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Colonial coral resilience by decreasing size: reaction to increased detrital influx during onset of the late Palaeozoic Ice Age

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Modern coral reefs and associated biodiversity are severely threatened by increasing terrestrial runoff. Similar scenarios could be suspected for geological times, but reef coral resilience is still an enigma. In late Visean-Serpukhovian (Mississippian foraminiferal zones/MFZ 14-16) times, a major glaciation phase of the late Palaeozoic Ice Age (LPIA) associated with enhanced terrestrial weathering and runoff coincides with a biodiversity crisis and coral reef decline. In this study, the impact of enhanced terrestrial runoff is tested on size variations of colonial corals *Aulina rotiformis* and *Lithostrotion decipiens* along a gradient of contemporaneous (Serpukhovian) open marine carbonate to near-shore siliciclastic facies in South China. Along this gradient, their sizes decrease from carbonate, through intermediate carbonate-siliciclastic, to siliciclastic facies. This is consistent with increasing abundance of terrestrial materials of high silicon, aluminium and phosphorus values. On a larger million-year-long interval (MFZ14-16) and for several palaeocontinents, size data of *Lithostrotion decipiens* and *Siphonodendron pauciradiale* show a distinct decline in late Visean, when enhanced terrestrial weathering occurred commonly with palaeosols developed during regression. This suggests that terrestrial sediment and nutrient input may have mainly controlled phenotypic plasticity in Mississippian reef corals, with a decrease in size as a component of resilience across the LPIA onset.

1. Introduction

Corals are the most dominant element in modern reef ecosystems and construct complex habitat environments that maintain a high biodiversity in marine settings [1–3]. However, they are being severely influenced by climate warming and terrestrial sediment input, resulting in obvious coral bleaching and mortality [4–6]. Monitoring and modelling studies indicate that some reef corals can adapt to these detrimental factors through their genetic variation or morphologic plasticity [7]. Although these biology-environment processes are increasingly being studied, they are constrained within a short-time scale and the long-term evolutionary trend of reef corals under environmental impact is still not well understood.

Studies on variation in reef corals under climate and environmental changes during geological times may provide insights into their secular evolutionary relationship. Accompanied with the Late Devonian mass extinction events, the largest stromatoporoid-coral reef ecosystems of the Phanerozoic collapsed and disappeared [8–11]. In the succeeding Mississippian, coral reefs gradually recovered and proliferated with high reef coral diversity in the late Visean (Middle

