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Implications for Ediacaran biological evolution from the ca. 602 Ma Lantian biota in China

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ABSTRACT

The morphologically differentiated benthic macrofossils of algae and putative animal affinities of the Lantian biota in China represents the oldest known Ediacaran macroscopic eukaryotic assemblage. Although the biota provides remarkable insights into the early evolution of complex macroeukaryotes in the Ediacaran, the uncertainty in its age has hampered any robust biological evaluation. We resolve this issue by applying a petrographic-guided rhenium-osmium (Re-Os) organic-bearing sedimentary unit study on the Lantian biota. This work confines a minimum age for the first appearance of the Lantian biota to 602 ± 7 Ma (2σ, including decay constant uncertainty). This new Re-Os date confirms that the Lantian biota is of early–mid Ediacaran age and temporally distinct from the typical Ediacaran macrobiotas. Our results indicate that the differentiation and radiation of macroscopic eukaryotes, and the evolution of the primitive, erect epibenthic ecosystem, occurred in the early–mid Ediacaran and were associated with highly fluctuating oceanic redox conditions. The radiogenic initial $^{187}Os/^{188}Os$ ratios derived from the Lantian (1.14 ± 0.02) and other Ediacaran shales invoke oxidative weathering of upper continental crust in the early–middle Ediacaran, which may have stimulated the evolution of life and oceanic-atmospheric oxygenation. Integrated with published Ediacaran chronological and geochemical data, our new Re-Os geochemical study of the Lantian black shale provides a refined, time-calibrated record of environment and eukaryote evolution during the Ediacaran.

INTRODUCTION

The Ediacaran Period (635–541 Ma) marks a pivotal time in the evolution of life, when complex macroscopic eukaryotes irreversibly attained ecological dominance (Xiao and Narbonne, 2020). Ediacaran stratigraphic successions host abundant fossil assemblages that mainly include acanthomorphic acritarchs (microscopic marine planktonic organisms of uncertain, and possibly various, taxonomic affinities) in the lower Ediacaran and macroscopic, morphologically complex, soft-bodied Ediacara-type fossils in the upper Ediacaran (Liu et al., 2015; Droser et al., 2017; Liu and Moczydłowska, 2019; Xiao and Narbonne, 2020). A remarkable biological evolution in the Ediacaran Period is the increasing macroscopic complexity exhibited by the Lantian biota, which occurs in the lower slope to basinal black shales of the Lantian Formation, China (Fig. 1). The Lantian biota probably represents the oldest known macroscopic fossil assemblage of morphologically differentiated benthic algae and putative animal affinities (Yuan et al., 2011; Van Iten et al., 2013; Wan et al., 2016) and provides a lineage into the origin and early evolution of multicellular organisms (Narbonne, 2011; Yuan et al., 2013).

Until now, the Lantian biota lacked any absolute age control, especially because the dearth of intercalated ash beds hinders zircon U-Pb dating. Moreover, the high hydrocarbon maturity (Zeng et al., 2016) and variable degrees of post-formation modification of the Lantian black shales have rendered previous Re-Os geochronology attempts unsuccessful. Yet, largely based on lithostratigraphic correlation between the Lantian (south Anhui) and Doushantuo Formations (Yangtze Gorges area), which are ~700 km apart (Fig. 1A), the Lantian biota was aged between 635 Ma and 551 Ma (Condon et al., 2005; Yuan et al., 2011). However, complex facies changes and diachronous lithostratigraphic boundaries in the Lantian and Doushantuo Formations make this lithostratigraphy-based temporal correlation uncertain. The youngest population of detrital zircons from Member II of the Lantian Formation yields a maximum depositional age of 590 ± 7 Ma (concordia U-Pb date; Lan et al., 2019; Fig. 1C). Further, low-Y monazite formed during early diagenesis from the same stratigraphic unit gave a U-Pb date of 612 ± 29 Ma, which has been inferred as a minimum depositional age of the Lantian Formation (Liu et al., 2020). However, the sampling depths of the aforementioned detrital zircon and monazite U-Pb dates are only loosely constrained. The absence of absolute age constraints on the Lantian biota severely hampers its correlation to other Ediacaran fossil assemblages and therefore hinders our understanding of the evolutionary trajectory. Thus, to constrain the age of the Lantian biota and calibrate Ediacaran chemo- and biostratigraphic records, and yield implications for life evolution and environmental changes, we present a petrographic-guided, Re-Os geochronology of the best-preserved, biota-bearing, organic-rich black shale of Member II of the Lantian Formation from a cored interval (Fig. 1).

