Biogeography and Ecological Setting of Indian Ocean Hydrothermal Vents

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Within the endemic invertebrate faunas of hydrothermal vents, five biogeographic provinces are recognized. Invertebrates at two Indian Ocean vent fields (Kairei and Edmond) belong to a sixth province, despite ecological settings and invertebrate-bacterial symbioses similar to those of both western Pacific and Atlantic vents. Most organisms found at these Indian Ocean vent fields have evolutionary affinities with western Pacific vent faunas, but a shrimp that ecologically dominates Indian Ocean vents closely resembles its Mid-Atlantic counterpart. These findings contribute to a global assessment of the biogeography of chemosynthetic faunas and indicate that the Indian Ocean vent community follows asymmetric assembly rules biased toward Pacific evolutionary alliances.

The 1977 discovery of hydrothermal vent communities dominated by giant vestimentiferan tubeworms, vesicomyid clams, and bathymodiolid mussels at the Galapagos Spreading Center quickly resulted in pioneering work on chemosynthesis, microbial symbioses in marine animals, and physiological and biochemical adaptations to extreme environments [reviewed in (*1*)]. Vent communities were immediately recognized as being composed of predominantly endemic species adapted for life in patchy, ephemeral, sulfide-rich environments (*2*), and exploration of ridge systems in different ocean basins has led to an appreciation of regional variations in species composition (*3*). Ecological, phylogenetic, geological, and geochemical factors that contribute to the evolution of distinct biogeographic provinces continue to be explored and defined. An unknown piece of this biogeographic puzzle has been the mid-ocean ridge systems of the Indian Ocean (Fig. 1A). It has been suggested that the Indian Ocean ridge system has served as a conduit for exchange of vent-endemic taxa between Pacific and Atlantic Oceans and that the Indian Ocean vent fauna might be allied to either Pacific or Atlantic provinces (*3*, *4*). Given multiple examples of evolutionary convergence toward symbiotic lifestyles in vent invertebrates, we expected that the remote Central Indian Ridge vents might also support independently evolved, previously unknown symbioses (*4*).

Closely spaced vent fields (those along adjacent spreading-ridge segments) share species and gene pools (*5*–*8*), whereas vent communities separated by larger gaps (e.g., East Pacific Rise versus the Juan de Fuca, Explorer, and Gorda Ridges of the northeast Pacific) have distinct faunal lists with few shared species (*9*). Between the East Pacific Rise and Mid-Atlantic Ridge, alliances of vent taxa are almost exclusively at generic, familial, or higher taxonomic levels (*10*). Ecological settings can also be disparate, with highly mobile, swarming shrimp dominating some Mid-Atlantic Ridge vents and sessile invertebrates dominating eastern Pacific vent fields (*11*).

Vent faunas of isolated back-arc basins in the western Pacific show some surprising alliances with Mid-Atlantic Ridge taxa at the generic level, suggesting a historical connection via the Indian Ocean (*4*). However, other western Pacific genera appear to be shared exclusively with eastern Pacific vents (*12*). On the basis of the biogeography of nonvent deep-sea invertebrates, the Indian Ocean vent fauna has been predicted to be more similar to Pacific than Atlantic fauna (*13*).

In April 2001, we conducted multidisciplinary investigations to address biogeographic questions and to understand geological and geochemical contexts of hydrothermal systems in the Indian Ocean (*14*). Our study focused on the southern portion of the Central Indian Ridge from 23°S to the Rodriguez Triple Junction near 25°30′S (Fig. 1B). This 275-km-long region is an intermediate-rate (50 to 60 mm year^{-1}) spreading system (*15*) and encompasses the five southern segments (S1 to S5) of the ridge (*16*). The rift valley throughout this area has a regional trend of NNW, is between 5- and 8-km wide, and has relief ranging from 1000 m near segment ends to 500 m near segment centers (*16*).

