

A serpentinite-hosted ecosystem in the Southern Mariana Forearc

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Several varieties of seafloor hydrothermal vents with widely varying fluid compositions and temperatures and vent communities occur in different tectonic settings. The discovery of the Lost City hydrothermal field in the Mid-Atlantic Ridge has stimulated interest in the role of serpentinization of peridotite in generating H₂- and CH₄-rich fluids and associated carbonate chimneys, as well as in the biological communities supported in highly reduced, alkaline environments. Abundant vesicomyid clam communities associated with a serpentinite-hosted hydrothermal vent system in the southern Mariana forearc were discovered during a DSV *Shinkai 6500* dive in September 2010. We named this system the “Shinkai Seep Field (SSF).” The SSF appears to be a serpentinite-hosted ecosystem within a forearc (convergent margin) setting that is supported by fault-controlled fluid pathways connected to the decollement of the subducting slab. The discovery of the SSF supports the prediction that serpentinite-hosted vents may be widespread on the ocean floor. The discovery further indicates that these serpentinite-hosted low-temperature fluid vents can sustain high-biomass communities and has implications for the chemical budget of the oceans and the distribution of abyssal chemosynthetic life.

Challenger Deep | convergent margin | hydrothermal vent |
Shinkai Seep Field | vesicomyid clam

Hydrothermal activity plays an important role in Earth evolution by modifying the composition of oceanic crust, affecting ocean chemistry, forming metal-rich deposits, and providing energy and nutrient sources for chemosynthetic biological communities. Several varieties of seafloor hydrothermal vents with widely varying fluid compositions and temperatures occur in different tectonic settings. Along divergent plate margins, three basic vent types have been identified. The first type is a basalt-hosted, high-temperature hydrothermal system with fluid temperatures up to approximately 400 °C and low H₂ and CH₄ concentrations, but high metal concentrations (e.g., TAG hydrothermal field, 26°10' N Mid-Atlantic Ridge (MAR)) (1). The second type is a serpentinite and gabbro-hosted, high-temperature system with fluid temperatures up to approximately 360 °C and high H₂, CH₄, as well as high metal concentrations (e.g., Rainbow hydrothermal field, 36°14' N MAR; Logatchev hydrothermal field, 14°45' N MAR) (2, 3). The third type is a serpentinite-hosted, low-temperature system with 40 to 90 °C fluid temperatures and high H₂, CH₄, but low metal concentrations (e.g., Lost City hydrothermal field, 30°07' N MAR) (4, 5). There, carbonate chimneys are produced by highly reducing, high pH (9 to 11) vent fluids (4, 5). The third type may be fueled by exothermic serpentinization reactions (4). However, magmatic heat contributions to the third type are also suggested based on heat balance modeling (6), like the other two types that derive their heat from magmatic intrusions. The distinction of these three basic types at divergent plate margins can be linked to

tectonic evolution of mid-ocean ridges, with fluid flow focusing along detachment faults to allow venting away from ridge axis (7). Along convergent margins, low-temperature hydrothermal systems with approximately 2 °C fluid temperatures associated with large serpentinite mud volcanoes in the Mariana forearc are well known (8–10). Serpentinite mud volcanoes erupt through interaction of fluids released from the subducting slab with faulted and/or mylonitized peridotite formed along deep-seated faults in the lithosphere of the overriding plate (11), producing serpentinite, H₂, CH₄, and high pH (up to 12.5) fluids (12).

The discovery of the Lost City hydrothermal field has stimulated interest in the role of serpentinization of peridotite in generating H₂- and CH₄-rich fluids and associated carbonate chimneys, as well as in the biological communities supported in highly reduced, alkaline environments (4, 5). Serpentinization of peridotite produces H₂-rich alkaline fluids, magnetite, and Fe-Ni alloys (13). Fischer-Tropsch-type reactions between H₂ and CO₂ using magnetite and Fe-Ni alloys as catalysts result in abiotic formation of CH₄ (14). Anaerobic oxidation of CH₄ generates H₂S, which is the food source for the sulfide-oxidizing bacteria that are symbiotic with chemosynthetic biological communities. Such serpentinite-hosted systems may have played important roles in the emergence of life on the Earth (15).

In this article, we report the discovery of a serpentinite-hosted ecosystem in the southern Mariana forearc, named the “Shinkai Seep Field (SSF)” (Fig. 1A). This field was serendipitously found during the YK10-12 cruise of the R/V *Yokosuka* in September 2010, intended to study the geology of the southern Mariana forearc in detail. The field program included 8 dives with DSV *Shinkai 6500* and 7 dives of the *Yokosuka Deep-Tow Camera*. The SSF was discovered during the DSV *Shinkai 6500* dive 1234 (observer: T.I.), which was a lithological transect of the inner trench slope of the Mariana Trench along approximately 143°E. The location of the SSF is approximately 11°39.09'N and approximately 143°02.94'E, at depth of 5,861 to 5,550 m (Fig. 1A and B) on a south-facing steep scarp of the inner trench slope of the Mariana Trench, approximately 80 km northeast of the Challenger Deep, Earth's deepest location.