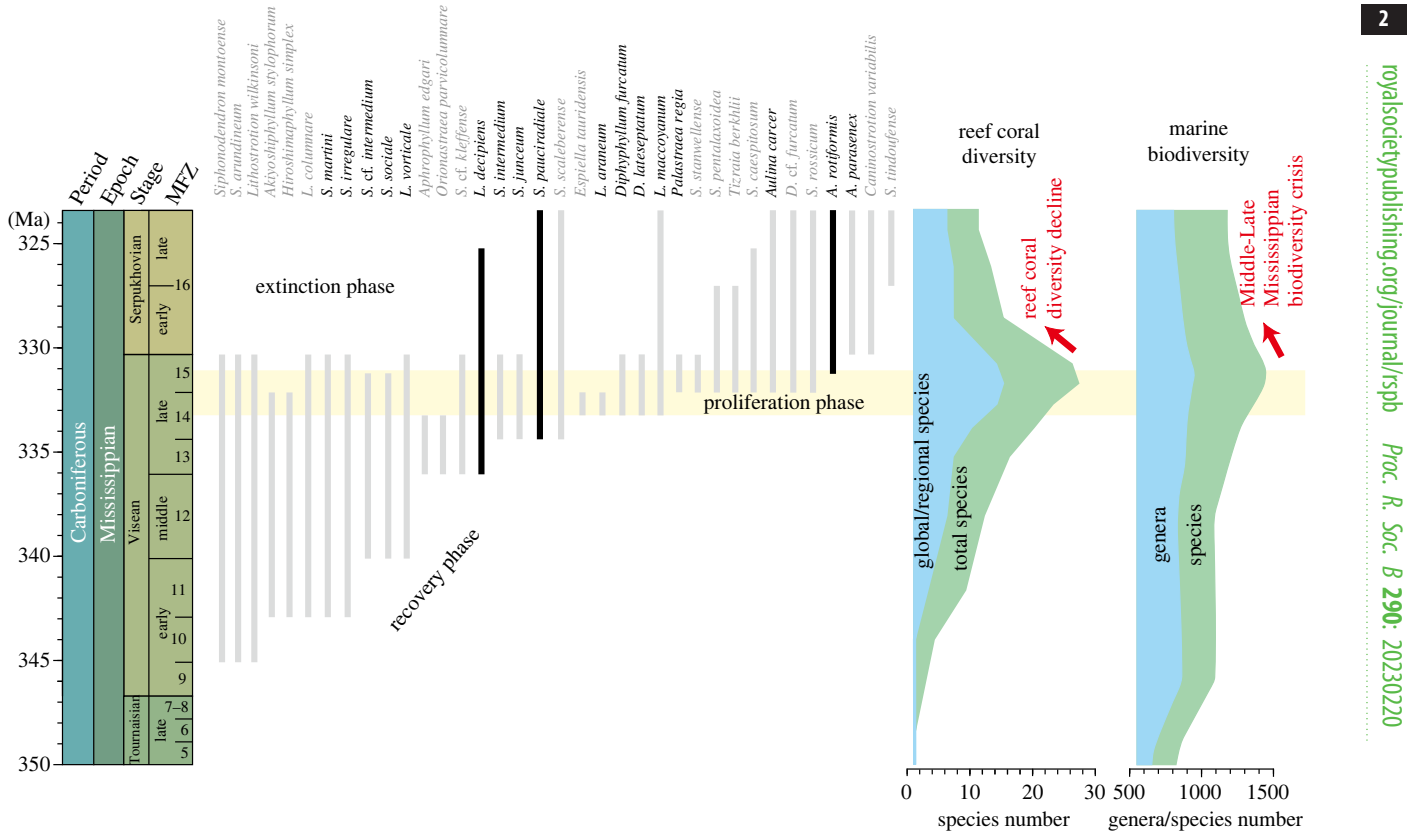

Figure 1. Evolutionary pattern of Mississippian reef coral diversity and total marine biodiversity, including recovery phase, proliferation phase and extinction phase of reef corals during early to late Visean, middle part of late Visean, latest Visean to Serpukhovian, respectively. The coral species in black and grey colours represent their global and regional distribution, respectively. The marine biodiversity curve is from [12], compiled based on the Paleobiology database (https://paleobiodb.org/classic). The black range bars indicate the studied reef coral species that cover the critical transition of the Middle-Late Mississippian biodiversity crisis. MFZ: Mississippian foraminiferal zone drawn based on [52].

Mississippian) [11] (figure 1). Then, a dramatic climate cooling occurred, probably initiated in the latest Visean and continued into the Serpukhovian (Late Mississippian), which can be associated with a major phase of the late Palaeozoic Ice Age (LPIA). This cooling was triggered by decreasing atmosphere CO_2 concentration resulting from both enhanced terrestrial silicate weathering and marine organic burial, evidenced from distinct positive shifts in strontium, carbon and oxygen isotopes sequentially [12]. Concurrently, sea-level fall and enhanced terrestrial input led to obvious marine carbonate decline [13,14]. These detrimental factors eventually caused the Middle-Late Mississippian biodiversity crisis and prominent ecological changes, characterized by collapse of coral reef ecosystems, decline in reef coral diversity, and changes in composition of coral communities [11,15–18] (figure 1).

In order to uncover the causal relationship between coral evolution and increased terrestrial sediment input across the onset of the LPIA, three cosmopolitan and long-range colonial rugose coral species were selected, the fasciculate form *Siphonodendron pauciradiale*, and the massive forms *Aulina rotiformis* and *Lithostrotion decipiens* (figure 1; electronic supplementary material, figure S1). They were collected from both reef and non-reef strata in the Yashui, Malanbian, Wangjiacun and Jianshanzi sections in Guizhou, Hunan and Anhui of South China and Gansu provinces of Northwest China, respectively (electronic supplementary material, figure S2*a*). These sections represent shallow water open platform carbonates (Yashui), mixed carbonate-siliciclastic (Malanbian) and near-shore siliciclastic settings (Wangjiacun and Jianshanzi) facies [19,20] (electronic supplementary material, figure S2*b–d*). The Yashui corals represent late Visean to late Serpukhovian ages, while the corals from the other sections are from the early part of the late Serpukhovian (electronic supplementary material, text and figure S3). In this study, the main aims are (i) to uncover morphologic responses of the same species in different facies from near-shore to open platform of the South China Block; (ii) to reveal the long-term ecological evolution of coral size across the climate cooling at the onset of the major LPIA, based on review of coral data from South China and other palaeocontinents globally and (iii) to discuss the potential relationship between ecological changes in reef corals and increased terrestrial runoff.

