricted migration of these small benthic organisms, contrasting the regional differences between coeval microbialites. Of course it is not possible to determine whether ostracods were more capable of lateral migration than ammonoids; benthic ostracods have benthic larvae (Boomer and Whatley, 1995), so ostracod migration processes presumably involved physical movement by agents such as ocean currents. Thus it is reasonable to assume on the basis of the widespread distribution of conodont animals and ostracods that the advective ocean circulation of Tethys was functioning satisfactorily immediately after the mass extinction.

3.3. Biomarker data in the Permian—Triassic transition

Luo *et al.* (2013) described biomarkers from one site in shallow marine microbialites from the northern part of the Yangtze Platform (South China), demonstrating abundance of bacteria in the microbialites, although this depends on the chemical biomarkers accurately reflecting the biotic composition of the physical sedimentary structures. Luo *et al.* (2014) presented biomarker evidence of vertical changes in seawater oxygenation through the Permian—Triassic boundary of South China sequences, which reflects the occurrence of planktic bacteria, with interpretation of blooms of green sulphur bacteria associated with vertical oxygenation variation. The notion of ocean overturn has been explored by numerous authors, and a prominent view was drawn from sulphur isotope data, where Paytan *et al.* (2011) showed the most negative point on the entire Late Precambrian to Phanerozoic sulphur isotope curve was at the Permian—Triassic boundary, followed by a rapid rise. The curve was interpreted by Paytan *et al.* (2011) as reflecting anoxic deep water followed by overturn. Zhou *et al.* (2017) presented biomarker evidence of expansion of photic zone euxinia on a global basis, including both upward and oceanward increase of euxinic conditions. Could such vertical changes have interrupted the pattern of normal shallow-marine circulation patterns and prevented advective migration of the microbial communities that created the post-extinction carbonate microbialites? Thus could this be the reason for geographic variations of microbialite construction? If so, then this is incompatible with the distribution patterns of organisms such as *H. parvus*, and molluscs and ostracods discussed above, that were able to travel across the shallow ocean.

3.4. Biomarker data in the Permian—Triassic transition

Azam *et al.* (1983) recognized the important role of bacteria in carbon fixation in the modern oceans and their key relationship with dinoflagellate plankton that are ubiquitous, a clear demonstration of the wide distribution of microbia in the oceans. However, as early as 1960, Kriss *et al.* (1960) identified geographic variations in bacterial distribution in ocean sediments and water column, indicating that climate has an influence on distribution. Li and Dickie (1996) showed that bacterial abundance correlates with latitudinal decrease in temperature towards the poles, emphasizing the importance of temperature control on bacterial populations. In a valuable overview of microbes in the modern oceans, Doblin and van Sebille (2016) summarized the key points that microbes are passengers in ocean currents; microbes are Lagrangian, effectively meaning that they passively drift with the currents. Modelling by Doblin and van Sebille (2016) predicted that modern microbes may drift as much as 3500 km in 500 days of ocean transport and be subjected to significant temperature variations along the way. Thus those microbes able to tolerate large temperature changes are likely to survive long distances of ocean transport (Fig. 3). Doblin and van Sebille (2016) also noted that microbes are highly sensitive to temperature variations and function best at their optimum temperatures, with important reduction of activity outside those temperature optima. Thus Doblin and van Sebille (2016) showed that in the modern oceans, planktic microbes with high tolerance to raised temperatures can survive and be transported long distances in the oceans. This range of information from modern ocean microbial distributions raises the possibility that the PTBMs were temperature-sensitive; however, this would be difficult to test, given that this is a period of isotope curve instability. Furthermore, Sun *et al.* (2012) interpreted post-extinction surface conditions after the end-Permian events, to have been very hot, thus whether there were geographic variations within the tropical to subtropical zones that might have controlled the geographic distribution of PTBM types remains an open question. The PTBMs occur in a relatively narrow latitudinal zone in presumed tropical and subtropical areas in Tethys, but whether lateral variations in