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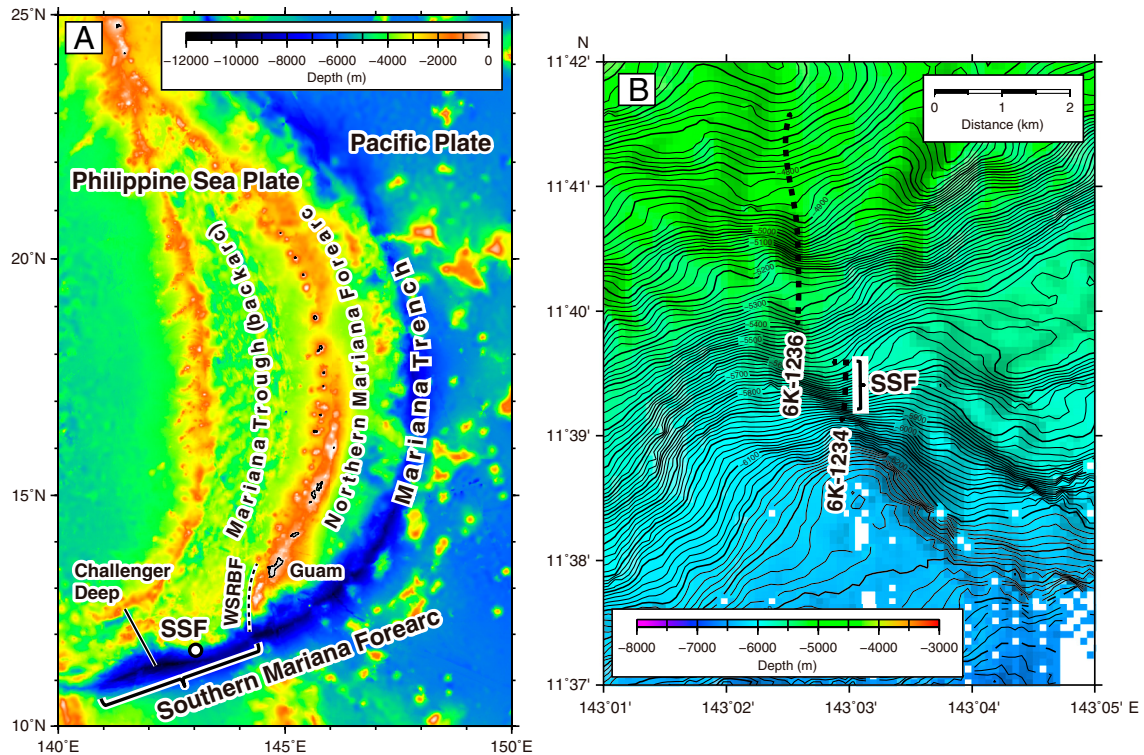


Fig. 1. Location of the Shinkai Seep Field (SSF). (A) Bathymetry of the Mariana Trench and location of the SSF. The West Santa Rosa Bank Fault (WSRBF) divides the Mariana forearc into the southern and northern parts (marked by a dotted line). (B) Detailed bathymetry of the SSF area obtained during the YK10-12 cruise. Contours in 20 m intervals. The tracks of the DSV *Shinkai 6500* dives 1234 and 1236 are shown by black dotted lines. Approximate location of the SSF is indicated. Dive 1236 recovered Eocene to Miocene subduction-related volcanics, not peridotites. The bathymetry in this area shows the absence of conical hills typical of serpentine mud volcanoes common in the northern Mariana forearc.

Geologic Background

The Mariana arc-trench system is a nonaccretionary convergent plate margin where the mantle of the overriding Philippine Sea Plate interacts with fluids released by the subducting Pacific Plate. Subduction to form the Izu-Bonin-Mariana arc-trench system began at approximately 51 Ma (16, 17). Forearc is an important component of a convergent plate margin and is a broad region between the trench axis and the associated volcanic arc. Along the Mariana forearc southwest of Guam, the West Santa Rosa Bank Fault at approximately 144°15'E marks a major tectonic boundary (18), dividing the Mariana forearc into a stabler northern part and a southern part which is more tectonically active. The southern Mariana forearc is noted for facing the Challenger Deep (Fig. 1A). A number of serpentine mud volcanoes exist in the northern Mariana forearc approximately 30 to approximately 100 km behind the trench axis (8–10), however none is known from the southern Mariana forearc. Instead, serpentinized peridotite crops out and has been sampled from the inner trench slope along the southern Mariana forearc (19, 20). The southern Mariana forearc is cut by numerous normal and strike-slip faults striking parallel and perpendicular to the trench axis, suggesting that the region is under north-south and east-west extension (18). Opening of the southern Mariana Trough (a backarc basin) and the presence of a short and narrow subducted slab west of the West Santa Rosa Bank Fault that is rolling back rapidly might be responsible for the different geologies of the two forearc parts (18, 21).

