Past endolithic life in metamorphic ocean crust

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Abstract

The known deep subsurface biosphere on Earth persists in diversified habitats, including deep within igneous rocks of the oceanic crust. Here, we extend the range of the deep subsurface biosphere to metamorphic ocean crust of a subduction zone. We report fossilised life in zeolite facies rocks, which formed by low grade metamorphism, from the southern Mariana trench. Dense carbonaceous spheroids, filaments, and *Frutexites*-like structures are preserved in these rocks, which are enriched in organic carbon but depleted in ¹³C. The distinct difference in the GDGT-0 *vs.* crenarchaeol and the branched *vs.* isoprenoid tetraether values between the inner and outer portions of these rocks indicate the *in situ* production of organic carbon. We demonstrate that these structures may result from the past activity of potential chemolithoautotrophs within the metamorphic crust, as implied by their morphologies, Raman spectra, carbon isotopes, and biomarker signatures, as well as the Fe oxidation state within whole rocks. We propose that fluid-rock reactions at temperatures within the tolerance of life during low grade metamorphism contributed to microbial subsistence within the biotope. The low grade metamorphic ocean crust of the subduction zone likely represents Earth's deepest, and one of its largest, microbial ecosystems, which may potentially influence the deep carbon cycle.

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Letter

The deep subsurface biosphere on Earth exists in a variety of hydrated subsurface regions with sufficient energy gradients (Orsi, 2018). Fumes *et al.* (2008) reviewed the microbial alteration textures in the meta-volcanic glasses and crusts of pillow lavas from submarine environments, showing that textural signatures and chemical tracers of microbial life can be well preserved in metamorphic rocks. Based on a heat conduction model, Plümper *et al.* (2017) estimated that microbial life could exist as deep as ~10 km below the seafloor. However, little is known about whether microbial life thrives in metamorphic rocks that form under low temperature, high pressure conditions at a convergent margin during the descent of a subducting plate. Among these metamorphic rocks, zeolite facies rocks (Fig. S-1) are first formed from metamorphism of basaltic rocks in subduction zones at depths of 1–14 km beneath the seafloor and temperatures of approximately 40–300 °C (Marshak, 2009). The temperature range of zeolite facies formation is partly within the tolerance of life (Takai *et al.*, 2008), making it the maximum metamorphic grade that can potentially host life in subduction zones. Thus, zeolite facies rocks in subduction zones may provide promising habitats for subsurface piezophilic microorganisms.

To test this hypothesis, we recovered metamorphic rocks that have been tectonically extruded through deep faults at the

seafloor from the subduction zone of the southern Mariana trench (SMT) at a water depth of 5500 to 6800 m (Fig. S-2, Table S-1), using the manned submersible *Jiaolong* during two R/V XYH09 cruises (June–July 2016 and May–June 2017). Extensive outcrops of metamorphic rocks were observed on the south and north slopes of the SMT (Fig. 1). X-ray diffraction (XRD) analyses show that these metamorphic rocks mainly consist of phillipsite, heulandite, gmelinite, analcite, natrolite, chabasite, chlorite, and celadonite (Table S-1), a mineral assemblage indicative of low grade zeolite facies metamorphism. The oxygen isotopic composition of carbonates extracted from these rocks ($\delta^{18}\text{O}_{\text{SMOW}} = 13.9$ to 25.3 ‰) reveals that they have been altered at temperatures between 20 °C and 89 °C assuming equilibrium with ¹⁸O-depleted fluids (–4 ‰; Table S-2).

Transmitted white light and scanning electron microscopy (SEM) observations revealed a high abundance of spheroidal objects with diameters of *ca.* 2–150 µm in zeolite and celadonite (Figs. 2a,b, S-3, S-4). They exhibit loose, net-like, or condensed-gel structures (Fig. S-4d). Nano-scale secondary ion mass spectrometry (NanoSIMS) and energy dispersive X-ray spectroscopy (EDS) element maps show that the spheroids are chiefly composed of carbon (C), nitrogen (N) and phosphorus (P), whereas the matrix is zeolite or celadonite (Figs. 2d–g, S-3c,f, S-4e, S-5). Raman spectra of the carbonaceous spheroids are characterised by two broad and overlapped first order bands, assigned as

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Figure 1 Representative metamorphic ocean crust on the north (a–b) and south (c–d) slopes of the SMT. (a) Yellow-green zeolite rocks coated by black manganese crusts (Dive JL118; 6695 mbsl). (b) White-yellow zeolite rock terrace (Dive JL119; 6001 mbsl). (c) Bluish-green celadonite rock outcrop (Dive JL122; 6300 mbsl). (d) Yellowish zeolite mound (Dive JL122; 6296 mbsl). Zeolite rocks in yellow indicate the presence of ferric iron.