2. Material and methods

In the geological record, the individual size of an entire coral colony is often impossible to obtain due to its preservation and/or inclusion into the rocks. Hence, the values of corallite diameter and septal number have been successfully applied to indicate variations in the size and complexity of rugose corals and discuss the relations of these parameters to environmental changes [21,22]. In this study, the values of corallite/tabularium diameter and septal number of individual corallites are used to represent coral size and complexity for each species. In total, these parameters were measured on 1561 corallites of 136 thin sections (approx. 4 × 5 cm) representing 74 colonies (sample length, width and height are approx. 10 cm to 20 cm) of three colonial rugose coral species *Aulina rotiformis*, *Lithostrotion decipiens* and *Siphonodendron pauciradiale*. They are from the Yashui, Malanbian, Wangjiacun and Jianshanzi sections (see electronic supplementary material, table S1). In order to unravel long-term evolution of coral size,

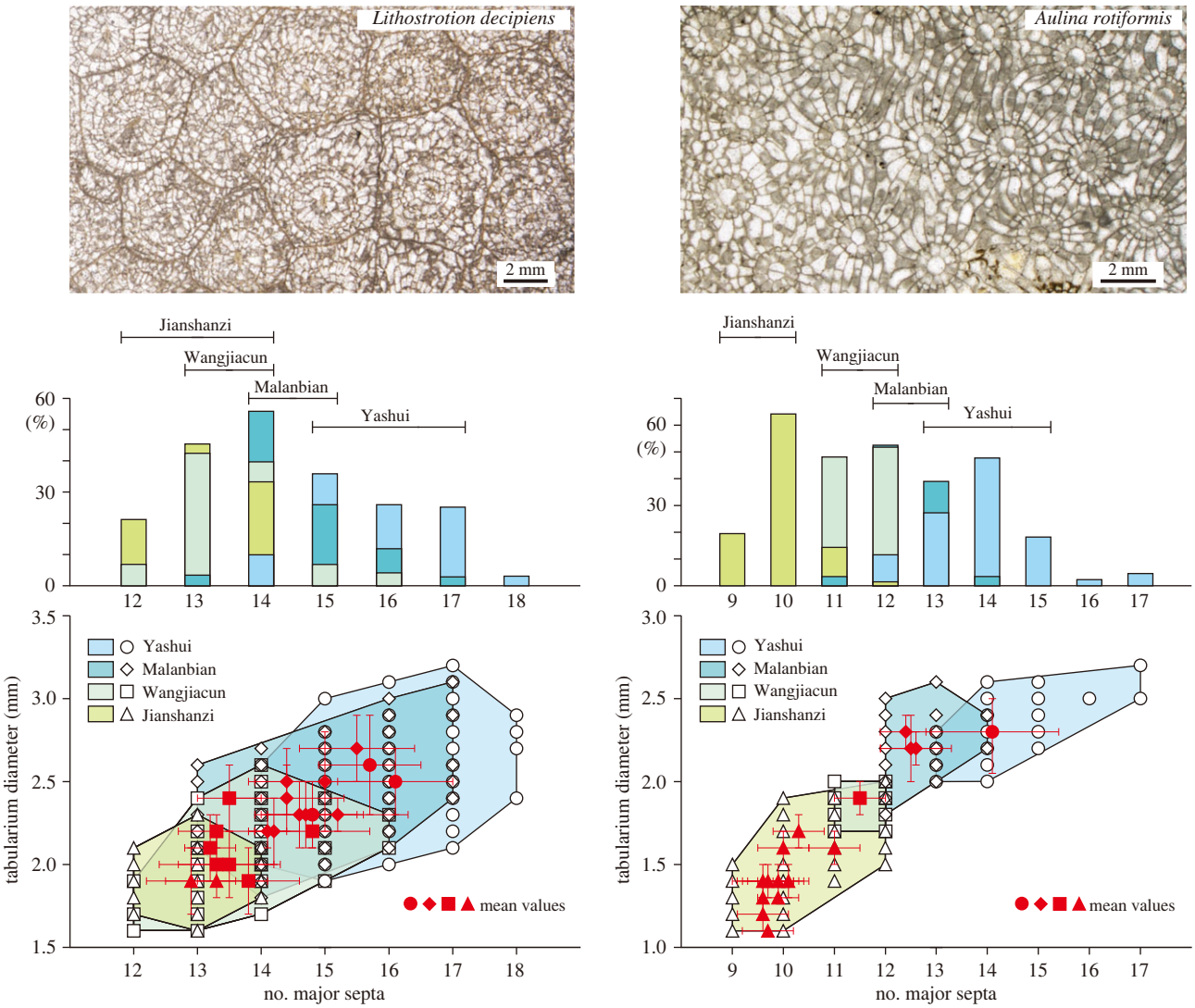

Figure 2. Variation in the septal number of the colonial coral species *Lithostrotion decipiens* and *Aulina rotiformis*, and correlation diagrams of tabularium diameter and septal number of *L. decipiens* and *A. rotiformis* in the Yashui, Malanbian, Wangjiacun and Jianshanzi sections.

