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Fossil evidence for serpentinization fluids fueling chemosynthetic assemblages

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Among the deep-sea hydrothermal vent sites discovered in the past 30 years, Lost City on the Mid-Atlantic Ridge (MAR) is remarkable both for its alkaline fluids derived from mantle rock serpentinization and the spectacular seafloor carbonate chimneys precipitated from these fluids. Despite high concentrations of reduced chemicals in the fluids, this unique example of a serpentine-hosted hydrothermal system currently lacks chemosynthetic assemblages dominated by large animals typical of high-temperature vent sites. Here we report abundant specimens of chemosymbiotic mussels, associated with gastropods and chemosymbiotic clams, in approximately 100 kyr old Lost City-like carbonates from the MAR close to the Rainbow site (36°N). Our finding shows that serpentinitization-related fluids, unaffected by high-temperature hydrothermal circulation, can occur on-axis and are able to sustain high-biomass communities. The widespread occurrence of seafloor ultramafic rocks linked to likely long-range dispersion of vent species therefore offers considerably more ecospace for chemosynthetic fauna in the oceans than previously supposed.

Bathymodiolus | Ghost City | ultramafic-hosted | mid-ocean ridge | ecogeochemy

High-temperature hydrothermal vents occur at very geographically restricted sites in the deep-sea, localized on spreading ridges and arc-related volcanoes. Typically, such vent fluids are metal- and H2S-rich and precipitate metallic sulﬁde chimneys on the seafloor (1, 2). These vents usually support high-biomass invertebrate communities, dominated by a small number of endemic species forming symbioses with diverse chemotrophic bacteria (e.g., vibrio, tubeworms, bivalve and gastropods), and bathymodiolin clams (1, 3). These symbioses exploit chemical energy from a variety of fluids enriched in reduced compounds, mostly hydrogen, to form carbon (4). These vents contain a variety of fluids enriched in reduced compounds, mostly hydrogen, to form carbon (4). Along slow and ultraslow spreading ridges, like the Mid-Atlantic Ridge (MAR), ultramafic mantle rocks can be exposed on the seafloor by large offsets faults (5). Seawater serpentization of these peridotites produces hydrogen, which subsequently reacts with CO2 to form methane (6, 7). Because of this, peridotite-hosted high-temperature vent sites on the MAR (e.g., Rainbow and Logatchev) exhibit elevated levels of methane and hydrogen contents in their fluids. Hydrothermal activity can also occur at off-axis ridge settings. A unique example of this is the Lost City vent field, discovered in the year 2000 on the Atlantis Massif, 30°07’N MAR, at 750- to 850-m depth (8). Here, exothermic serpentization processes may largely drive the hydrothermal convection, although a contribution of magmatic inputs is not excluded (9). The main difference between this off-axis vent field and the other known vent fields on the MAR-axis is that the majority of the Lost City vent fluids are metal-poor, low-temperature (40–91 °C), and have high pH (9–11). Further, the Lost City fluids are also highly enriched in H2 and CH4 and comparatively lower in H2S (10). On contact with ambient seawater these alkaline fluids precipitate chimney structures up to 60 m high composed of carbonates (aragonite and calcite) and brucite (Mg(OH)2) (11–13). Sulﬁde minerals are mostly absent from these chimneys, contrasting strongly with on-axis hydrothermal vent structures (13, 14). The Lost City site has generated considerable interest because this sort of system was likely to have been common in early Earth history and represents a plausible geochemical environment for the emergence of life on this, and potentially other, planets (15, 16).

In the context of the MAR peridotite-hosted vent ﬁelds another remarkable feature of Lost City is the lack of typical high-biomass animal assemblages dominated by large chemosynthetic invertebrates: There are currently no Bathymodiolus mussel beds or bivalve-shrimp swarms, although the diversity of other invertebrates (particularly small gastropods and polychaete worms) is described as being equivalent to that of high-temperature MAR vent communities (11, 17). Only two living specimens of Bathymodiolus aff. azoricus have been found at Lost City (18, 19), whereas hundreds of broken shell fragments downslope away from the active chimney areas (19, 20) suggest that the population size might have been much larger in the past and is now almost extinct (19). Dead B. azoricus shells have also been recently reported from carbonate chimneys at an inactive site near Lost City (21).