The Kairei vent field (2415 to 2460 m) at 25°19.23′S, 70°02.42′E in segment S1 immediately north of the Rodriguez Triple Junction (Fig. 1B) was discovered by Japanese scientists in August 2000 (*17*). The segment is ~20-km-long and terminates in 4200-m-deep basins at a nontransform discontinuity to the north and at the triple junction to the south. The eastern rift-valley wall has a stair-step morphology; Kairei is located on a 10° to 30° slope high on the rift valley wall on one of the steps, nearly 1800-m shallower than the rift valley floor and >7 km from the central axis of the rift valley. The main area of high-temperature (306° to 365°C) venting occurs along a WNW trend, extends ~80-m along the rift wall, and is ~30-m wide. Large accumulations of weathered sulfides and peripheral relict sulfide chimneys suggest that the site has been active for a long time (> tens of years) and that there has been migration or focusing of flow to the current configuration of three high-temperature mounds. Diffuse, lower-temperature flow is mainly restricted to sides of these black-smoker complexes. End-member, high-temperature fluids sampled from multiple orifices have identical chemistries with ~15% greater chlorinity than local ambient seawater (540 mmol kg^{-1}) and iron concentrations of ~5 mmol kg^{-1} (ambient seawater [Fe] is <1 nmol kg^{-1}).

We discovered the Edmond vent field (23°52.68′S, 69°35.80′E; 3290 to 3320 m) (*18*) approximately 160-km NNW of Kairei (Fig. 1B). Earlier hydrothermal plume work suggested the presence of active seafloor vents in this region (*19*, *20*). We integrated

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geological structure, inferred from multibeam bathymetry, with near-bottom water-column surveys to locate the seafloor origin of the hydrothermal plume signal. The Edmond Field is located at the northern end of segment S3 on the eastern rift-valley wall, $\sim$6 km from the adjacent rift axis. The vent field (100 m by 90 m) is constructed on a small protrusion that extends south from the eastern rift wall that forms the northeast corner of a $\sim$60-m-deep basin. The seafloor structure at the nontransform discontinuity that marks the northern end of the segment is characterized by a zone of cross-cutting, low-relief ridges and valleys that have orientations parallel, perpendicular, and oblique to the NNW trend of the rift valley (Fig. 1B). Similar cross-cutting ridge-crest structures are important in controlling sites of hydrothermal venting at the TAG (Trans Atlantic Geotraverse) hydrothermal field on the Mid-Atlantic Ridge (*21*, *22*).

The Edmond Field is dominated by old, disaggregated sulfide structures and massive sulfide talus, indicating that hydrothermal activity has been focused at this site over long periods of time, as at Kairei. Orange-brown, iron-oxyhydroxide sediments are common at Edmond, accumulating to several cm in depressions and coating many of the sulfide structures and much of the talus. Hydrothermal venting at Edmond exhibits a wide range of styles and chimney morphologies (*23*). High-temperature venting is manifest as discrete clusters of large (up to 20-m tall and 2-m in diameter) chimneys with vigorous black-smoker fluids emanating from multiple orifices and "beehive" structures (*24*). Within and between chimney clusters, smaller (up to 5-m high), branched, candelabra-like structures with orifice diameters of $\sim$2 to 20 cm ornament the seafloor and discharge black-smoker fluids at slower flow rates. Extensive diffuse flow and blocks of anhydrite suggest that sub-surface seawater entrainment and mixing processes occur over a broad area, providing varied microhabitats for microbial activity, including sediments covered by extensive microbial mats.

Hydrothermal fluids (273° to 382°C) collected from four sites at Edmond had chlorinities about 70% greater than ambient seawater, making them some of the hottest brines yet sampled on mid-ocean ridges. Edmond fluids have high iron concentrations of $\sim$14 mmol kg^{-1}. Iron enrichment at Edmond relative to Kairei is a result of the higher chlorinity and temperature of Edmond fluids. Edmond and Kairei fluids are characterized by low pH ($\sim$3 measured at 25°C and 1 atm) and several mmol kg^{-1} of H_2S. Despite high iron concentrations, large amounts of dissolved sulfide are transported in vent fluids and are available for biological metabolic processes.