GEOLOGICAL BACKGROUND

During the Ediacaran Period, the Yangtze block of the South China craton (Fig. 1A) consisted of a shelf to the northwest, a deep

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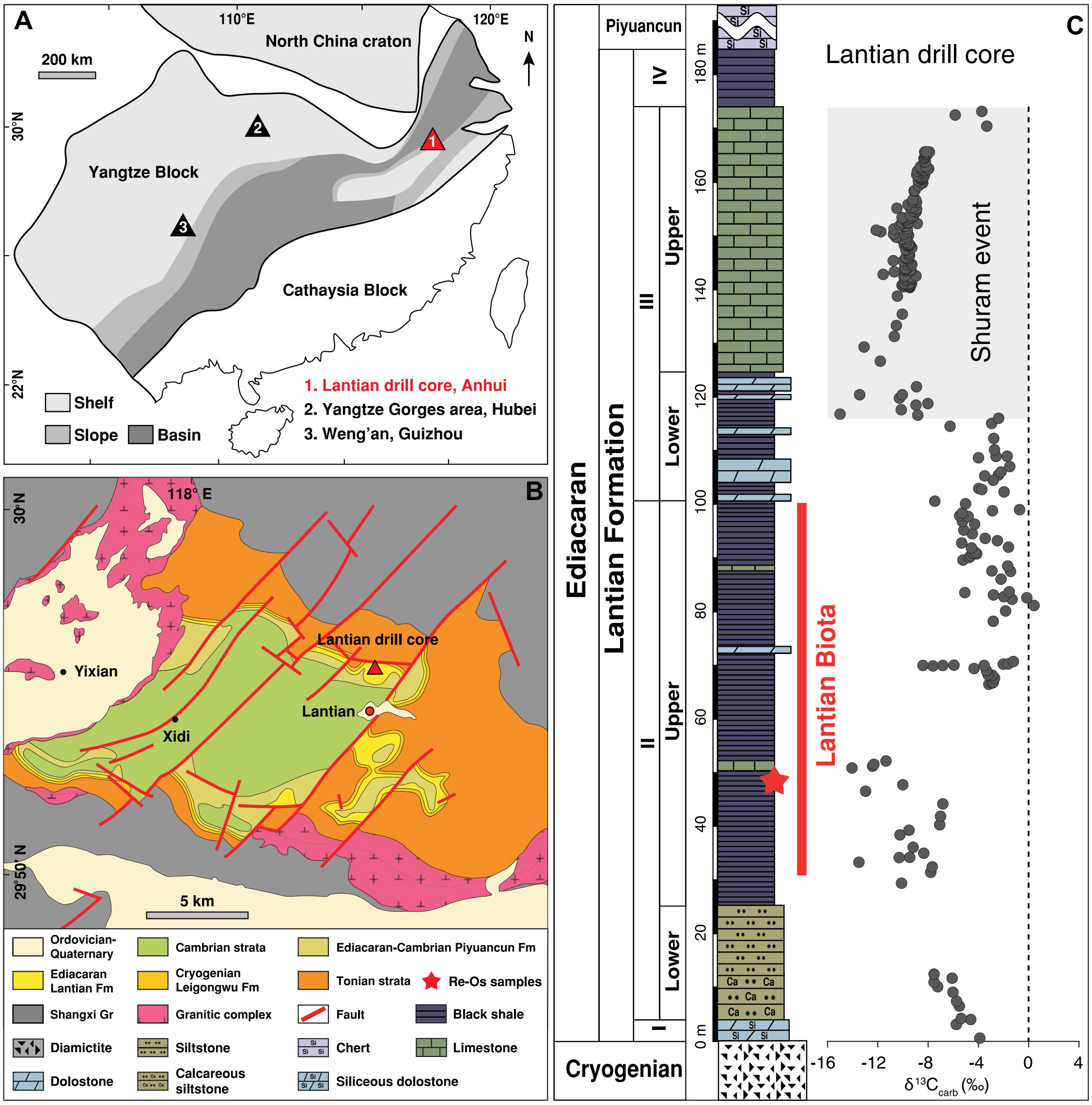