Supporting these observations, the enrichment of reduced compounds in Lost City hydrothermal ﬂuids indicates that these, and similar peridotite-hosted vents, hold the energetic potential to support large aggregations of Bathymodiolus mussels, a genus widely distributed along the MAR axis (22). B. aff. azoricus at Lost City hosts the same symbiont phylotypes as the methanotrophic and thiophosphatic endosymbionts of both B. azoricus and B. puteoserpentis from on-axis sites on the MAR (18), where the methanotrophic symbiont fixes carbon from methane and the chemolithoautotrophic uses sulfide to form CO2 (23–25). In addition to methane, DeChaine et al. (18) suggest that B. aff. azoricus at Lost City could also be utilizing hydrogen, although hydrogen-oxidizing symbionts have yet to be identiﬁed. These authors further


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suggested that hydrogen sulfide would be poorly available for mussels at Lost City (18), based on measured sulfide concentrations from Lost City end-member fluids. However, this hypothesis is not supported by the comparison of the end-member total dissolved sulfide versus temperature ratios between Lost City and the on-axis vent fields (Table S1). The maximum temperature of the habitat of Bathymodiolus mussels lies around 15°C, and it requires significant dilution of the end-member fluids in cold seawater. In this temperature range, the sulfide concentration resulting from the dilution of Lost City end-member fluids should be rather similar to the levels experienced by mussels from on-axis vent fields (22, 26). Recent data (27), moreover, suggest that fluids issuing from flanges on the flanks of Lost City chimneys may indeed have a higher H\textsubscript{2}S/temperature ratio than the end-member fluid. Given the potential availability of these reduced compounds in the Lost City vent fluids for symbionts and free-living chemotrophic microbial populations (28, 29), there is therefore no reason to suppose that Lost City-type fluids should exclude the formation of dense chemosynthetic faunal assemblages.

The findings contained in this paper support the hypothesis that Lost City-type fluids can sustain such communities, while providing further evidence for the suggestions of Kelley et al. (17, 30) that low-temperature hydrothermal circulation on slow-spreading ridges has a widespread distribution. We report previously unreported Lost City-like carbonates containing fossil Bathymodiolus shells of large size at high densities, together with smaller numbers of two species of chemosynthetic bivalves and four gastropod species. This fossil assemblage is 110,000 years old (based on radiocarbon isotope) and contains similar species to the Bathymodiolus mussel beds from high-temperature vents elsewhere on the MAR. Although geographically close to the Rainbow hydrothermal vent field, the Ghost City carbonates and fossils were clearly mal vent field, the Ghost City carbonates and fossils were clearly found, in addition to the carbonates, three shells of thysanid bivalves, numerous pieces of serpentinized peridoidite, and some troctolites and gabbros. The carbonates are white to ivory in color, ranging from 750 to 25 cm\textsuperscript{3} in volume, and most have thin (up to 1 mm) exterior ferric oxhydroxide (ferrihydrite with Mn component) black crusts upon which solitary corals have grown (Fig. 2 A and B and Fig. S2). The carbonate textures range from “layered” (Fig. 2C and Fig. S3), with significant porosity (close to 40%, n = 4), to “massive.” This carbonate matrix, which encloses mussel shells with a density of up to 4 shells per 10 cm\textsuperscript{2}, lacks metallic oxide or sulfide minerals and consists of varying proportions of authigenic carbonate cements and infilling pelagic calcitic and aragonitic fossils (foraminifera, coccoliths, and a few pteropods; Fig. 2D and Fig. S3). The authigenic carbonate cements consist of aragonite, commonly occurring as radial aggregates of acicular crystals, calcite, and sparser rosettes of glendonite crystals (Fig. 2 E and F and Fig. S4). The infilling pelagic sediments have δ\textsuperscript{18}O values of 3.63 ± 0.25‰ and δ\textsuperscript{13}C values of 0.93 ± 0.17‰ (n = 4). Mixed calcite/aragonite authigenic cements have δ\textsuperscript{18}O and δ\textsuperscript{13}C values of 4.88 ± 0.19‰ and −0.66 ± 1.18‰, respectively (n = 9) (Table 1). The authigenic carbonates and the infilling pelagic sediment show good separation between δ\textsuperscript{13}C and δ\textsuperscript{18}O on a canonical discriminant analysis (CDA) scatterplot, supporting distinct mineralization process (Fig. 3 and Table S2). Isotopic measurements of a series of subsamples from one authigenic carbonate crust gave U/T\textsuperscript{9} ages ranging from 46 ± 0.3 kyr to 193 ± 11 kyr (n = 4) (Table 2). These samples, however, display a wide range of initial δ\textsuperscript{13}C/U values (from approximately 129 to 183‰), suggesting that their U/T\textsuperscript{9} ages may be possibly biased due to postformation interaction with seawater or diagenesis (31). One of these subsamples is characterized by a δ\textsuperscript{13}C/U\textsubscript{initial} value (150 ± 1‰; Table 2) close to the modern seawater signature (146.6 ± 2.6‰) (31), which suggests that its U/T\textsuperscript{9} ratio may be considered as the most representative of the formation age of Ghost City carbonates. The corresponding U/T\textsuperscript{9} age (110 ± 0.9 kyr) lies in the same range as the older chimneys from Lost City (122 ± 12 kyr) (32) and suggests that