the corallite and tabularium diameter values of two stratigraphically long-ranging and geographically widely distributed species, *L. decipiens* and *S. pauciradiale*, were also compiled for the western (Europe and North Africa) and eastern (China) Palaeotethys Ocean from the late Visean to Serpukhovian. The European and African data are based on figured specimens, for China the data of the Yashui section are used (electronic supplementary material, table S1).

Thin-section photographs of studied Chinese rugose corals were taken using a Nikon SMZ25 microscope. The coral identification is according to [23,24]. The microfacies around the coral colonies and skeletons are identified following the classification schemes proposed by [25]. Elemental mapping photographs were obtained using energy-dispersive spectroscopy (EDS) analyses with large area mapping (LAM) technique under the field emission scanning electron microscope (Tescan MAIA3 GMU) with EDS (Oxford Ultim Max 170). The thin sections were imaged in a partial vacuum using secondary electron detectors at an accelerating voltage of 20 keV for acquisition rate approximately 130 000 cps s^{-1}.

3. Results

(a) Coral size

In the studied four sections, each representing a different palaeoenvironment, *A. rotiformis* and *L. decipiens* are well developed during the same stratigraphic interval (*Bradyina cribrostomata* Zone) (electronic supplementary material, figure S3). The plots for both tabularium diameter and septal number show that there is a clear trend when the results are separated by sections. In the carbonates of the Yashui section, both species attain the largest sizes, whereas the smallest size values (*ca*. average values of 31% and 23% smaller for *A. rotiformis* and *L. decipiens*, respectively, than those at Yashui) are observed in the siliciclastic facies of the Jianshanzi section (figure 2). The specimens from the Malanbian and Wangjiacun sections fall in between the two end-members according to the siliciclastic content of the section; hence sizes in Malanbian are larger than in Wangjiacun.

The long-term dataset for the western and eastern Palaeotethys Ocean reveals that the coral sizes for *L. decipiens* and *S. pauciradiale* obviously changed during the late Visean, around the Asbian-Brigantian boundary (ABB). The average coral sizes are significantly larger before that boundary than in the latest Visean and Serpukhovian (values about 10% and 20% smaller for *L. decipiens* and *S. pauciradiale*, respectively) (electronic supplementary material, table S1). For the *S. pauciradiale*, the decline in size values across the ABB is well expressed for both shallow marine bioclastic carbonate facies and coral reef facies, and the latter contains larger coral size than that of shallow bioclastic carbonate facies. Sufficient