As at Kairei, high-temperature fluids from Edmond appear to be uniform in composition. Within-field homogeneity of fluid chemistry at Kairei and Edmond is similar to the pattern observed on more slowly spreading ridge systems, such as the Mid-Atlantic Ridge (*25*), where fluids typically seem to be derived from a single source. On faster-spreading ridges, high-temperature fluids even a few meters apart can be chemically unique (*26*). Kairei and Edmond hydrothermal fluids contain about 15 mmol kg^{-1} total gas. This is at the lower end of gas concentrations seen in hydrothermal fluids but is about 1.5 times gas concentrations seen in brines at the Juan de Fuca Ridge (*27*) and at 9° to 10°N on the East Pacific Rise (*28*). There are major differences in the composition of gases at the Kairei and Edmond Fields: Kairei fluids contain high H_2 concentrations (8.5 mmol kg^{-1}), whereas Edmond H_2 concentrations are more typical of vent fluids (0.2 mmol kg^{-1}). High H_2 concentrations have been seen in ultramafic-hosted systems, but there they are usually accompanied by high CH_4 concentrations (*29*). Methane concentrations are low at Kairei and Edmond (0.2 and 0.4 mmol kg^{-1}, respectively) and ultramafic rocks were not recovered in dredges conducted in the vicinity of either Kairei or Edmond.

Although a complete account of microbial diversity at Central Indian Ridge vent fields is beyond the scope of this study, previously

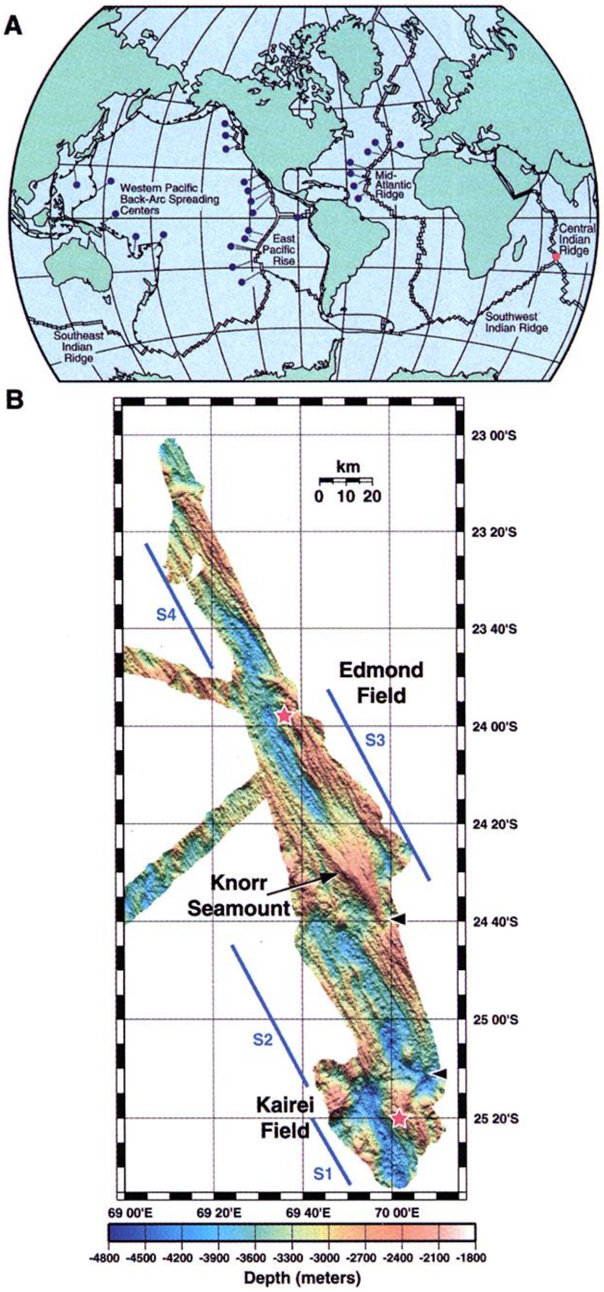

Fig. 1. Maps showing location of study sites. **(A)** Map of the global mid-ocean ridge. Red dot indicates location of Kairei and Edmond Fields on the Central Indian Ridge. Blue dots denote known hydrothermal systems elsewhere on mid-ocean ridges and back-arc spreading centers. **(B)** Multibeam bathymetry data (shaded relief) from cruise KN162-13 of the first four ridge segments [S1-S4 (*15*)] that compose the southern Central Indian Ridge. Red stars mark locations of Kairei and Edmond Fields on the eastern wall of the rift valley and >6 km from the ridge axis. Also shown is the location of Knorr Seamount, a large volcano nearly 40-km long by 18-km wide and triangular in shape, with a rifted summit reaching 1700 m above the rift valley floor. Arrowheads indicate nontransform discontinuities of the ridge axis.