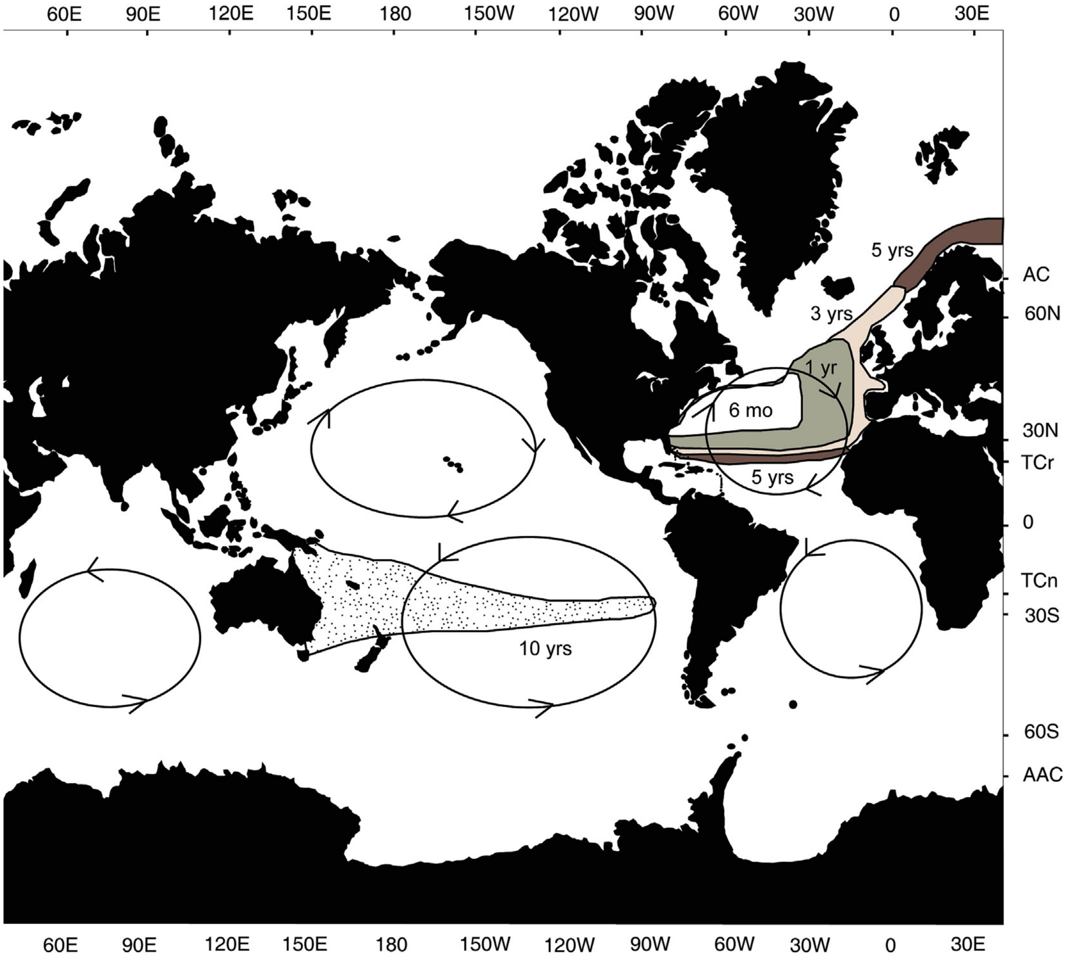

Fig. 3 Compiled maps of modelled distributions of drifted particles, after van Sebille (2014). The Pacific Ocean drift shows a modelled distribution of particles released from the east coast of Australia after 10 years of model run; the model used is called adrift.org.au. Particles are carried by the South Pacific Ocean gyre in an anticlockwise direction, and after 10 years have travelled most of the distance across the Pacific Ocean. The Atlantic Ocean shows model runs of up to 5 years in the Gulf Stream and its extension, the North Atlantic Drift. These two modelled distributions show distances covered that are comparable to what may have been the size of Tethys Ocean in the Permian—Triassic time. If surface-ocean wind-driven and coriolis-influenced currents at that time operated in the way they do today, then it may be expected that pelagic organisms would have been transported across the Tethys Ocean, for example the conodont animal that carried *Hindeodus parvus* elements.

temperature between eastern and western Tethys existed or not may not be easy to prove.

Modern bacteria have a complex relationship with ocean circulation, including even chemoautotrophic ammonia-oxidising bacteria, shown by Hollibaugh *et al.* (2002) to be not only distributed across the global ocean system but also to show regional variations. Hellweger *et al.* (2014) modelled the behaviour of microbes in the modern ocean and remarkably concluded that microbes have the ability to evolve in very short time periods, considered shorter than the time it takes for ocean currents to disperse them. If this model is considered in relation to the PTBMs, it is an interesting idea that microbia could have undergone evolution during the migration process, an avenue for future investigation.