Figure 1. Geological maps and stratigraphic column for the Lantian Formation (China) (modified after Wang et al., 2017). (A) Generalized paleogeographic map of the Yangtze Block during the early–middle Ediacaran Period showing the approximate location of shelf, slope, and basinal facies. Numbered triangles indicate locations of areas/sections mentioned in the text, with the Lantian area highlighted in red. (B) Geological map of the Lantian area showing the location of the Lantian drill core. (C) Litho- and chemo-stratigraphy of the Lantian drill core highlights the horizon that was sampled for Re-Os geochronology in this study. Carbonate carbon isotopic data are from Wang et al. (2017). Gr—Group; Fm—Formation.

basin to the southeast, and a narrow slope in between, with the water depth deepening toward the southeast (based on the present geographic orientation; Jiang et al., 2007). The complete Ediacaran stratigraphic successions in the Yangtze block are recorded in various sedimentary facies and are well-known for their extraordinarily well-preserved fossil biotas, including the two probably oldest Ediacaran biotas (i.e., the Lantian biota in Anhui and the Weng'an biota in Guizhou; Fig. 1A). The Lantian Formation in the eastern Yangtze block was deposited in slope-basinal facies (Fig. 1A), which overlies the terminal Cryogenian diamictite of the Leigongwu Formation and underlies the Ediacaran–Cambrian transitional Piyuancun Formation (Fig. 1C). Samples were collected for Re-Os geochronology from a cored interval of the Lantian Formation near Lantian village (29.952°N, 118.038°E; Fig. 1B), Xiuning County, Anhui Province, China (Wang et al., 2017). In the drill core (Fig. 1C), the Lantian Formation begins with a 4-m-thick unit of light-gray siliceous cap dolostone of Member I. The overlying Member II (97 m) consists of a lower subunit of gray, calcareous siltstone interbedded with argillaceous limestone and an upper subunit of black shale with rare argillaceous limestone interbeds. Further upsection, Member III (73 m) is composed of interbedded gray, argillaceous dolostone and black shale, followed by ca. 50 m of gray limestone. The uppermost Lantian Formation, Member IV, consists of 10 m of black shale. Carbonaceous compression macrofossils and pyritized fossils occur almost continuously in the upper subunit of Member II (Yuan et al., 2011; Wang et al., 2017). Black shale samples for Re-Os geochronology were collected from a 50 cm interval of the Lantian drill core (Figs. 1C and 2A), which is 48.0 m above the base of the Lantian Formation (Wang et al., 2017).

METHODS AND RESULTS

To target the best-preserved shale with the least post-depositional isotope exchange for Re-Os dating (Stein and Hannah, 2014), we used a petrographic-guided approach. Fresh core samples without post-formation veining and weathering (Fig. 2A) were imaged by X-ray computed tomography (CT) and X-ray fluorescence (XRF). An ~50 cm core interval consisting of well-laminated, organic-rich black shale with two inter-layered pyrite horizons (0.5–2 cm) was studied (see the Supplemental Material[1] for complete analytical protocols). Our CT imagery (Fig. 2A) and XRF scan (Table S1 in the Supplemental Material) revealed well-preserved sedimentary lamination (Fig. 2A) and relatively homogenous elemental patterns (Fig. 2B) for the Lantian shales, which suggest a stable depositional environment with no evidence of chemical weathering (e.g., Si, Al, and Fe; Table S1). Nine samples were selected over an interval of ~25 cm for Re-Os isotope analysis

[1]Supplemental Material. Analytical methods and data. Please visit https://doi.org/10.1130/GEOL.S.18822305 to access the supplemental material, and contact editing@geosociety.org with any questions.