Dive Observations and Sample Descriptions

The DSV *Shinkai 6500* dive 1234 observed close association of serpentinized peridotite and vesicomid clams (Fig. 2A–E), however, no active fluid venting was observed. Dive 1234 collected more than 30 live vesicomid clams, along with peridotite, subordinate gabbro and a fragment of a white to ivory colored

potential vent chimney (total 18 rocks, total weight approximately 77 kg), but no water samples because *Shinkai 6500* was not prepared to do this. The lithologies encountered indicate that this section of the dive was on lithospheric mantle partially covered with locally derived debris flow deposits and ooze. Highly fractured outcrops of serpentinized peridotite were commonly observed during the dive (Fig. 2C). Fractures in the serpentinized

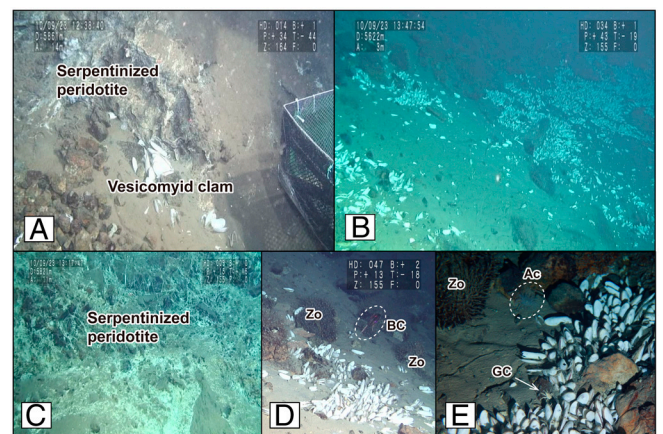


Fig. 2. Field photographs taken during the DSV *Shinkai 6500* dive 1234. (A) Live vesicomid clams on fractured and cemented serpentinized peridotite. (B) Extensive vesicomid clam community at 5,622 m depth. (C) An outcrop of fractured serpentinized peridotite filled with aragonite. (D) Close-up view of the vesicomid clam community at 5,622 m depth, showing close association with zoanths (Zo) and a *Beroe* comb jelly (BC; enclosed by a white dotted circle) with illuminated spots. (E) Close-up view of the vesicomid clam community at 5,622 m depth, showing close association with zoanths (Zo), an actinarian (Ac; enclosed by a white dotted circle), and a galatheid crab (GC; pointed to by a white arrow).

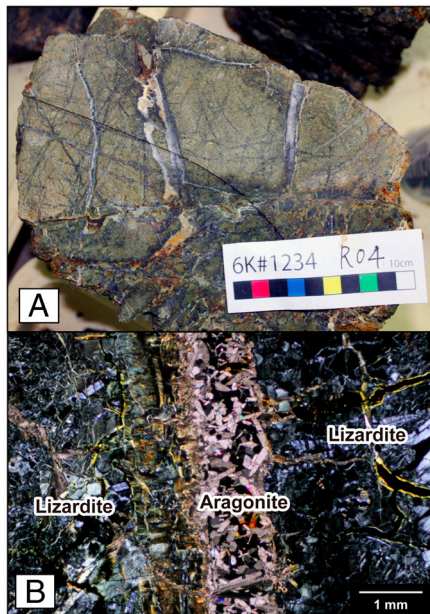


Fig. 3. Serpentinized peridotite recovered during the DSV *Shinkai 6500* dive 1234. Veined serpentinized peridotite (sample #6K-1234-R04). (B) Photomicrograph showing the vein is primarily composed of aragonite (sample #6K-1234-R04). The host is now composed of lizardite. Crossed polars.

peridotites and spaces between clasts in peridotite breccias commonly were filled with white minerals (Fig. 3A). Thin section observation (Fig. 3B) and X-ray diffraction (XRD) analyses confirm that the serpentine mineral is lizardite and the vein mineral is aragonite (CaCO₃). These serpentinized peridotites include amphibole, like those from the dredge site approximately 50 km east of the SSF (20). Scanning electron microscope (SEM) observation and XRD analyses of the potential chimney fragment indicate that it consists mostly of brucite (Mg(OH)₂) and acicular aragonite (Fig. 4A and B). Brucite chimneys are also known in the Pacman Seamount (a serpentinite mud volcano) in the northern Mariana forearc (9), as well as in the Lost City field (4, 5, 22).