Despite the ease of migration of modern microbes in the oceans discussed above, some indication of geographic variability in living microbialites is shown in the occurrence of microbialites in ocean-facing settings. The most famous examples are Shark Bay (for stromatolites) and Lake Thetis and Lake Clifton (thrombolites) in western Australia (Burne and Moore, 1987, 1993), well known as unique environments with non-normal salinities. However, in open marine normal-salinity waters the presence of giant stromatolites in Exuma Sound, eastern Bahamas (Reid *et al.*, 1995), is also unique because such structures are not found elsewhere, not even in other places in the Bahamas, for reasons that are not clear. These modern examples show how microbialites are subject to unidentified localized controls of occurrence and types that may have parallels in the PTBMs.

An area of potential future exploration is the relationship between microbialite distribution and the effects of the Siberian volcanic eruptions, considered to be approximately synchronous with the extinction (Reichow *et al.*, 2009). Svensen *et al.* (2009) reconstructed the huge extent of the Siberian traps in North—Central Russia, but of key potential importance is the geographic distribution of the effect of the eruption for which there is no current clarity. Climate models such as that of Kiehl and Shields (2005) provide a valuable overview of global changes, but the scale does not permit discrimination of effects within an area the size of Tethys. The possibility of distinguishing the results of eruptions on eastern Tethys from those farther west awaits further work.

3.5. Microbialite calcification

Late Permian reefs do not have any similar calcimicrobes to those in the post-extinction microbialites; *Renalcis*-type calcimicrobes have not been found, see Kershaw *et al.* (2012) for discussion. In contrast, the occurrence of *Renalcis*-type microbes in reef limestones not involved in mass extinctions is well known. For example, the Devonian reef systems in Europe, Canada and Australia all contain renalcids as reef frame constructors; and the Cambrian reefs are rich in renalcids in various sites worldwide (personal observations in South China, see also Zhuravlev, 2001). The corollary is that the South China PTBM sites largely lack identifiable classic stromatolites and thrombolites, yet such structures are also widespread geographically and temporally in geological history.

It might be argued that calcification of microbia to form calcimicrobes was stimulated in only the eastern Tethys, but that does not match the evidence of active ocean currents discussed above, that may be presumed to have equalized saturation throughout the Tethys Ocean if ocean currents modelled by Kidder and Worsley (2004) applied. Microbes that produced calcimicrobes were likely all benthic given their tendency to form microframeworks on the sea floor, which could explain their geographic limitation because they were not carried by ocean currents. There is also the problem of the lack of renalcid-group calcimicrobes in the Late Permian reefs below the microbialites, if they were present, why did they not calcify? Riding (1992) argued that calcimicrobes calcified in Earth history depending on seawater saturation of carbonate, which implies that the lack of renalcid groups in the Late Permian reefs is an indicator that saturation had not reached the level required to calcify the renalcid-like structures seen in the post-extinction microbialites. Kershaw *et al.* (2012) pointed out that the Late Permian reefs are rich in calcified structures believed to be organic, such as *Archaeolithoporella* and *Tubiphytes*, in addition to the abundant hypercalcified sponges and corals and copious contemporaneous marine inorganic cement, yet lack the renalcid calcimicrobes that appear in abundance across the Yangtze Platform directly after the extinction. Perhaps, as argued by Kershaw *et al.* (2012), the loss of all these calcified Late Permian organisms during the extinction provided extra carbonate saturation needed for renalcid-like organisms to calcify, instead of the argument put forward by many authors that upwelling of bicarbonate-rich deep ocean water was the stimulus for post-extinction microbialite growth. One point for future consideration is whether the calcified structure of renalcid fossils does represent a single type of organism, or whether it may have formed the calcified remains of more than one type of microbial life, so that those in the Devonian had different saturation requirements from those in the Permian—Triassic boundary. It is a great pity that no modern equivalents are alive today to test such an idea.

4. Conclusions

This discussion makes clear that major questions remain unanswered with regard to the processes that controlled the formation and distribution of the Permian—Triassic boundary microbialites. Because the biostratigraphically important pelagic organisms that held conodont fossils of the taxon *H. parvus* were able to spread through the ocean system quickly after the extinction, there is no clear reason why microbialite sequences are composed of distinctly different kinds of microbial constructions on a regional basis. Possible controls may be one or more of the following:

1) Because microbial organisms were benthic, they may have lacked planktic stages for migration.
2) Eastern Tethyan seas may have been more saturated with respect to calcium carbonate to stimulate microbial calcification.
3) Tethyan ocean circulation may have been limited, perhaps by large-scale upwelling disrupting ocean surface circulation, reducing lateral migration of microbial communities.
4) Microbes may have been under local to regional environmental controls, the mechanisms of which are not yet recognized in the facies; the possibility of climatic differences between East Tethys and West Tethys in relation to the Siberian eruptions, for example, is one area for future investigation.

There may be other controls in addition to these four that could emerge in future research.

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