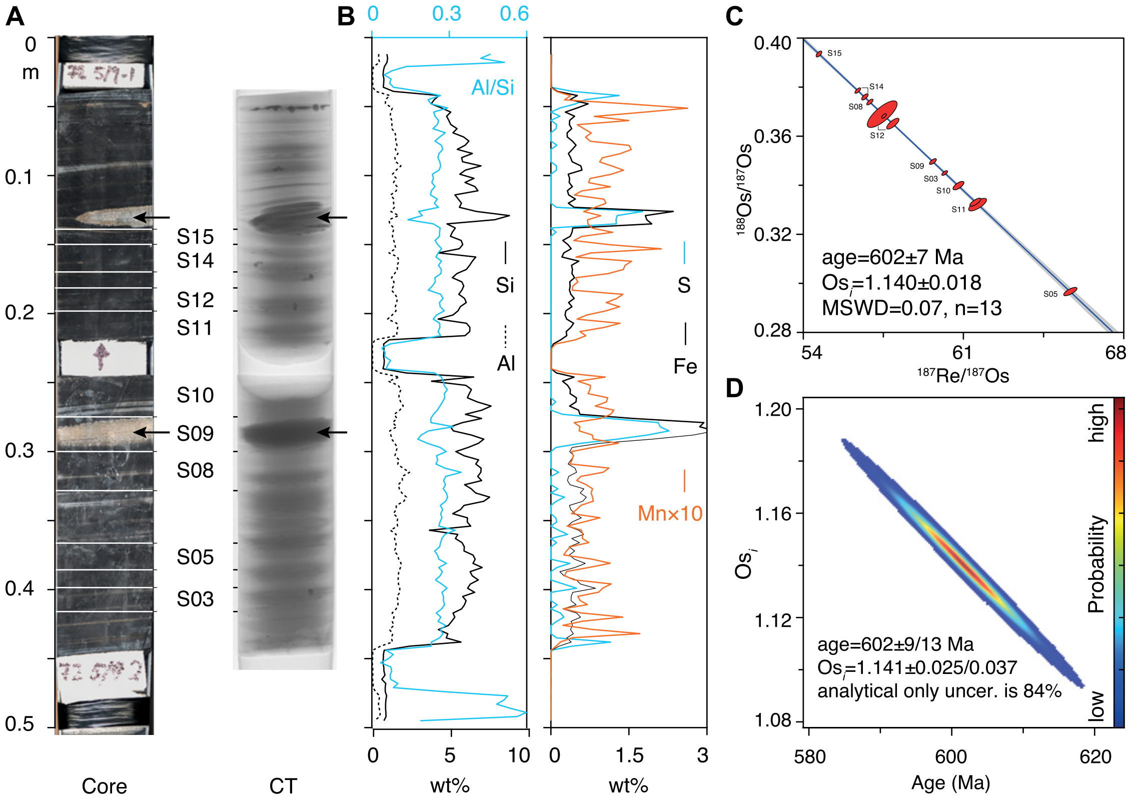

Figure 2. Results of petrographic-guided Re-Os dating of the Lantian biota (China). (A) The core section studied (0.5 m in length) is from the 72 5/9 interval of the drill core (Fig. 1), which is 48.0 m above the base of the Lantian Formation. The computed tomography scan reveals clear sedimentary lamination of the organic-rich black shales. Arrow highlights the presence of syn-sedimentary pyrite nodules. (B) Relatively homogenous elemental patterns of shales (excluding syn-sedimentary pyrite nodules) from micro X-ray fluorescence scanning (Table S1 [see footnote 1]) further confirm no post-formation disturbance of the samples studied. (C) Re-Os data from nine samples yield an inverse isochron age (n = 13, Model 1, mean square of weighted deviates [MSWD] = 0.07, probability = 1) of 602 ± 7 Ma (2σ, including decay constant uncertainty throughout this study) and an initial ^{187}Os/^{188}Os (Os*i*) value of 1.14 ± 0.02 using an inverse isochron approach (Li and Vermeesch, 2021). (D) A Monte Carlo simulation (Li et al., 2019) yielded identical results to those from an inverse isochron approach, within uncertainty (602 ± 9/13 Ma, 1.141 ± 0.025/0.037; uncertainties are presented as analytical only/model uncertainty included), and indicates that analytical uncertainty is the predominate source (84%) of uncertainties for the final age. CT—computed tomography, uncer.—uncertainty.