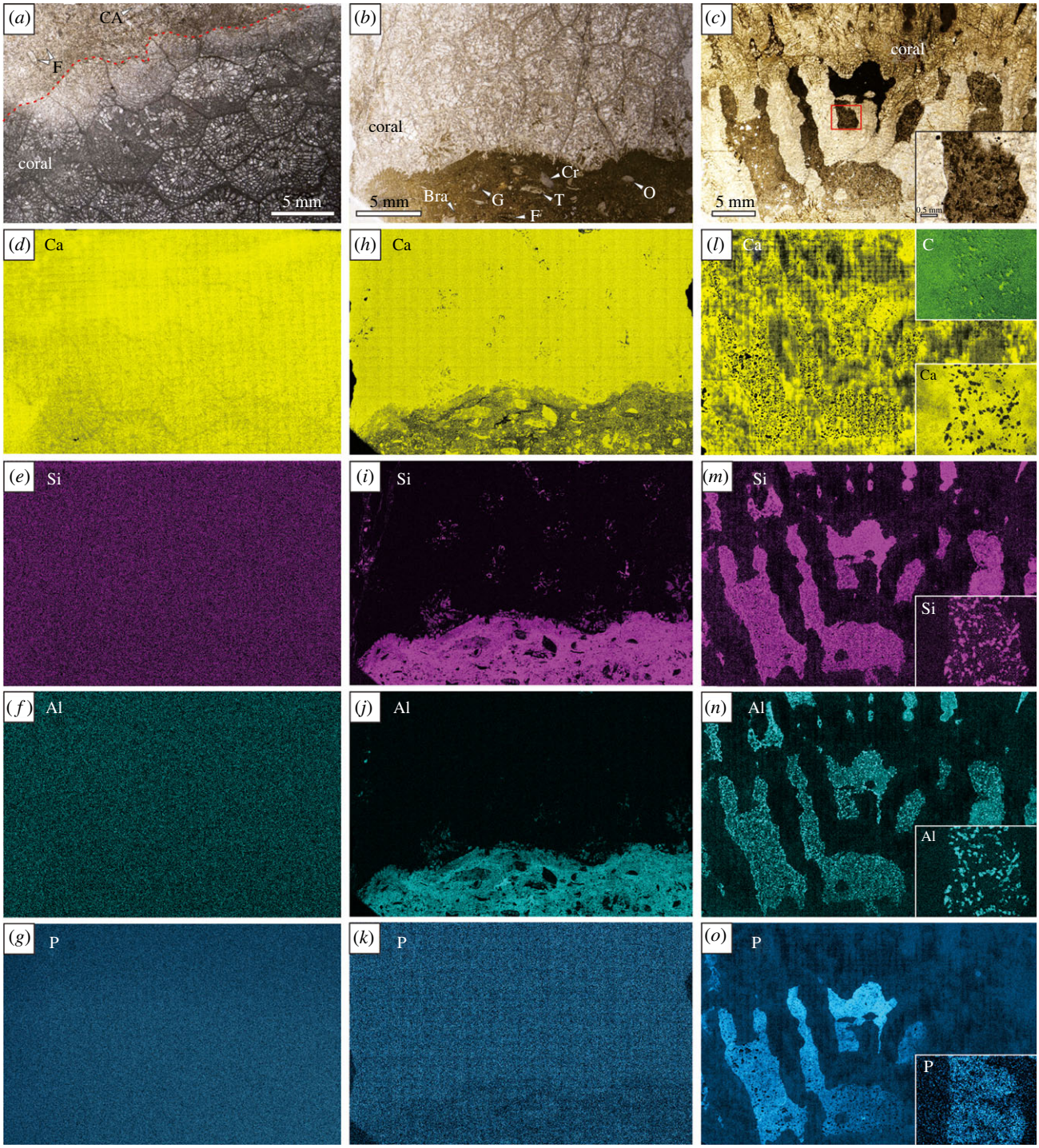

Figure 3. Thin-section photographs (*a–c*) and their corresponding elemental–mapping photographs (*d–o*) of the colonial coral species *Lithostrotion decipiens* in the Yashui, Malanbian and Wangjiacun sections. Bra: brachiopod, CA: calcareous algae, Cr: crinoid, F: foraminifer, G: gastropod, O: ostracod, T: trilobite, Al: aluminium element, C: carbon element, Ca: calcium element, P: phosphorus element, Si: silicon element. The inset photographs in (*c*,*l–o*) are the amplification of the red rectangle in (*c*).

data to demonstrate such a size decline at the ABB for *L. decipiens* are currently only available for shallow marine bioclastic carbonate facies (electronic supplementary material, table S1).

(b) Coral taphonomy

The preservation of the *L. decipiens* colonies and the microfacies of the sediments they are embedded in, have been studied in selected characteristic colonies from the Yashui, Malanbian and Wangjiacun sections of the South China Block. At Yashui, the colony is well preserved with the corallites tightly connected in cerioid form. The surrounding facies is bioclastic packstone with abundant foraminifers and calcareous algae (figure 3*a*). The colonies at Malanbian are relatively well preserved and are featured by slightly broken coral skeletons and argillaceous bioclastic packstone. The latter is composed of diversified marine fauna including crinoids, foraminifers, brachiopods, gastropods, ostracods and trilobites, among which micrite and siliciclastic mud fill in (figure 3*b*). At Wangjiacun, colonies are poorly preserved, containing destroyed skeletons with smooth and continuous surfaces, leaving irregular spaces between corallites. These interspaces are absent of marine skeletal fossils, but are

occupied by abundant fossils of microbes, silt-sized quartz grains and micrite (figure 3*c*).