Abundant live vesicomid clams were encountered between 5,861 and 5,550 m with the most extensive and diverse communities at 5,622 m at the base of an exposed section of serpentinized peridotite breccia (Fig. 2B). Vesicomid clams host symbiotic bacteria within vacuoles in their gills. We know of no other descriptions of vesicomid clams anywhere on the Mariana forearc, although *Bathymodiolus* mussel communities are known from the South Chamorro Seamount (a serpentinite mud volcano) in the northern Mariana forearc (23, 24). Although no active fluid venting was observed during dive 1234, the clustering of biological activity along the breccia horizon at 5,622 m suggests that the fluids responsible for nourishing the clams mainly vented along the base of this exposure, forming the most important SSF biological site.

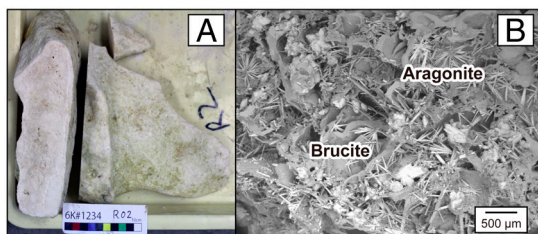


Fig. 4. Potential chimney fragment recovered during the DSV *Shinkai 6500* dive 1234. (A) Sectioned block of a potential chimney fragment (sample #6K-1234-R02) (B) SEM photomicrograph of a potential chimney fragment (sample #6K-1234-R02) showing the association of brucite (forming a lamellar texture) and aragonite (forming acicular crystals).

The organisms other than the vesicomid clams viewed or collected at this field included actinarians, zoanthids, a *Beroe* comb jelly, buccinid snails, and galatheid crabs (Fig. 2D and E). No vesicomid clam communities were found during a subsequent dive (dive 1236) on the slope above the end of dive 1234, which recovered Eocene to Miocene subduction-related volcanics (Fig. 1B). This observation clearly indicates that this community is hosted solely by serpentinized peridotite.

Shinkai Seep Field Vesicomid Clams

On the basis of shell morphology, the vesicomid clams are within the clade including the species assigned to genus *Abyssogena* proposed by Krylova et al. (25) (Fig. 5A). Based on partial DNA sequences (507 base pair) of mitochondrial DNA cytochrome oxidase *c* subunit I (COI) region, this species appears to be more closely related genetically to the vesicomid clam described as *Abyssogena southwardae* by Krylova et al. (25) from the high-temperature serpentinite and gabbro-hosted Logatchev hydrothermal field (26, 27), and from the seep sites in the West Florida Escarpment and the Barbados Accretionary Prism (28) (Fig. 5B). Carbon and nitrogen isotopic compositions of soft tissues from the clams were obtained to determine the consumed food substrate and trophic level. The highly depleted $\delta^{13}\text{C}$ values (−34.9 to −33.7‰) for the SSF vesicomid clams are consistent with other vesicomid clams with thiotrophic symbionts using dissolved CO₂