D and G, and a very wide second order band of disordered carbonaceous matter (DCM; Fig. 2c). The morphologies and chemical compositions of the SMT carbonaceous spheroids resemble those of a fossilised microbial community found in serpentinised mantle rocks (Klein *et al.*, 2015; Plümper *et al.*, 2017).

Microscopic filaments, which are composed of DCM (Figs. 2i,j, S-6b; Video S-1), are also present in the SMT metamorphic rocks (Figs. 2h, S-6a,c,d). These filaments, $\sim 2.0\ \mu\text{m}$ wide and $\sim 30\text{--}200\ \mu\text{m}$ long, are typically tubular, non-septate and unbranched. The tubular nature of the carbonaceous filaments, the existence of a “hollow” lumina shown in Video S-1, and the range of widths exhibited by the filaments, are consistent with a biological origin (Buick, 1990). Morphologically, they resemble microbial filaments found in zeolite-carbonate interfaces in sub-seafloor basalts (Ivarsson *et al.*, 2008).

Millimetre scale *Frutexites*-like structures composed of zeolite and celadonite also occur in the matrix (Figs. 2k,l, S-7; see Supplementary Information). The close spatial associations and bulbous arborescent morphology of the SMT *Frutexites*-like structures, as well as the occurrence of carbonaceous matter concentrated in zeolite and celadonite minerals, indicate that the organic matter may have been formed by microbial activity during subduction metamorphism. Similar *Frutexites*-like structures were previously found in subsurface rock samples and attributed to chemoautotrophic communities (Heim *et al.*, 2017).

Geochemical analyses show that contents of total organic carbon (TOC) in metamorphic rocks range from 0.008 wt. % to 0.379 wt. %, while contents of total inorganic carbon (TIC) range from 0.004 wt. % to 0.141 wt. %. $\delta^{13}\text{C}_{\text{TOC}}$ values vary between $-22.4\ \text{‰}$ and $-29.5\ \text{‰}$ (average = $-25.2\ \text{‰}$), whereas TIC is more enriched in ^{13}C ($\delta^{13}\text{C}_{\text{TIC}} = -14.5\ \text{‰}$ to $-6.1\ \text{‰}$; Table S-2). Carbonates derived from circulating unmodified seawater and the mantle typically have $\delta^{13}\text{C}$ values of approximately 0 and $-7\ \text{‰}$, respectively (Fig. 3; Deines, 2002). The low $\delta^{13}\text{C}_{\text{TIC}}$ values and their large shift in the SMT metamorphic rocks indicate that organic matter was oxidised into ^{12}C -enriched CO_2 , which shifted the isotopic values of the dissolved inorganic carbon pool from which carbonate precipitated. Similar $\delta^{13}\text{C}_{\text{TIC}}$ values were also recorded in altered basalts on the Costa Rica Rift and attributed to microbial metabolic processes (Torsvik *et al.*, 1998). The $\delta^{13}\text{C}_{\text{TOC}}$ values recorded in the SMT metamorphic rocks are typically lower than $\delta^{13}\text{C}_{\text{TOC}}$ values (-17.5 to $-21.3\ \text{‰}$) of the surrounding sediments (Fig. 3b; Table S-2). This clearly indicates that the source of organic carbon in such rocks is different from those in the surrounding sediments. Abiotic organic synthesis in the oceanic lithosphere, including Fischer-Tropsch-type reactions ($150\text{--}350\ ^\circ\text{C}$), re-speciation and high temperature reactions ($>400\text{--}500\ ^\circ\text{C}$) of C-O-H fluids during magma cooling, and carbonate decomposition to CH_4 ($<800\ ^\circ\text{C}$),