unknown chemolithoautotrophic thermophilic (70° or 80°C) and heterotrophic bacteria were isolated from Kairei and Edmond sulfides. Microaerophilic, hydrogen-oxidizing, and nitrate-reducing isolates are closely related to a bacterial lineage within the Aquificales (EX-H1) (*30*, *31*), first isolated from vent sulfides near 9°50′N on the East Pacific Rise (*30*). On the basis of 16S rRNA sequence comparison, Kairei isolates are $\sim$98% similar to EX-H1 and $>$99% similar to hydrogen-oxidizing isolates obtained from the Edmond Field (*32*). One additional isolate from Edmond was only 95% similar in 16S rRNA sequence to EX-H1 (*33*). Two hydrogen-oxidizing isolates (*34*) from Edmond sulfides were grown at 90°C and represent the first *Aquifex* spp. ever recovered from deep-sea hydrothermal vents. These isolates are $\sim$98% similar (in terms of 16S rRNA) to *Aquifex pyrophilus* (*35*). Thermophilic methanogens closely related to *Methanococcus* sp. were also isolated from Kairei. A bacterial sulfate-reducing isolate related to *Thermodesulfobacterium* ($\sim$94% similar in 16S rRNA sequence) (*36*) was obtained from sulfide of an active black smoker (335°C) at Kairei. New thermophiles from Kairei and Edmond represent a glimpse into the potentially vast microbial diversity at these sites.