**Ghost City Carbonates**

Eight carbonate blocks were dredged during the MoMAR-DREAM cruise (MoMAR 08 Leg 2, August–September 2008) from the northwestern flank of the Rainbow massif, which is situated on a nontransform offset at 36°14.15N, 33°53.50W (Fig. 1 and Fig. S1). This site, which we name Ghost City, is 1,200 m northeast of the Rainbow vent field at around 2,100 m water depth. The dredge from which the carbonates were collected sampled a transect around 800 m long on the seafloor and recovered, in addition to the carbonates, three shells of thysanid bivalves, numerous pieces of serpentinized peridoidite, and some troctolites and gabbros. The carbonates are white to ivory in color, ranging from 750 to 25 cm\textsuperscript{3} in volume, and most have thin (up to 1 mm) exterior ferric oxhydroxide (ferrihydrite with Mn component) black crusts upon which solitary corals have grown (Fig. 2 A and B and Fig. S2). The carbonate textures range from “layered” (Fig. 2C and Fig. S3), with significant porosity (close to 40%, n = 4), to “massive.” This carbonate matrix, which encloses mussel shells with a density of up to 4 shells per 10 cm\textsuperscript{2}, lacks metallic oxide or sulfide minerals and consists of varying proportions of authigenic carbonate cements and infilling pelagic calcitic and aragonitic fossils (foraminifera, coccoliths, and a few pteropods; Fig. 2D and Fig. S3). The authigenic carbonate cements consist of aragonite, commonly occurring as radial aggregates of acicular crystals, calcite, and sparser rosettes of glendonite crystals (Fig. 2 E and F and Fig. S4). The infilling pelagic sediments have δ\textsuperscript{18}O values of 3.63 ± 0.25‰ and δ\textsuperscript{13}C values of 0.93 ± 0.17‰ (n = 4). Mixed calcite/aragonite authigenic cements have δ\textsuperscript{18}O and δ\textsuperscript{13}C values of 4.88 ± 0.19‰ and −0.66 ± 1.18‰, respectively (n = 9) (Table 1). The authigenic carbonates and the infilling pelagic sediment show good separation between δ\textsuperscript{13}C and δ\textsuperscript{18}O on a canonical discriminant analysis (CDA) scatterplot, supporting distinct mineralization process (Fig. 3 and Table S2). Isotopic measurements of a series of subsamples from one authigenic carbonate crust gave U/T\textsuperscript{9} ages ranging from 46 ± 0.3 kyr to 193 ± 11 kyr (n = 4) (Table 2). These samples, however, display a wide range of initial δ\textsuperscript{13}C/U values (from approximately 129 to 183‰), suggesting that their U/T\textsuperscript{9} ages may be possibly biased due to postformation interaction with seawater or diagenesis (31). One of these subsamples is characterized by a δ\textsuperscript{13}C/U\textsubscript{initial} value (150 ± 1‰; Table 2) close to the modern seawater signature (146.6 ± 2.6‰) (31), which suggests that its U/T\textsuperscript{9} ratio may be considered as the most representative of the formation age of Ghost City carbonates. The corresponding U/T\textsuperscript{9} age (110 ± 0.9 kyr) lies in the same range as the older chimneys from Lost City (122 ± 12 kyr) (32) and suggests that