Figure 2 Representative carbonaceous spheroids (a–g; sample JL122-G01), filaments (h–j; sample JL122-G01), and *Frutexites*-like structures (k–m; sample JL122-G02) preserved in metamorphic rocks. (a) SEM-BSE image showing the distribution of spheroids composed of disordered carbonaceous matter (DCM, red arrows) in celadonite. (b) Enlarged view of DCM shown with a green rectangle in (a). (c) Raman spectrum collected at location marked by a green spot in (b), showing the characteristic first order (D band at ~1365 cm⁻¹ and G band at ~1590 cm⁻¹) and second order (between ~2500 and 3000 cm⁻¹) bands of DCM. (d–g) SEM-EDS images corresponding to (b), showing that DCM comprising of carbon (C) and nitrogen (N) is embedded by celadonite with celadonite grains on the inside (green arrows). (h) Transmitted white light photomicrograph of filaments. (i) Micro-Raman image of a filament. Reds and greens represent DCM and celadonite, respectively. (j) Three dimensional CLSM image of filaments using 488 nm laser excitation. (k) Transmitted white light photomicrographs of *Frutexites*-like structures. (l) Micro-Raman image of the white box shown in (k). White dotted lines indicate the contour of *Frutexites*-like structure. Reds, greens, blues and pinks represent DCM, celadonite, quartz and feldspar, respectively. (m) Average Raman spectra of DCM and minerals from (l).

Figure 3 (a) Total organic carbon isotopes in serpentinites from Iberian Margin (Schwarzenbach *et al.*, 2013). (b) Carbon isotopes in zeolite-rich metamorphic rocks and surrounding sediments from the SMT. (c) Carbon isotope variations found in nature (Schidlowski, 2001). The right hand column shows carbon isotope fractionation variations in four different carbon fixation pathways by autotrophic microorganisms (1: 3-hydroxypropionate cycle; 2: reductive tricarboxylic acid (rTCA) cycle; 3: Calvin-Benson-Bassham cycle; 4: reductive acetyl-CoA pathway). Data for the dissolved organic carbon field are from Bauer (2002).

may also produce organic matter with a similar range of $\delta^{13}\text{C}$ values, but they dominantly form methane and short chain hydrocarbons (Andreani and Ménez, 2019) and their required temperatures are inconsistent with the low temperature (20–89 °C) zeolite facies rocks studied here. Although some evidence suggests abiotic carbonaceous matter can be formed during low temperature alteration of ocean crust (<150 °C), it would have a distinct chemical composition containing aromatic carbon and short aliphatic chains (Sforna *et al.*, 2018). Raman analysis shows that the intensity ratio of the D and G bands for DCM is 0.76 (Fig. 2c), which is distinctly higher than that for graphite from the Loch Maree Group (0.21), but falls within those for organic matter from the Applecross, Aultbea and Cailleach Head Formations (0.47–1.02; Muirhead *et al.*, 2016). This clearly indicates that such organic carbon in SMT metamorphic rocks is not graphite. Similar $\delta^{13}\text{C}_{\text{TOC}}$ values were found in serpentinite muds from mud volcanoes on the Mariana forearc (Eickenbusch *et al.*, 2019), and serpentinites from the Iberian Margin (Schwarzenbach *et al.*, 2013). Alongside an isotopic offset of TOC relative to marine dissolved organic carbon, Raman and lipid biomarker analyses provide strong evidence that such organic carbon is primarily derived from chemolithoautotrophic microorganisms instead of abiotic production (Schwarzenbach *et al.*, 2013; Klein *et al.*, 2015). Thus, carbon isotope data suggest that this organic carbon in SMT metamorphic rocks is of biological origin.

Glycerol dibiphytanyl glycerol tetraether lipids (GDGTs) analyses reveal that the GDGTs concentrations in the outer portions of metamorphic rocks (OPMR; GDGT-0: 5.445–8.784 ng/g; crenarchaeol: 14.527–17.427 ng/g; branched GDGT: 2.471–3.538 ng/g) are comparable to those of the surrounding sediments (GDGT-0: 4.939–11.385 ng/g; crenarchaeol: 10.783–26.826 ng/g; branched GDGT: 2.196–7.665 ng/g), but notably higher than those in the inner portions of metamorphic rocks (IPMR; GDGT-0: 0.086–0.800 ng/g; crenarchaeol: 0.012–0.192 ng/g; branched GDGT: 0.044–0.597 ng/g; Table S-3). Crenarchaeol is considered to be a specific biomarker for Thaumarchaeota that grows chemoautotrophically by utilising ammonium or other electron donors (Pester *et al.*, 2011), whereas GDGT-0 is most