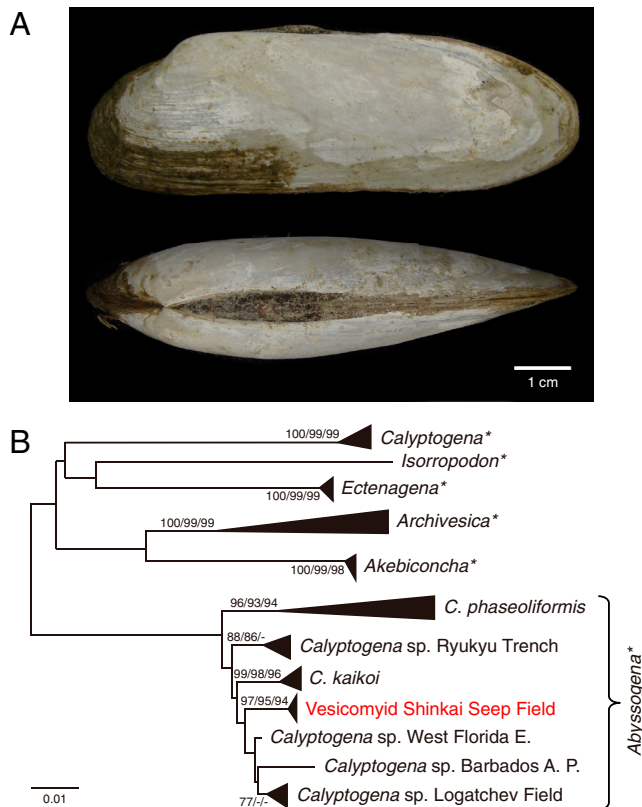


Fig. 5. Phylogenetic analysis of vesicomid clam from the SSF. (A) Specimen photograph (exterior of left valve and dorsal view). (B) Phylogenetic tree based on COI nucleotide sequences listed in Table S1. Bootstrap values (NJ/MP/ML) are shown beside nodes when the values are higher than 70. Scale bar represents 0.01 changes per nucleotide base. Operational taxonomic units (OTUs) with asterisk are expressed as the genus names proposed by Krylova and Sahling (36). OTUs without asterisk are expressed as the species names originally registered in the DNA Data Bank of Japan. All of these are assigned to genus *Abyssogena* proposed by Krylova and Sahling (36). *Calyptogena* sp. from Logatchev field, Barbados Accretionary Prism and West Florida Escarpment are now described as *Abyssogena southwardae* by Krylova et al. (25). A. P., Accretionary Prism. E., Escarpment.

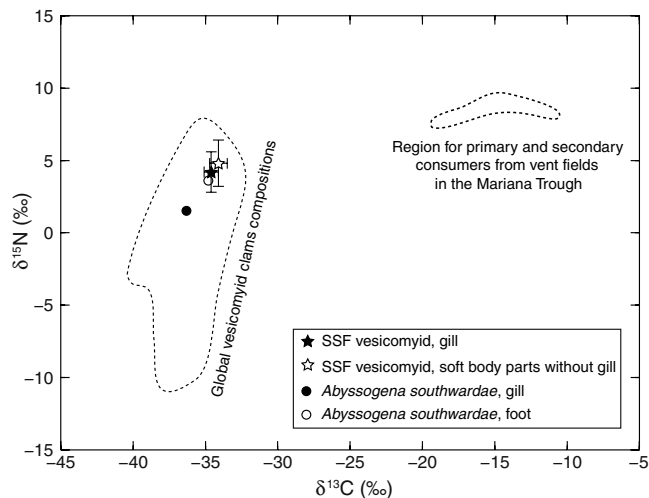


Fig. 6. Soft tissue stable isotopic analysis of vesicomid clam from the SSF. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ relationship for SSF vesicomid clam. $\delta^{13}\text{C}$ of gills ($n = 3$) and soft body parts without gill ($n = 3$) are -34.6 ± 0.5 (1 sigma) and $-34.1 \pm 0.6\%$, respectively. $\delta^{15}\text{N}$ of gills ($n = 3$) and soft body parts without gill ($n = 3$) are 4.2 ± 1.4 and $4.8 \pm 1.6\%$, respectively. Data for the vesicomid clam described as *Abyssosogena southwardae* by Krylova et al. (25) are shown for comparison (27). The global vesicomid clam compositions are based on (39–45). Region for primary and secondary consumers from vent fields in the Mariana Trough (46) is shown to demonstrate the isotopic difference from vesicomid clams.

from seawater and/or vent water as their carbon source (Fig. 6). The $\delta^{15}\text{N}$ values (3.1 to 6.3‰) are similar to those of vesicomid clams from other localities (Fig. 6). Although vesicomid clams are among the dominant invertebrates of chemosynthesis-based communities found at hydrothermal vents, cold seeps, and whale carcasses, there have been no live examples from a serpentinite-hosted hydrothermal system including serpentinite mud volcanoes, except for the high-temperature serpentinite and gabbro-hosted system at Logatchev (26, 27) and the Vema Fracture Zone (although the hydrothermal activity in this location has yet to be documented) (25, 29). Fossil vesicomid clams have however recently been reported from two sites near the high-temperature serpentinite and gabbro-hosted system at Rainbow (30, 31). It should be noted, however, that one of these sites, the Ghost City field, was not a high-temperature system when it was active approximately 110 kyr ago (31). The SSF vesicomid clam community is therefore an important live example of a low-temperature serpentinite-hosted hydrothermal system from either convergent or divergent margins, extending our knowledge about the biogeography of these clams.

Discussion

The serpentinization processes at several MAR hydrothermal sites are controlled by the interactions of seawater and peridotite with variable influence of magmatic heat (via gabbroic intrusions) (6). In contrast, the SSF is located in a deep inner trench slope of a convergent margin where magmatic heat contribution is unlikely. The serpentinization process at the SSF is instead likely controlled by persistent fluid flow from the subducting slab, although the bathymetry of the SSF indicates that it is not associated with a discernible serpentinite mud volcano (Fig. 1B). Fluids from Mariana serpentinite mud volcanoes have affinities with slab-derived fluids (32). The source of these fluids is dehydration of sediment and altered basalt at the top of the subducting Pacific Plate (12). The large volumes of slab-derived fluid available in a convergent margin setting appears to allow higher fluid-rock ratios than is possible in a mid-ocean ridge setting. Persistent fluid flow could eventually result in pervasive serpentinization of the peridotite beneath the SSF. It should be noted

that the serpentinized peridotites from the SSF as well as from the dredge site approximately 50 km east of the SSF (20) include amphibole, suggesting a hydrous mantle beneath the forearc in this region.