**Fig. 1.** Location of the Ghost City fossil hydrothermal field at different scales. (A) Large scale map showing hydrothermal vents hosted by volcanic rocks (red dots) and gabbros and peridotites (green dots); Ghost City is in the vicinity of the Rainbow hydrothermal field. (B) Standard multibeam bathymetrical map of three MAR segments between 36°00 and 36°20N. These segments show a typical slow-spreading axial valley offset by two nontransform discontinuities. Both Rainbow and Ghost City are located at the northern end of the segment centered on 36°10N. (C) High resolution multibeam bathymetrical map acquired at low ship speed during the Flores cruise of the R/V L’Atalante showing the Rainbow vent field on the western flank of the Rainbow massif; the Ghost City fossil site is located on the northwestern flank of this gabbroic and peridotitic structure approximately 1,200 m northeast of the Rainbow vent field, at a depth of 2,100 m.
Ghost City carbonate formation is significantly older than the first evidence of Rainbow vent activity (23 ± 1.5 kyr) (33). Additionally, the same carbonate sample exhibits a radiogenic strontium isotopic ratio (87Sr/86Sr) of 0.70916 ± 0.00006, close to seawater ratios.

Among known authigenic carbonates from oceanic environments where ultramafic rocks are exposed, such as vein-filling aragonites in serpentinites (34, 35), samples from Ghost City are texturally and mineralogically most similar to those from Lost City, particularly the carbonates of old (up to 25 kyr) inactive chimneys (13). According to these authors, the Lost City inactive structures display well-defined fluid flow paths, retaining significant porosity (up to approximately 35%) and are characterized by dark or black exteriors that contrast to white, ivory, or gray interiors. The outer walls of these structures become dark due to manganese precipitation associated with aging and are colonized by serpulid worms and corals (13). In older inactive chimneys the internal microchannels are progressively in-filled with micritic calcite; brucite, which is undersaturated in seawater, tends to disappear in these chimneys (12). Another feature indicative of prolonged postformation interaction with seawater is near seawater Sr isotope values in carbonate minerals, as seen in both the Lost City inactive chimneys (13) and Ghost City samples. One mineralogical distinction of Ghost City carbonates is the presence of glendonite. Glendonite in Ghost City carbonate crust exhibits a characteristic star shape and is associated with acicular aragonite crystals surrounding the benthic fossils. Glendonite is a pseudomorph after ikaite, a very unstable hydrous calcium carbonate associated with cold water (<6°C) depositional systems, including glaciomarine and deep water settings (36, 37). Original ikaite precipitation is favored by elevated alkalinity, high pH (>10) and dissolved phosphate enrichments. Glendonite was not reported in Lost City carbonates, but the presence of ikaite in the walls of active chimneys was suspected from the observation of rapid dissolution of elongated carbonate crystals during sampling (13).