likely to be synthesised by both Thaumarchaeota and methanogenic archaea in deep seafloor environments that grow chemoautotrophically by utilising H_2 (Weijers *et al.*, 2009). Crenarchaeol and branched GDGTs can be produced in seafloor environments (Lincoln *et al.*, 2013; Pan *et al.*, 2016), even though they are commonly regarded as typical water column and soil biomarkers, respectively. In the OPMR, the GDGT-0 *vs.* crenarchaeol ratios (GCR; 0.4 to 0.5) are similar to those of the surrounding sediments (0.3–0.5), indicating that Thaumarchaeota is a preponderant group of Archaea (Fig. 4; Schouten *et al.*, 2002). In the IPMR, the GCR ranges from 1.4 to 59.5 indicating a substantial methanogenic source for GDGT-0 (Weijers *et al.*, 2009), as detected in Lost City chimneys and Iberia Margin brucite-calcite veins (Lincoln *et al.*, 2013; Klein *et al.*, 2015). In addition, the branched *vs.* isoprenoid tetraether (BIT) values for the IPMR range from 0.42 to 0.97, with an average value of 0.72 ($n = 5$; Fig. 4). These values are distinctly higher than those observed for the OPMR (average = 0.15, $n = 2$) and surrounding sediments (average = 0.19, $n = 6$), but almost identical to those observed for low temperature hydrothermal deposits (average = 0.63, $n = 4$; Pan *et al.*, 2016). Collectively, these tetraether lipid signatures further corroborate the *in situ* contribution of organic carbon by chemolithoautotrophic life in the IPMR.

H_2 generated by anaerobic basalt-fluid reactions during low grade metamorphism can function as an electron donor to provide energy for known chemolithoautotrophic life in metamorphic ocean crusts (Du *et al.*, 2019). Ferrous iron in basaltic minerals, such as pyroxene and olivine, can be oxidised to ferric iron through the dissociation of water during metamorphism and result in the generation of H_2 (Bach, 2016). Previous laboratory experiments demonstrated that H_2 could be generated through anaerobic basaltic mineral-water reaction at low to moderate temperatures (30 °C to 200 °C; Stevens and McKinley, 2000). High GCR ranging from 1.4 to 59.5 (Fig. 4), together with trace iron in zeolite facies rocks, strongly support this hypothesis. Besides H_2 , ammonium could provide another potential electron donor for chemolithoautotrophic life in metamorphic rocks, as indicated by high contents of crenarchaeol and NH_4^+ (average = 8.8 ppm; Table S-4) in

Figure 4 Ternary diagram showing the relationships of the fractional abundances of acyclic glycerol dibiphytanyl glycerol tetraether lipids (GDGT-0), crenarchaeol and sum of all branched GDGTs (Br-GDGTs) in different environments.

some of metamorphic rocks. Ammonia can be derived from the abiotic mineral catalysed reduction of N_2 , NO_2^- and NO_3^- (Brandes *et al.*, 1998) or microbial nitrate reduction coupled with H_2 oxidation (Cowen *et al.*, 2003) in the upper ocean crust. These autotrophic metabolisms in the metamorphic crust may evolve during rock aging and decrease with decreasing intensity of fluid-rock reactions (Türke *et al.*, 2018).

The low grade metamorphic ocean crust described here represents previously underexplored habitats for chemolithoautotrophic life on Earth. From the P-T phase diagram (Fig. S-1), this habitable niche, with temperatures below the upper limit for life (122 °C; Takai *et al.*, 2008), is expected to extend up to approximately 14 km into the ocean lithosphere of the subduction zone, far deeper than either the known basalt-hosted deep biosphere that is dominant in the upper 300–500 m of the ocean crust (Furnes *et al.*, 2008), or the ultramafic rock-hosted deep biosphere that is predicted as deep as ~10 km below the seafloor (Plümper *et al.*, 2017). However, it still remains unclear how long this endolithic life was sustained and to what extent it impacts crustal biogeochemical cycles. Future works in other deep sea localities are needed to further comprehend this deep subsurface ecosystem and its potential role in the deep carbon cycle in the region scale geological context.

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Author Contributions

XP designed research. XP, ZG, MD, KT and HX participated in the cruise. XP, ZG, MD, KT, ADC, DP and HX performed research and analysed data. All authors discussed the results and wrote the paper. XP, ZG, and MD contributed equally to this work.

Additional Information

Supplementary Information accompanies this letter at <http://www.geochemicalperspectivesletters.org/article2017>.

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