(c) Elemental mapping

LAM of elements was conducted for the corresponding *L. decipiens* colonies described above in the Yashui, Malanbian and Wangjiacun sections (figure 3*d–o*). In the Yashui section, the element mapping reveals the dominance of calcium (Ca) in both *L. decipiens* colonies and adjacent matrix, characterized by strong chemical signals of the same colour. Silicon (Si), aluminium (Al) and phosphorus (P) are absent, indicated by weak colour (figure 3*d–g*). In the Malanbian section, most parts of *L. decipiens* colonies are characterized by high values of Ca (bright colour), and low values of Si, Al and P (black or dark colour), except for a few broken coral skeletons with low Ca and high Si and Al values. Different from Yashui, the coral surrounding facies at Malanbian is featured by relatively low values of Ca and high values of Si and Al content, whereas the fossils have high Ca and low Si and Al values. This phenomenon is more obvious in the dark argillaceous areas (figure 3*h–k*). The interspaces between *L. decipiens* skeletons at Wangjiacun are represented by low values of Ca, and high values of Si, Al and P content. Enlargement of internal sediments consists of abundant microbial fossils with high values of carbon (C), Si, Al and P, and low values of Ca, and silt-sized quartz grains and micrite with obviously high Si and Ca values, respectively (figure 3*l–o*).

4. Discussion

Turbid waters are a major challenge for modern zooxanthellate scleractinian corals due to the tight link of photosynthesis and calcification. The latter is significantly lower in dark environments [26]. Therefore, increased terrestrial sediment influx due to continental weathering is expected to have important (paleo)ecological consequences [4,6,27]. In modern marine systems, scleractinian reef coral species display high phenotypic plasticity in skeletal morphology under terrestrial sediment influence and/or light attenuation, such as coral colony flattening [26–29]. Based on laboratory experiments in the short time duration of hours and days, it is suggested that modern corals of larger size can be more efficient in active sediment rejection by ciliary activity, mucus entanglement, tissue expansion and tentacular action [30,31]. Since the coral polyp is not preserved in fossil material, similar reactions and mechanisms can only be assumed for the past. In the coral skeleton itself, the development of dissepiments is probably related to tissue expansion for shedding of sediments [32]. A few case studies on Palaeozoic rugose corals also show that phenotypic plasticity occurs in coral morphology, characterized by a decrease in corallite diameter and septal number and/or foliose and massive forms resulting from terrestrial input [e.g.21,22,27]. This size decline in rugose corals indicates that the continuous sediment influx is probably beyond their active-rejection capability. In addition, variation in Palaeozoic coral morphology may also be induced by light scarcity resulting from turbid water and/or deep-water depth [33,34]. This last hypothesis implies that Palaeozoic corals relied on photosynthesis, which has not been fully demonstrated yet [11]. However, the past studies lack coral size records in spatially equivalent strata of various facies, resulting in still ambiguous insights into the relationship among terrestrial runoff, water depth and coral growth. In this study, the size values of two colonial coral species *A. rotiformis* and *L. decipiens* are compiled and show a decrease from the Yashui (carbonate facies), Malanbian (carbonate-siliciclastic intermediate facies) and Wangjiacun and Jianshanzi (siliciclastic facies) sections (figure 2). The simultaneous and similar morphological response of an array of fossil species is ascribed to phenotypic plasticity, especially where the species coexist [35]. Although the more abraded intervals might in theory have affected the sampled corals by affecting the distribution of corallite size in the preserved coral faunas, we do not see any evidence for this phenomenon, such as lack of eroded surfaces in the strata where coral skeletons are well preserved (electronic supplementary material, figures S1 and S3). Hence, the studied size data can represent the variation trend in coral phenotypic plasticity. They show that the size value of coral species *A. rotiformis* and *L. decipiens* continuously declines together with an increase in coral skeleton abrasion and likely smothering from Yashui, through the Malanbian, to the Wangjiacun sections, which are accompanied with obvious increase in terrestrial siliciclastic sediments characterized by high values of Si and Al content (figures 2 and 3). The lack of crystallization and low to undetectable manganese (Mn) content in the coral colonies and their surrounding microfacies indicates that they have retained primary seawater elemental signature without obvious diagenesis (figure 3*a–c*; electronic supplementary material, figure S4). This trend to smaller coral sizes implies that enhanced sediment input could have controlled coral growth and mortality. The decline in coral size could be probably attributed to the decrease in their growth rate resulting from the depletion of available energy, as a consequence of increased energy requirements for respiration, sediment removal and repair of damaged tissues [36,37]. This hypothesis is supported by Devonian and Modern coral communities with similar morphological forms under siliciclastic input and turbid environments [27]. An example from the Mississippian of the UK shows that in addition to reduction of corallite sizes, fasciculate *Siphonodendron* colonies almost abandon budding, resulting in unusually several cm-long more or less straight corallites [22]. This may be an additional reaction of branching colony forms to cope with terrestrial sediment input.