(Fig. 2A). The Re and total Os abundances of the samples range from 4 ppb to 12 ppb and 155–490 ppt, respectively (Table S2). Using the inverse isochron approach (Li and Vermeesch, 2021), the ^{187}Re/^{188}Os (139–221) and ^{187}Os/^{188}Os (2.54–3.37) ratios yield an isochron age of 602 ± 7 Ma (2σ with decay constant uncertainty throughout this study), with an initial ^{187}Os/^{188}Os (Os_i) value of 1.14 ± 0.02 (n = 13, Model 1, MSWD = 0.07, probability = 1.0; Fig. 2C) . An identical age (602 ± 9 Ma) and Os_i (1.14 ± 0.03) are obtained (Fig. 2C) from Monte Carlo simulation (Li et al., 2019). The low MSWD is expected because the samples have very limited spread in ^{187}Re/^{188}Os, and indicates a predominant analytical contribution of uncertainties (84%; Fig. 2C).

DISCUSSION AND CONCLUSION

A ca. 602 Ma Age for the Lantian Biota

Our petrographic-guided approach allows targeting the best-preserved shales for Re-Os dating, and we successfully obtained a 602 ± 7 Ma Re-Os date from the middle of Member II of the Lantian Formation. This provides the first direct absolute age constraint on the Lantian biota. The upper boundary of the Lantian biota interval is near the Member II–III boundary of the Lantian Formation (Fig. 1C). This boundary horizon is suggested to be below the Shuram event interval (574.0 ± 4.7 Ma–567.3 ± 3.0 Ma; Rooney et al., 2020; Fig. 3A) and concurrent with another negative carbon isotope excursion (CIE, Fig. 1C), which is interpreted as an equivalent to the one near the Member II–III boundary of the Doushantuo Formation in the Yangtze Gorges area (Jiang et al., 2007; Zhu et al., 2007). The absolute age of this CIE is not constrained but has been correlated to the 580 Ma Gaskiers glaciation (Condon et al., 2005; Fig. 3A). We tentatively follow this interpretation, and therefore the Lantian biota is assumed to be older than 580 Ma (Fig. 3B), which is supported by our new Re-Os date. There are no age constraints on the lower boundary of the Lantian biota. Based on the correlated date of 635 Ma for the base of the Lantian Formation and our new Re-Os date (602 ± 7 Ma), and without the availability of additional high-precision dates, we tentatively propose that the nominal age of the lower boundary of the Lantian biota is ca. 615 Ma with an uncertainty on the order of a few million years.

In contrast to the deepwater, *in situ* preserved Lantian biota, the Weng'an biota is hosted in shelf-facies phosphorite of the Doushantuo Formation in the Weng'an area (Fig. 1A). It is a rich microfossil assemblage consisting mainly of reworked and redeposited acanthomorphic acritarchs, multicellular algae, tubular microfossils, putative animals, and animal embryos (Xiao et al., 2014). Similar microfossil assemblages have been recovered from chert nodules in the lower part (Member II) of the Doushantuo Formation (Liu and Moczydłowska, 2019; Ouyang et al., 2021). The lowest occurrence of such chert nodules is ∼2.8 m above the cap dolostone (Ouyang et al., 2021), with an estimated age close to 632 Ma (Condon et al., 2005). These age constraints demonstrate that the Lantian biota occurred later than the Ediacaran microfossil assemblages but with a significant temporal overlap (Fig. 3B). Our new black shale Re-Os date (602 ± 7 Ma) further suggests that the Lantian biota is older than the first occurrence of soft-bodied Ediacara-type fossils (Fig. 3B). The layers that contain these oldest Ediacara-type fossils are stratigraphically below the Shuram Event (Macdonald et al., 2013) and geochronologically no later than 574.17 ± 0.66 Ma in Newfoundland (Matthews et al., 2021) and 574.0 ± 4.7 Ma in northwestern Canada (Rooney et al., 2020).