The oxygen and carbon isotope values of the Ghost City authigenic carbonates are consistent with those observed in serpentinization contexts. The 18O enrichment during fluid/rock interaction results in carbonates with high δ18O values (>2‰) (11, 38). The Ghost City carbon isotope signatures (δ13C = −2.6 to 0.7‰) are comparable to those measured in carbonates from serpentinite-hosted systems, like the South Chamorro Seamount (δ13C = −2.1 to −1.3‰) and the Conical Seamount (δ13C = −2.9 to −0.1‰) in the Mariana forearc (39–41), and lie within the wide range of carbonate isotope signatures reported for Lost City (−7 to +13‰) (11). Carbonates with the lower

Table 1. Mean, standard deviation, and range of oxygen and carbon isotopic compositions of carbonates and mussel shells

<table>
<thead>
<tr>
<th></th>
<th>(n)</th>
<th>δ18O ± SD (‰ VPDB)</th>
<th>δ13C ± SD (‰ VPDB)</th>
<th>Min/Max</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GHOST CITY</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In-filled pelagic sediments</td>
<td>4</td>
<td>3.63 ± 0.25</td>
<td>3.27/3.85</td>
<td>0.93 ± 0.17</td>
</tr>
<tr>
<td>Authigenic carbonates</td>
<td>9</td>
<td>4.88 ± 0.19</td>
<td>4.48/5.09</td>
<td>−0.66 ± 1.18</td>
</tr>
<tr>
<td>Bathymodiolus shells</td>
<td>3</td>
<td>4.93 ± 0.40</td>
<td>4.52/5.31</td>
<td>−0.30 ± 1.99</td>
</tr>
<tr>
<td><strong>LOST CITY</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vent carbonates (11)</td>
<td>50</td>
<td>−6/5</td>
<td>−11.9</td>
<td>−7/13</td>
</tr>
<tr>
<td>Methane (11, 44, 45)</td>
<td></td>
<td></td>
<td></td>
<td>−13.6/−8.8</td>
</tr>
<tr>
<td><strong>RAINBOW</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Living Bathymodiolus shells</td>
<td>5</td>
<td>2.32 ± 0.59</td>
<td>1.67/2.99</td>
<td>2.78 ± 0.41</td>
</tr>
<tr>
<td>Methane (44)</td>
<td></td>
<td>−17.7/−15.8</td>
<td></td>
<td></td>
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</tbody>
</table>

Comparison of carbonates and mussel shells from Ghost City, Lost City, and Rainbow high-temperature hydrothermal vent site.
isotopic signature reflect a mixed inorganic carbon source with contributions from seawater (δ13C\textsubscript{DIC} = 0‰) and an isotopically lighter-DIC source. Owing to the very low concentration of inorganic carbon in serpentinization fluids, the most likely origin for this 13C depleted DIC is the oxidation of methane. Methane in serpentinization fluids are characterized by light carbon isotopic signatures (e.g. δ13C\textsubscript{CH4} = 27‰ in the Zambales ophiolite, −10.3‰ at Logatchev, −16.1‰ at Rainbow, and −11.9‰ at Lost City) (42–45), which can be further fractionated by methanotrophic microbes converting methane into inorganic carbon. While abiotic methane oxidation is kinetically inhibited at low temperature (46), microbial oxidation of methane can occur in subseaﬂoor habitats with various electron acceptors (e.g., oxygen and sulfate) during the mixing of seawater with end-member fluids (47, 48). According to Proskurowski et al. (48), the fractionation factor resulting of anaerobic or aerobic methane oxidation can be as high as 1.039 (49, 50) and will result in further depletion of the initial carbon isotope ratio by at least −13‰. Only a small fraction (approximately 5%) of this 13C depleted methane is thus sufﬁcient to explain the slightly negative carbon isotopic signature of some Ghost City carbonates. An additional contribution from biogenic methane formed during the subseaﬂoor mixing of seawater and the end-member fluid, as described in Proskurowski et al. (48), cannot be ruled out. This assumption is supported by the identiﬁcation of both methanogenic and anaerobic methanoxidizing Archaea at Lost City, particularly in the less active chimneys where seawater mixing is occurring (28). In Lost City-type conditions, seawater is the only source of HCO\textsubscript{3}− and mixing is required to compensate the poor supply of this ion from the ﬂuid. As a consequence, the substantial isotopic fractionation resulting of biogenic methane formation that was observed at basalt-hosted diffuse vents (48) may not be achieved due to limiting inorganic carbon conditions. The relative importance of biogenic methane is therefore difﬁcult to estimate from Ghost City samples’ isotopic ratios.