Accompanied with terrestrial sediment input, nutrients could also be loaded into the marine shallow continental shelf, which would increase primary productivity and organic burial rates in marine sediments, such as on modern coral reefs [38,39]. Sediments with organic components tend to be more harmful for reef corals, due to (i) its flocculating action that promotes the aggregation of fine sediment into larger particles and (ii) its acceleration of the proliferation of microbes [39–41]. This observation may be transferable into deep-time. At Wangjiacun, abundant microbes are present in the interspaces between coral skeletons, associated with abundant terrestrial materials and nutrients indicated by high values of Si, Al and P (figure 3*m–o*). Microbial respiration could result in reduction of O_2 and pH values, thus initiating coral tissue degradation [37,39]. This hypothesis is manifested by the severe abrasion of coral skeletons with smoothly and irregularly fragmented skeletons in the Wangjiacun section (figure 3*c*).

Although case studies uncover changes in coral size under the influence from terrestrial input [e.g.21,22,28], their long-term causal relationship is still not well understood. In this study, the long-range and cosmopolitan corals *L. decipiens* and *S. pauciradiale* from the late Visean to Serpukhovian

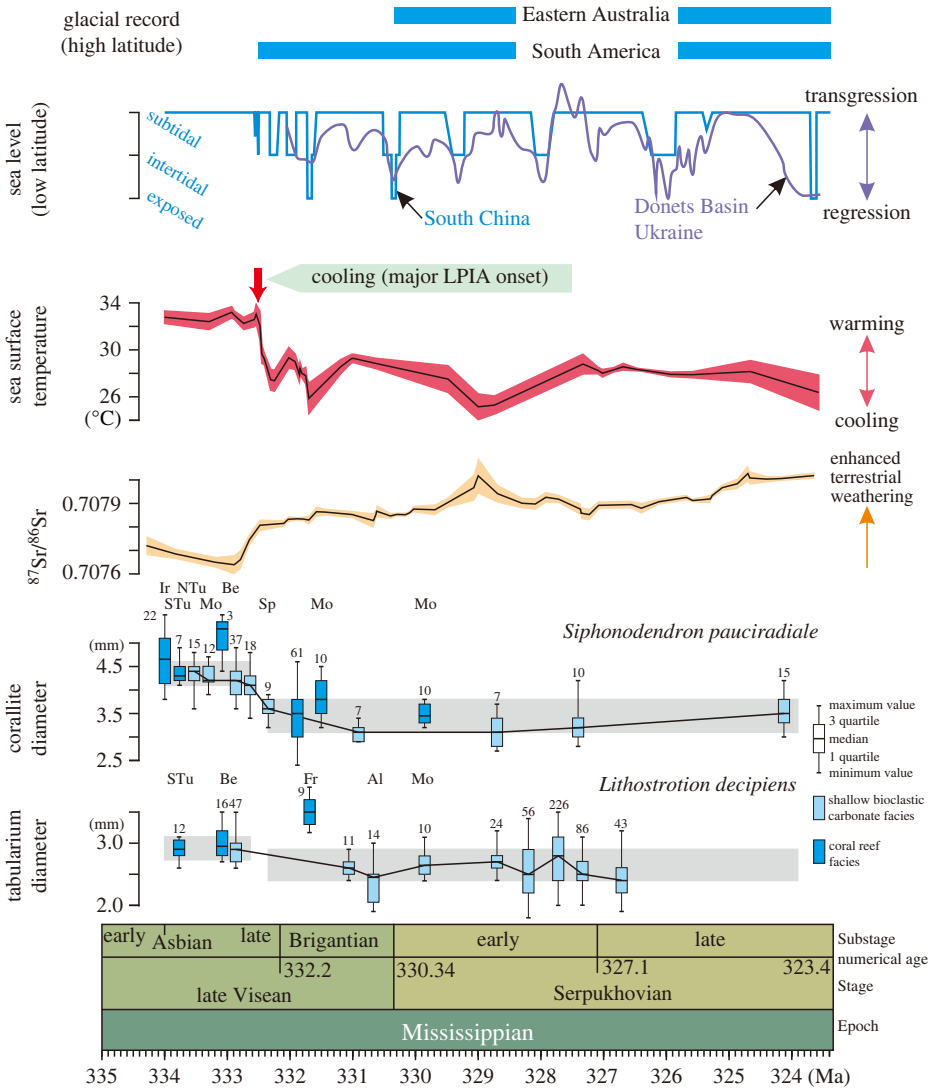

Figure 4. Size evolutionary pattern of the colonial coral species *Siphonodendron pauciradiale* and *Lithostrotion decipiens* based on global data (electronic supplementary material, table S1), and their relations to the changes in terrestrial weathering ($^{87}Sr/^{86}Sr$), sea surface temperature, low-latitude sea-level and high-latitude glacial deposits from the late Visean to Serpukhovian stages [12]. The number on the bar represents the counted number of corallites. The grey shaded bars represent the one- and three-quartile values of the coral size data. The unlabelled bars indicate the data from the Yashui section in South China. Al: Algeria, Be: Belgium, Fr: France, GB: Great Britain, LPIA: Late Palaeozoic Ice Age; Mo: Morocco, NTu: northern Turkey, Sp: Spain, STu: southern Turkey.

successions in China, Europe and North Africa enable the study of their evolutionary trend in size during this time (figure 1). Based on these compiled data from different palaeocontinents, it shows that a distinct decline in size values (10–20%) both for *L. decipiens* and *S. pauciradiale* across the ABB (late Visean) is very well expressed in the shallow marine bioclastic carbonate facies within the Palaeotethys Ocean. This phenomenon is also present in the species *S. pauciradiale* in the coral reef facies, which contains larger coral size than that of the shallow bioclastic carbonate facies (figure 4). This obvious size decline may be due to ecotypic variants within a single evolving lineage that is related to genetic variation within these coral species. It could be interpreted as an anagenetic evolutionary trend, resulting in the gradual shift to morphologically smaller forms [22,42,43]. However, this trend did not lead to any speciation event in the Serpukhovian. Indeed, the two studied species are the ancestors of smaller and morphologically more simple forms [44,45], but those speciation events took place in the early Asbian several million years before the ABB [46]. In consequence, the variations in coral sizes around the ABB are thought to reflect the capability of the two species to adapt to environmental pressure. Hence, taxonomic studies on these fossils should consider and probably better define intra-specific morphological variability.