The potential vent chimney sample from the SSF further constrains the origin of the SSF fluids. Systematic chemical variation of the fluids across the northern Mariana forearc is documented among the serpentinite mud volcanoes. The trench-proximal mud volcanoes (e.g., Pacman Seamount) have fluids with lower alkalinity and higher Ca, and brucite chimneys. In contrast, trench-distal mud volcanoes (e.g., South Chamorro Seamount) have fluids with higher alkalinity and lower Ca, and carbonate chimneys. This systematic variation reflects progressive devolatilization of the slab with increasing depth and temperature beneath the forearc (9, 12). The potential chimney sample from the SSF largely consists of brucite, consistent with the observation in the trench-proximal serpentinite mud volcanoes.

We thus interpret that the SSF represents a serpentinite-hosted ecosystem supported by fault-controlled fluid pathways connected to the decollement within a forearc (convergent margin) setting. Our DSV *Shinkai 6500* diving and earlier dredging (19, 20) indicates that the deep geology of the southern Mariana forearc is dominated by peridotite and is heavily faulted, suggesting that more SSF-type seeps exist along the southern Mariana forearc, and perhaps, along the other nonaccretionary convergent margins like the Tonga forearc where extensive peridotite exposures in the deep forearc also are known (33). Our discovery supports the prediction that serpentinite-hosted vents may be widespread on the ocean floor (5, 30, 31). The discovery further indicates that these serpentinite-hosted low-temperature systems can sustain high-biomass communities. Therefore, this discovery could help us better understand how seafloor hydrothermal activity contributes to the chemical budget of the oceans and the distribution of abyssal chemosynthetic life.

Methods

SEM and XRD Analyses. SEM observations of the potential chimney fragment were made at Southern Methodist University (Dallas, USA) on a Leo-Zeiss 1450VP5E electron microscope equipped with an EDAX Genesis 4000 XMS SYSTEM 60 energy-dispersive spectrometer. XRD analyses of the chimney fragment were also made at Southern Methodist University with a Rigaku Ultima III XRD system. XRD analyses of the vein minerals of the fractured peridotite were made at Shizuoka University (Shizuoka, Japan) with a Rigaku RINT 2200 XRD system.

DNA Sequence Information for the SSF Vesicomid Clams. Phylogenetic relationships of the SSF vesicomid clams were determined at Japan Agency for Marine-Earth Science and Technology (JAMSTEC) based on partial DNA sequences (507 base pair) of mitochondrial DNA cytochrome oxidase c subunit I (COI) region, employing the method of Kojima et al. (34). The obtained sequences were aligned by CLUSTALW mounted in MEGA version 4 (35) with the sequences of the vesicomid species which are proposed as type species of the five genera (*Calyptogena*, *Ectenagena*, *Archivesica*, *Akebiconcha* and *Isorropodon*) by Krylova and Sahling (36), as well as all the available sequences of genus *Abyssosogena* in the DNA Data Bank of Japan (Table S1). Reconstruction of the phylogenetic tree was conducted by neighbor joining (NJ) (Kimura 2-parameter distance), maximum parsimony (MP), and maximum likelihood (ML) methods, using MEGA version 5.05 (37) (Fig. 5B).

Stable Carbon and Nitrogen Isotopic Compositions of the SSF Vesicomid Clams. Samples were prepared at JAMSTEC. The whole clam specimens were stored at -80°C prior to dissection and isotope analyses. After thawing to room temperature, samples of gill and other soft tissues were dissected from the specimens, and were rinsed in filtered seawater. Prior to isotope analyses, samples were dried and powdered, and lipid was extracted following the method of Ohkouchi et al. (38). Carbon and nitrogen isotopic compositions were determined at the Japan Chemical Analysis Center with a Delta V advantage isotope ratio mass spectrometer coupled with an elemental analyzer via ConFlo IV interface. Analytical precisions observed by repeated measurements of authentic and laboratory standards were better than 0.2‰ for carbon and nitrogen. The results are expressed relative to Pee Dee Belemnite and atmospheric nitrogen standards in the usual notation (Fig. 6).