The geological context, as well as petrographic and isotopic data, provides supporting evidence that the Ghost City carbonates were formed 110,000 years ago from venting of metal-poor ﬂuids. Despite the proximity with the Rainbow high-temperature vents ﬁeld, the lack of polymetallic sulﬁde precipitates in the Ghost City carbonate samples precludes a high-temperature metal-rich hydrothermal ﬂuid contribution in their formation. More likely, these ﬂuids were formed from low-temperature hydrothermal circulation related to serpentinization and were probably close in composition to those currently venting at Lost City.

**Ghost City Fossils**

We counted 146 specimens of the mussel *Bathymodiolus aff. azoricus* on the exposed surfaces of the eight Ghost City carbonate blocks (Fig. 4 and Fig. S4). The shells range in length from 5 mm to 84 mm, which is comparable to living *B. azoricus* shells from high-temperature hydrothermal vent ﬁelds on the MAR (51). Very few of the Ghost City mussel shells are fragmented, and quite a few specimens have articulated valves, with a ratio of 3.6 disarticulated to articulated shells (n = 73). Some of the small articulated mussel shells are nested within larger articulated specimens (Fig. 2D). These features are indicative of in situ growth and a lack of post mortem transport. This interpretation is supported by the isotope composition of the Ghost City *B. aff. azoricus* shells (δ18O = 4.93 ± 0.40‰, δ13C = −0.30 ± 1.99‰, n = 3; Table 1), values that are more similar to the Ghost City authigenic carbonates than living *Bathymodiolus* shells from the Rainbow high-temperature hydrothermal vent site (CDA analysis; Fig. 3 and Table S2). The other benthic fossils enclosed within the Ghost City carbonate samples (Fig. 4) comprise serpulid tubes (>30); the vesicomyid clam *Phreagena* sp. (n = 2); the thyasirid clam *Thyasira* sp. (n = 1); the limpet *Paralepetopsis* aff. *ferrugivora* (n = 15); and the snails *Protolira* aff. *thorvaldssoni* (n = 32), *Phymorhynchus* sp. (n = 1), *Anatoma* sp. (n = 2), and *Lirula* sp. (n = 1). These also show variable preservation, but in general the shells that were originally aragonitic (the gastropods and clams) show more dissolution and recrystallization than the mixed calcite/aragonite mussel shells, an observation consistent with prolonged seawater interaction (Fig. S5). The Ghost City mollusk assemblage shares ﬁve taxa with living MAR axial high-temperature vent communities (3, 52–54), including two locally at Rainbow (*Bathymodiolus* and *Protolira*), and two taxa associated with sedimented vent sites (Table S3). The Ghost City *Phreagena* sp. is also found at the recently described Clamstone site, an inactive (approximately 25 kyr BP) serpentine-hosted sedimented vent ﬁeld near Rainbow (approximately 1.2 km east of Ghost City, at a depth of 1,980 m) (55). Thyasirid clams that may be conspecific with the Ghost City *Thyasira* sp. occur at Clamstone (55), Anay’s Garden, a sedimented vent site in the Logatchev area (52, 56, 57), and have also been reported in