Unlike present-day studies, genotypes are difficult to access for fossil species, due to lack of genomic material, soft part anatomy and biochemical signatures [47]. This suggests that genetic differentiation in fossil species can reasonably be excluded by study of (i) examined variation within conspecific samples and (ii) study of samples from contemporaneous strata with geographical closeness [47]. These points are fulfilled for the studied gradient on the South China Block and nearby East Qilian Mountain. Hence, we conclude that morphological changes in the same coral species reflect phenotypic plasticity ascribed to environmental changes. From the late Visean to Serpukhovian, sea surface temperature obviously changed with the onset of the LPIA around the ABB, as evidenced from the occurrence of high-latitude glacial deposits, low-latitude eustatic sea-level fall and a positive shift in brachiopod oxygen isotope values [12,48,49] (figure 4). This dramatic climate cooling (drop of approx. 5°C in sea surface temperature

in low latitudes) was probably induced by enhanced terrestrial silicate weathering and runoff indicated by a positive shift in strontium, carbon and oxygen isotopes, resulting from coeval Variscan orogeny and terrestrial plant proliferation [12,50,51] (figure 4). Hence, the prominent reduction in reef coral size across the ABB is consistent with coeval enhanced terrestrial weathering and dramatic climate cooling (figure 4). This suggests a causal link between this decline in coral size and enhanced terrestrial sediment input during a glacial period (figure 4). This implies that the corals alter their morphology towards small forms to adapt to the new state of phenotype-environment match (figure 4).

This study uncovers the relationship between reef coral evolution and increased terrestrial runoff during the critical transition of the LPIA onset (Mississippian foraminiferal zones 14–16). The smaller coral sizes of the latest Visean and Serpukhovian could be a consequence of resilience under long-term terrestrial sediment impact. These findings can provide insights into the long-term evolution and regulation of modern marine coral reefs as corals containing the ability to decrease in size are more resilient under high sedimentation from terrestrial runoff. Consideration of future coral reef conservation, which is mostly based on short-term observations and trends, including the almost immediate impact and effect of natural and man-made detrital input on coral reefs, may benefit from this long-term perspective.

Data accessibility. The supplementary figures and table are available online in the Dryad Digital Repository [53].

Authors' contributions. L.Y.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, resources, software, validation, writing—original draft and writing—review and editing; W.L.: conceptualization, data curation, formal analysis, resources, software, validation and writing—review and editing; M.A.: conceptualization, data curation, formal analysis, methodology, validation and writing—review and editing; D.J.B.: conceptualization, formal analysis, validation and writing—review and editing; X.W.: funding acquisition, resources, validation and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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