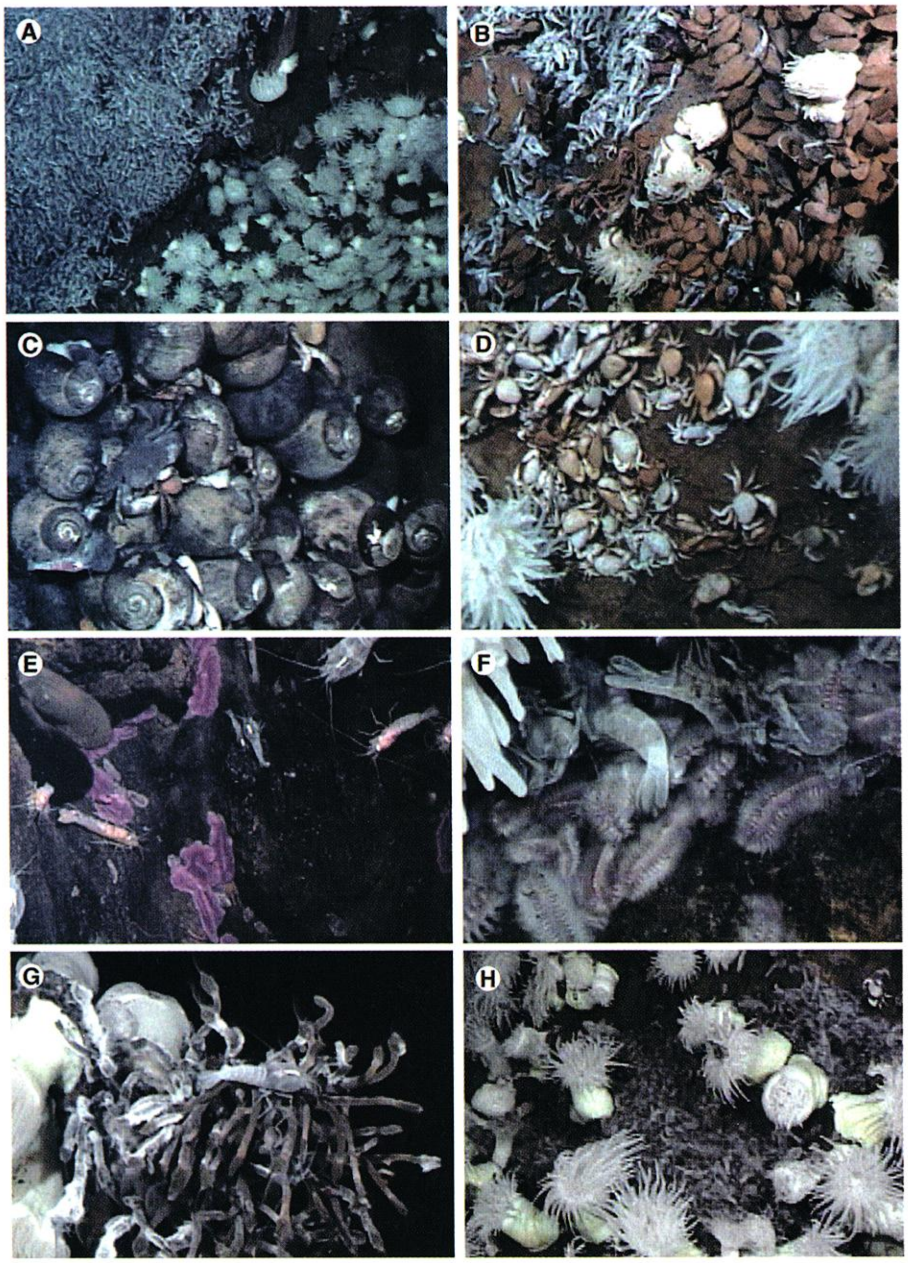

Fig. 2. Invertebrates of Central Indian Ridge hydrothermal vents. (**A**) Discrete boundary between shrimp (*Rimicaris* aff. *exoculata*, top left) and anemones (*Marianactis* sp., lower right). (**B**) Mussels (*Bathymodiolus* aff. *brevior*), shrimp, and anemones. (**C**) Hairy gastropods (*Alviniconcha* n. sp.) and brachyuran crabs (*Austinograea* n. sp.). (**D**) Brachyuran crabs and anemones. (**E**) Red turbellarian flat worms and shrimp [*Chorocaris* n. sp. (narrow-bodied) and *R.* aff. *exoculata* (wide-bodied)]. (**F**) Bristleworm (*Archinome* sp.) on shrimp molts. (**G**) Stalked barnacles (*Neolepas* n. sp.) and shrimp. (**H**) Anemones and shrimp molts.

The invertebrate community of the Kairei Field is characterized by an abrupt transition (Fig. 2A) between the centrally located complexes of black smokers dominated by dense swarms of shrimp (*Rimicaris* aff. *exoculata*) in 10° to 20°C fluids and an ambient-temperature (1° to 2°C) peripheral zone dominated by anemones (*Marianactis* sp.). Shrimp are also common outside the zone of active venting as solitary individuals rather than as swarms. At the base of shrimp swarms, mussels (Fig. 2B), hairy gastropods (Fig. 2C), and "scaly-foot" gastropods [family indeterminate; see (*37*)] occur in separate clusters of up to several hundred individuals. Brachyuran crabs [*Austinograea* n. sp.; see (Fig. 2D)], turbellarian flatworms (Fig. 2E), nemerteans, and a second shrimp species [*Chorocaris* n. sp.; see (Fig. 2E)] occur in sometimes dense but isolated patches in the narrow transition zone separating anemones and swarming shrimp. Other gastropods (limpets and provannid snails), large white polynoid (*Branchinotogluma* n. sp.) and archinomid [*Archinome* sp.; see (Fig. 2F)] polychaetes, and clusters of stalked neolepadine barnacles [*Neolepas* n. sp.; see (Fig. 2G)] were observed frequently in this transition zone, as were accumulations of shrimp molts (Fig. 2H). Vesicomyid shells were collected within $<$1 km of the Kairei Field (*17*), but no live clams have been observed.

The invertebrate fauna of the Edmond Field is a subset of that found at Kairei. As at Kairei, the biomass at Edmond is dominated by dense swarms of shrimp and by peripheral beds of anemones in areas of diffuse flow and on inactive sulfides. The Edmond vent field is distinguished from Kairei by the relative paucity or complete absence of certain species that are components of the Kairei Field, despite their visually similar habitats. Among the invertebrates observed at Kairei but not at Edmond are stalked neolepadine barnacles, scaly-foot gastropods, archinomid polychaetes, nemerteans, and turbellarians. Faunal differences observed between Kairei and Edmond are most likely related to contemporary quality and availability of microhabitat rather than geographic or bathymetric isolation.