Implications for the Ediacaran Eukaryote Evolution

Putative animal fossils, including four genera and five species, are reported from the Lantian biota (Yuan et al., 2011; Wan et al., 2016). They are typically centimeter-scale in size and show relatively complex morphological and

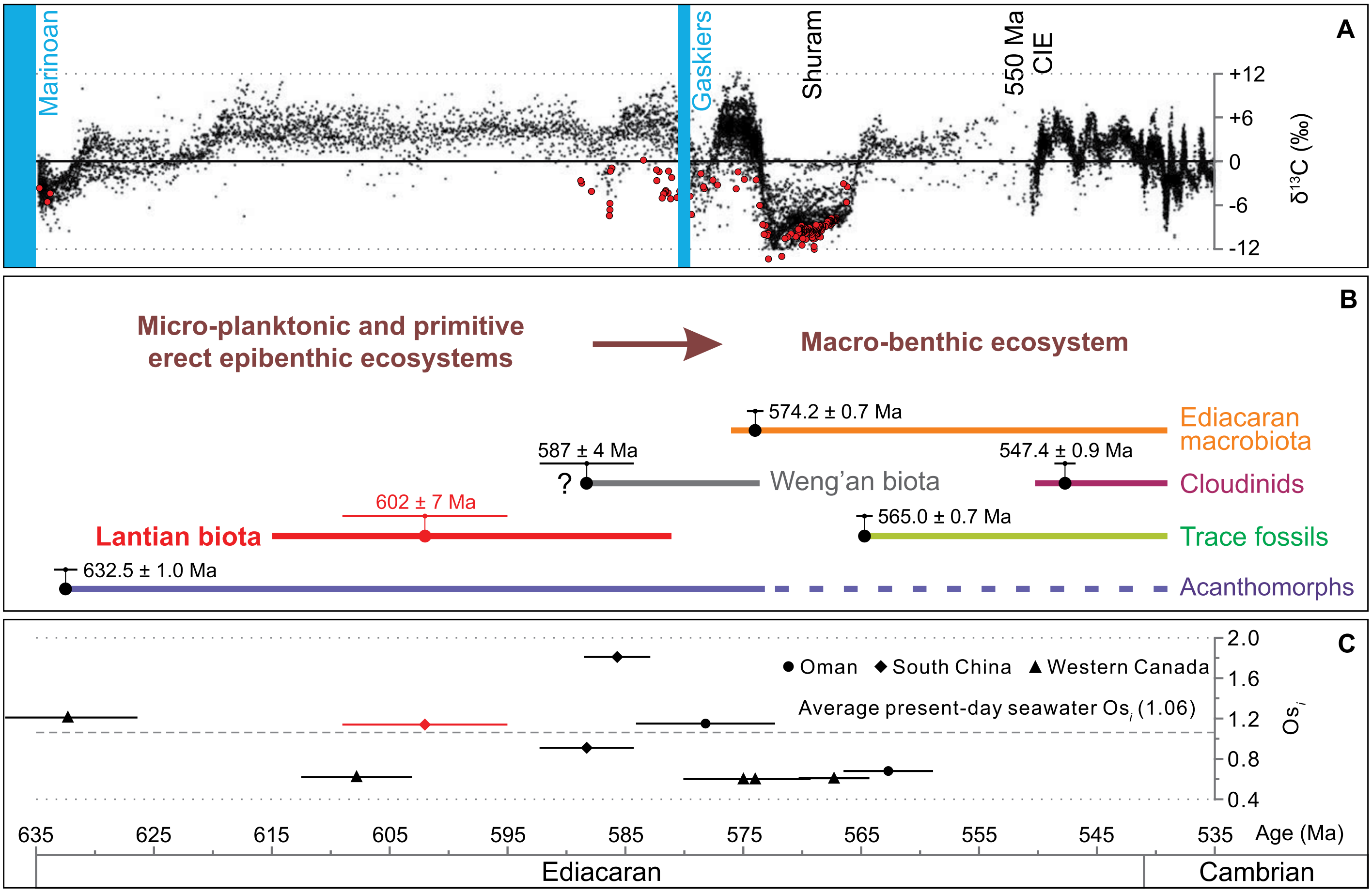

Figure 3. Integrated carbon isotopic profile (A), fossil ranges (B), and initial osmium isotopic data (C) of the Ediacaran Period, modified after Yang et al., 2021; data for Os*i* are given in Table S3 (see footnote 1). Carbonate $\delta^{13}C$ data from the Lantian Formation are highlighted in red. CIE—carbon isotope excursion.