**Table 2. U-Th ages for Ghost City carbonate samples**

<table>
<thead>
<tr>
<th>Sample</th>
<th>Corrected U-Th age (kyr) ± 2σ</th>
<th>Initial 234U (%) ± 2σ</th>
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<tbody>
<tr>
<td>S1</td>
<td>195 ± 11</td>
<td>183 ± 10</td>
</tr>
<tr>
<td>S2</td>
<td>110 ± 0.9</td>
<td>150 ± 1</td>
</tr>
<tr>
<td>S3</td>
<td>65 ± 11</td>
<td>170 ± 1</td>
</tr>
<tr>
<td>S4</td>
<td>46 ± 0.3</td>
<td>129 ± 1</td>
</tr>
</tbody>
</table>

Fig. 4. Fossils from Ghost City carbonates. (A) Carbonate block with numerous specimens of *Bathymodiolus aff. azoricus*, showing varying degrees of shell preservation. (B) Silicone rubber cast of vesicomyid bivalve *Phreagena*, right valve interior. (C) Thyasirid bivalve, left valve interior. (D) Gastropod *Lirula vitreus*, oblique apertural view. (E) Gastropod *Anatoma sp.*, oblique view of damaged specimen. (F) Silicone rubber cast of gastropod *Phymorhynchus*, side view. (G) Silicone rubber cast from carbonate containing three *Protolira* aff. *thorvaldssoni* gastropod specimens (black arrows) and a single limpet (white arrow). (H) Limpet *Paralepetopsis* aff. *ferrugivora*, apertural view of slightly corroded specimen.
soft sediments at Lost City (20). Thus, the Ghost City mollusk fauna is a mixture of MAR vent species from sedimented sites and more typical chimney habitat mussel bed communities. Although Ghost City fauna has a higher biomass, the mollusc species list is not greatly different from Lost City communities, with three mollusk species shared between the two sites: *B. azoricus*, *Thyasira* species, and the gastropod *Lurifax* (see Table S3).

**High-Biomass Vent Communities Supported by Serpentinization Fluids**

The Ghost City carbonates demonstrate that (i) high-biomass populations of *Bathymodiolus* mussels and other symbiont-hosting mollusks can be supported by metal-depleted and likely alkaline fluids, similar to the serpentinization-related vent fluids described at Lost City; and (ii) these communities have been present on the axis of the MAR for at least 110,000 years. The flexible *B. azoricus* dual symbiosis responds to variations in the methane-to-sulfide ratio in the environment (24, 25), making this species particularly well adapted to the variety of fluid chemistries that are found on the MAR (8, 58). The Ghost City fossil mussels might therefore also have relied on methanotrophy and, potentially, on sulfide, or even hydrogen, oxidation as primary energy pathways. Although the geological setting is different, there is evidence that some other *Bathymodiolus* species are able to exploit diverse energy sources present in a serpentinization context. At the South Chamorro serpentinite seamount in the Mariana forearc, mussels thrive in sedimented cracks in seafloor carbonate cement, and based on soft tissue carbon and sulfur isotopic data, Yamanaka et al. (41) suggest that the mussels host both methanotrophic and thiotrophic symbionts, utilizing both methane from serpentinization reactions and sulfur produced by sulfate reducing bacteria in the sediment. Additionally, vesciomyids (4, 59) and many of the studied large thysanids (4, 52) species host sulfide-oxidizing symbionts, and the presence of representative species in the Ghost City carbonates suggests that a threshold amount of sulfide was present in the Ghost City environment.

**Implications**

It is unclear why communities of symbioint-hosting molluscs, including high densities of large *Bathymodiolus* mussels, do not currently persist at Lost City, when they have been present in the past as shown by accumulations of dead shells. Because *Bathymodiolus* azoricus is able to exploit variable chemical energy sources, the most likely explanation is to be searched for in the ecological processes that govern community dynamics in fragmented habitats. One possible cause of this extinction may be related to the dispersal potential of vent species. Lost City is located further from the ridge axis than Ghost City and may have lacked of sufficient larval flow from high-temperature Rainbow-like vent field communities after a major disturbance event.