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- Humphris SE, Tivey MK (2000) A synthesis of geological and geochemical investigations of the TAG Hydrothermal Field: insights into fluid flow and mixing processes in a hydrothermal system. *Ophiolites and Oceanic Crust: New Insights from Field Studies and the Ocean Drilling Program*, eds Y Dilek et al. (Geol Soc of America Spec Paper 349, Boulder, CO), pp 213–235.
- Charlou JL, et al. (2002) Geochemistry of high H₂ and CH₄ vent fluids issuing from ultramafic rocks at the Rainbow hydrothermal field (36°14'N, MAR). *Chem Geol* 191:345–359.
- Schmidt K, et al. (2007) Geochemistry of hydrothermal fluids from the ultramafic-hosted Logatchev hydrothermal field, 15°N on the Mid-Atlantic Ridge: temporal and spatial investigation. *Chem Geol* 242:1–21.
- Kelley DS, et al. (2001) An off-axis hydrothermal vent field near the Mid-Atlantic Ridge at 30°N. *Nature* 412:145–149.
- Kelley DS, et al. (2005) A serpentinite-hosted ecosystem: the Lost City hydrothermal field. *Science* 307:1428–1434.
- Allen DE, Seyfried WE, Jr (2004) Serpentinization and heat generation: constraints from Lost City and Rainbow hydrothermal systems. *Geochim Cosmochim Acta* 68:1347–1354.
- McCaig AM, et al. (2007) Oceanic detachment faults focus very large volumes of black smoker fluids. *Geology* 35:935–938.
- Fryer P (1996) Tectonic evolution of the Mariana convergent margin. *Rev Geophys* 34:89–125.
- Fryer P, Wheat CG, Mottl MJ (1999) Mariana blueschist mud volcanism: implications for conditions within the subduction zone. *Geology* 27:103–106.
- Stern RJ, Fouch MJ, Klempner SL (2003) An overview of the Izu-Bonin-Mariana subduction factory. *Inside the Subduction Factory*, ed J Eiler (AGU, Washington DC), pp 175–222.
- Fryer P, et al. (2006) Variability in serpentinite mudflow mechanisms and sources: ODP drilling results on Mariana forearc seamounts. *Geochim Geophys Geosyst* 7(Q08014), 10.1029/2005GC001201.
- Mottl MJ, Wheat CG, Fryer P, Gharib J, Martin JB (2004) Chemistry of springs across the Mariana forearc shows progressive devolatilization of the subducting plate. *Geochim Cosmochim Acta* 68:4915–4933.
- Früh-Green GL, et al. (2004) Serpentinization of oceanic peridotites: implications for geochemical cycles and biological activity. *The Seafloor Biosphere at Mid-ocean Ridges*, ed WSD Wilcock (AGU, Washington DC), pp 119–136.
- Holm NG, Charlou JL (2001) Initial indications of abiotic formation of hydrocarbons in the Rainbow ultramafic hydrothermal system, Mid-Atlantic Ridge. *Earth Planet Sci Lett* 191:1–8.
- Shock EL, Schulte MD (1998) Organic synthesis during fluid mixing in hydrothermal systems. *J Geophys Res* 103(E12):28513–28527.
- Reagan MK, et al. (2010) Fore-arc basalts and subduction initiation in the Izu-Bonin-Mariana system. *Geochim Geophys Geosyst* 11(Q03X12), 10.1029/2009GC002871.
- Ishizuka O, et al. (2011) The timescales of subduction initiation and subsequent evolution of an oceanic island arc. *Earth Planet Sci Lett* 306:229–240.
- Fryer P, et al. (2003) Why is the Challenger Deep so deep? *Earth Planet Sci Lett* 211:259–269.
- Bloomer SH, Hawkins JW (1983) Gabbroic and ultramafic rocks from the Mariana Trench: an island arc ophiolite. *The Tectonic and Geologic Evolution of Southeast Asian Seas and Islands: Part 2*, ed DE Hayes (AGU, Washington DC), pp 294–317.
- Ohara Y, Ishii T (1998) Peridotites from the southern Mariana forearc: Heterogeneous fluid supply in mantle wedge. *Island Arc* 7:541–558.
- Gvirtzman Z, Stern RJ (2004) Bathymetry of Mariana trench-arc system and formation of the Challenger Deep as a consequence of weak plate coupling. *Tectonics* 23(TC2011), 10.1029/2003TC001581.
- Ludwig KA, et al. (2006) Formation and evolution of carbonate chimneys at the Lost City Hydrothermal Field. *Geochim Cosmochim Acta* 70:3625–3645.
- Fryer P, Mottl MJ (1997) “Shinkai 6500” investigations of a resurgent mud volcano on the Southeastern Mariana forearc. *JAMSTEC J of Deep Sea Res* 13:103–114.