structural differentiation (Wan et al., 2016). The new age constraint on the Lantian biota indicates that metazoans were possibly present and differentiated by the early–middle Ediacaran, consistent with the molecular clock analyses that suggest the development of fundamental clades and body plans of animals during the Ediacaran (Erwin et al., 2011; dos Reis et al., 2015). This inference is supported by the early–middle Ediacaran microfossil assemblages that host evidence for the presence of animal embryos, embryo cleavage, and putative animal body parts (Yin et al., 2015; Xiao et al., 2014).

Eight genera and 13 species of macroalgal fossils have been recognized as the main components of the Lantian biota (Yuan et al., 2013). Together with contemporary microalgal fossils preserved in the Weng'an biota and acanthomorphic acritarch assemblages (Liu and Moczydłowska, 2019; Ouyang et al., 2021), the fossils represent a major episode of radiation and diversification of algae in the early–middle Ediacaran. This bloom of algae may have facilitated oceanic oxygenation and the evolution of metazoa in the Ediacaran (Brocks et al., 2017). Several Lantian algal taxa span into the late Ediacaran macrobiotas, and one, *Flabelophyton*, shows a trend of increasing body size (Wan et al., 2020). The shared taxa between the temporally and taxonomically distinct Lantian biota and late Ediacaran macrobiotas imply their possible evolutionary connections.

The Ediacaran Period represents a critical transition in ecological evolution (Fig. 3B) that marks the replacement of matground-based ecosystems by modern-style ecosystems (Butterfield, 2007). Most members of the Lantian biota were erect epibenthic taxa (Yuan et al., 2011; Wan et al., 2016). Our new Re-Os date (602 ± 7 Ma) confirms that epibenthic communities were present by the early–middle Ediacaran contemporaneous with the prevailing micro-planktonic ecosystem (Xiao and Narbonne, 2020).

The 602 ± 7 Ma isochron from the Lantian Formation yields an Os_i value of 1.14 ± 0.02 (Fig. 2C). A statistically identical isochron age of 607.8 ± 4.7 Ma reported from the Old Fort Point Formation in western Canada yields a considerably different Os_i (0.62 ± 0.03; Kendall et al., 2004), implying a regional paleoenvironmental control on the Os isotopic composition of seawater for the two depositional sites. Yet, existing data show that the Os_i of early–middle Ediacaran (635-580 Ma) seawater is radiogenic; the majority of values are close to that of the present-day seawater (Fig. 3C), which suggests that seawater Os was predominantly derived from oxidative weathering of the upper continental crust during this time interval. Continental weathering may also suggest an increase in nutrient availability that may have stimulated the evolution of life and ocean-atmosphere oxygenation in the Ediacaran. Yet, given that available Os_i data are very limited, additional Os stratigraphic studies are warranted to further evaluate this hypothesis.

Redox proxies of the Lantian Member II black shale indicate persistent euxinia with a transient interval of oxygenation (Wang et al., 2017). However, the in situ preserved macroscopic (centimeter-scale) algae and possible metazoans of the Lantian biota clearly require oxygenation on ecological time scales, indicating episodic brief oxygenation below the storm wave base but within the euphotic zone in the early Ediacaran. This discrepancy could be reconciled by the significant difference between geochemical and ecological time scales (Yuan et al., 2011; Wang et al., 2017). The depositional setting and geochemistry of the Lantian Formation imply that deep and stenothermal environments rather than stable oxygenated conditions played a prominent role in the origin of the Lantian organisms, similar to the hypothesis proposed for the origin of the Ediacara-type organism (Sperling et al., 2016; Boag et al., 2018).

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