Another explanation could be that the focused flow chimney complex at Lost City lacks the mild temperature diffuse flow areas (<15°C) with substantial concentrations of electron donors like methane or sulfide, that characterize suitable habitat for vent mussels (22). Further investigation of Lost City habitat conditions and population genetics will help discriminating between these hypotheses.

The findings further support the hypothesis of a widespread occurrence of hydrothermal fluid circulation hosted in exposed ultramafic rocks on the ocean floor (60). The estimated duration of serpentinization-related fluid venting (over 10 kyr to 100 kyr time scales) (32) contrasts strongly with the geographically restricted and short-lived high-temperature vent fields known to date. Our results indicate that exposed mantle rocks undergoing serpentinization could host deep-sea chemosynthetic vent communities in a wide range of geological settings, including slow and ultraslow spreading ridge axes, off-axis Oceanic Core Complexes (61), continental margins (62), and serpentinite seamounts in forearc settings (63). The exploration of ultramafic rock exposures in the deep sea is thus a fertile area for the understanding both long-range larval dispersal of vent species and the specific requirements for settlement and growth of chemosynthetic animals.

**Methods**

**XRD Analyses.** Analyses of carbonate matrix, oxide crust, and mussel shells were made at the STS laboratory (UPMC Univ Paris 06) on a Siemens D501. *Bathymodiolus* aff. *azoricus* mussel shells were scrubbed in distilled water with a toothbrush immediately upon collection to remove loosely attached biogenic and inorganic particles. Sample powders of original calcitic outer layer and aragonitic inner layer of the shells were drilled from a depth of approximately 0.1 mm.

**Optical Petrography.** Polished thin sections of carbonates were observed using a stereomicroscope Zeiss StReO Discovery V20 (Fig. 2 and Fig. S1) Porosity measurements were made using JMicrovision software (www.jmicrovision.com).

**Carbon and Oxygen Stable Isotopes Analyses.** Analyses of three *Bathymodiolus* aff. *azoricus* shells and 13 carbonate matrix (authigenic carbonate and infillings of sedimentary fill) were carried out on a VG Micromass 602 mass spectrometer. Additionally, five shells of living *B. azoricus* from the Rainbow vent field were analyzed. Powdered samples from mussel shells for the isotopic analyses (3–4 mg) were obtained from the cleaned outer layer using a rotary drill with a diamond-tipped burr. The shell sample powders were pretreated with 1.5 % NaClO for 30 min to remove organic contaminants, rinsed three times with distilled water following a protocol modified after (64, 65). All carbonate powders were acidified in 100% phosphoric acid at 0°C with substantial concentrations of electron donors (64, 65). All carbonate powders were acidified in 100% phosphoric acid at 0°C under vacuum. The produced CO2 was collected and analyzed using the mass spectrometer. Isotopic data are reported in conventional delta notation relative to the Vienna Pee Dee Belemnite (VPDB). The standard used for the analyses was an internal standard calibrated on the NBS-19. Standard deviation for δ13C and δ18O is ±0.10‰.

**Uranium/Thorium and Stratium Analyses.** Analyses were made in the Pôle Spectrométrie Océan (Brest) on a Neptune MC-ICPMS. For uranium and thorium isotope measurements, about 2 mg of carbonate sample was dissolved in 7.5M HNO3 and spiked with a mixed 238U/239Th spike (66). U and Th were separated chemically using conventional anion exchange techniques adapted from previous studies (67). U and Th concentrations and isotope ratios were then measured in the MC-ICPMS. The carbonate age was corrected for detrital contamination (inherited 230Th) by using measured 232Th to 238Th concentrations and assuming a typical 232Th/238Th ratio (150,000) for the contaminant detrital phase, but this correction was insignificant on the calculated age (about 1%) (68). Strontium was isolated using Sr resin and the isotope ratios were measured using the MC-ICPMS. Isotope ratios were normalized to 87Sr/86Sr = 0.1194 and corrected from 87Rb and 86Kr interferences on the 86Sr and 88Sr signal, respectively.

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