- Yamanaka T, et al. (2003) Stable isotope evidence for a putative endosymbiont-based lithotrophic *Bathymodiolus* sp mussel community atop a serpentine seamount. *Geomicrobiol J* 20:185–197.
- Krylova EM, Sahling H, Janssen R (2010) *Abyssogena*: a new genus of the family Vesicomidae (Bivalvia) from deep-water vents and seeps. *J Moll Stud* 76:107–132.
- Gebruk AV, Chevalloné P, Shank T, Lutz RA, Vrijenhoek RC (2000) Deep-sea hydrothermal vent communities of the Logatchev area (14°45'N, Mid-Atlantic Ridge): Diverse biotopes and high biomass. *J Mar Biol Assoc UK* 80:383–393.
- Sowthward EC, et al. (2001) Different energy sources for three symbiont-dependent bivalve molluscs at the Logatchev hydrothermal site (Mid-Atlantic Ridge). *J Mar Biol Assoc UK* 81:655–661.
- Peek AS, Gustafson RG, Lutz RA, Vrijenhoek RC (1997) Evolutionary relationships of deep-sea hydrothermal vent and cold-water seep clams (Bivalvia: Vesicomidae): Results from the mitochondrial cytochrome oxidase subunit I. *Mar Biol* 130:151–161.
- Auzende J-M, et al. (1989) Direct observation of a section through slow-spreading oceanic crust. *Nature* 337:726–729.
- Lartaud F, et al. (2010) Fossil clams from a serpentinite-hosted sedimented vent field near the active smoker complex Rainbow MAR, 36°13'N: insight into the biogeography of vent fauna. *Geochim Geophys Geosyst* 11(Q0AE01), 10.1029/2010GC003079.
- Lartaud F, et al. (2011) Fossil evidence for serpentinization fluids fueling chemosynthetic assemblages. *Proc Natl Acad Sci USA* 108:7698–7703.
- Mottl MJ (1992) Pore waters from serpentinite seamounts in the Mariana and Izu-Bonin forearcs, Leg 125: Evidence for volatiles from the subducting slab. *Proc ODP Sci Results* 125:373–385.
- Bloomer SH, Fisher RL (1987) Petrology and geochemistry of igneous rocks from the Tonga Trench: A non-accreting plate boundary. *Jour Geol* 95:469–495.
- Kojima S, Fujikura K, Okutani T (2004) Multiple trans-Pacific migrations of deep-sea vent/seep-endemic bivalves in the family Vesicomidae. *Mol Phylogen Evol* 32:396–406.
- Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Mol Biol Evol* 24:1596–1599.
- Krylova EM, Sahling H (2010) Vesicomidae (Bivalvia): current taxonomy and distribution. *PLoS ONE* 5(4):e9957, doi:10.1371/journal.pone.0009957.
- Tamura K, et al. (2011) MEGA5: Molecular Evolutionary Genetics Analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol Biol Evol* 28:2731–2739.
- Ohkouchi N, Kawamura K, Kawahata H, Taira A (1997) Latitudinal distributions of terrestrial biomarkers in sediments from the Central Pacific. *Geochim Cosmochim Acta* 61:1911–1918.
- Boulégué EL, et al. (1987) Geochemical and biogeochemical observations on the biological communities associated with fluid venting in Nankai Trough and Japan Trench subduction zones. *Earth Planet Sci Lett* 83:343–355.
- Fisher CR, et al. (1988) Microhabitat variation in the hydrothermal vent mussel, *Bathymodiolus thermophilus*, at the Rose Garden vent on the Galapagos Rift. *Deep Sea Res* 35:1769–1791.
- Kennicutt MS, II, et al. (1989) An upper slope “cold” seep community: Northern California. *Limnol Oceanogr* 34:635–640.
- Saino T, Ohta S (1989) ¹³C/¹²C and ¹⁵N/¹⁴N ratios of vesicomid clams and a vestimentiferan tube worm in the subduction zone east of Japan. *Palaeogeogr Palaeoclimatol Palaeoecol* 71:169–178.
- Kim ES, et al. (1990) Carbon, nitrogen and sulfur isotopic ratios in hydrothermal vent animals from the mid-Okinawa Trough. *JAMSTECR Deepsea Res* 6:129–137 in Japanese with English abstract.
- Rau GH, et al. (1990) $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ of *Calyptogena phaseoliformis* (bivalve mollusc) from the Ascension Fan-Valley near Monterey, California. *Deep Sea Res* 37:1669–1676.
- Fiala-Médioni A, et al. (1993) Source of energy sustaining the *Calyptogena* populations from deep trenches in subduction zones off Japan. *Deep Sea Res Part I* 40:1241–1258.
- Van Dover CL (2002) Trophic relationships among invertebrates at the Kairei hydrothermal vent field (Central Indian Ridge). *Mar Bio* 141:761–772.