At all known vent fields, endo- and episymbioses between bacteria and invertebrates are responsible for sustaining the high biomass of vent communities (*1*). Indian Ocean vent fields are no exception (*38*). *Rimicaris* aff. *exoculata* supports episymbiotic, chemoautotrophic bacteria within its branchial chambers, and its tissues are isotopically indistinguishable from those of *Rimicaris exoculata* on the Mid-Atlantic Ridge (Table 1), consistent with a similar diet of chemoautotrophic bacteria and a trophic status as a primary consumer (*39*, *40*). Kairei and Edmond mussels and hairy gastropods host endosymbiotic, chemoautotrophic bacteria in their gills. Carbon isotope compositions of Kairei mussel gill tissues [*Bathymodiolus* aff. *brevior*, $\delta^{13}C$ = –31.3 per mil (‰)] resemble values observed in other vent bathymodiolid mussels containing endosymbionts (e.g., *Bathymodiolus brevior*, *B. thermophilus*). Nitrogen isotope compositions ($\delta^{15}N$) of Kairei mussels are more negative ($\delta^{15}N$ = –8.1‰) than those of mussels from Mariana or East Pacific Rise vents ($\delta^{15}N$ = –5 to +8‰), suggesting that different nitrogen sources are exploited or that a given source can have site-specific isotopic variability. A striking difference in carbon isotopes is seen in gill tissues of hairy gastropods at Kairei (*Alviniconcha* n. sp., $\delta^{13}C$ = –10.8‰) versus Mariana Trough (*Alviniconcha hessleri*, $\delta^{13}C$ = –28.9‰). This difference suggests that carbon metabolism of bacterial endosymbionts in the two host species may be different. Heavier carbon isotope values of Kairei hairy gastropod gills are consistent with reliance on methanotrophic symbionts that use volcanogenic methane or on chemoautotrophic symbionts that use form II ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) as the carboxylating enzyme, or they may be evidence for CO_2-limitation (*41*, *42*). Further molecular characterization and phylogenetic analysis of Indian Ocean symbionts will allow us to determine their metabolic capabilities and their evolutionary relationships to corresponding symbionts of Pacific and Atlantic invertebrates.

The scaly-foot gastropod is a candidate for bacterial symbiosis based on anatomical details of the digestive system, but $\delta^{13}C$ values of its tissues (–17.7‰) are neither enriched nor depleted in ^{13}C relative to values measured in deep-sea invertebrates dependent on photosynthetically derived organic material (*43*). Tests for RuBisCO activity in the gills of scaly-foot gastropods and microscopic examination of gill tissues for symbionts are negative. Nitrogen isotope values of scaly-foot gastropod gills are relatively light ($\delta^{15}N$ = 3.1‰) compared with nitrogen isotope values of Kairei hairy gastropods ($\delta^{15}N$ = 6.4‰), which is consistent with a symbiotic association in scaly-foot gastropods (*44*).

On the basis of this overview, the physical setting and ecology of the Kairei and Edmond Fields differ only in detail from known vent sites on mid-ocean ridges, yet the invertebrate species composition is such that the fauna belongs to a newly found biogeographic province. As reported by Hashimoto *et al.* (*17*) and as demonstrated here (Table 2), this fauna has a strong evolutionary link to Pacific vent taxa, with a single conspicuous exception. One-third of the 36 invertebrate taxa identified from the Kairei Field belong to genera that until now were known only from Pacific vent fields, and as many taxa may belong to new genera (*45*). Only one species, the dominant shrimp (*Rimicaris* aff. *exoculata*), belongs to a genus that is known exclusively from Atlantic vents. Eleven genera are known from both Pacific and Atlantic vents. At least one species, the scaly-foot gastropod, may represent a new family. The absence at Kairei of certain taxonomic groups that are common at Pacific vents—alvinellid polychaetes and vestimentiferan tubeworms—is notable. Small crustaceans, except copepods, were also not found in Kairei samples. The absence of amphipods is especially surprising, because they are often abundant at Pacific and Atlantic vents (*46*, *47*).

Molecular systematic analyses were used to assess taxonomic affiliations of seven invertebrate species found at Kairei with related invertebrate taxa from vent sites in other ocean basins (*48*). Sequence divergence between Kairei *Rimicaris* individuals and *R. exoculata* from the Mid-Atlantic Ridge is 0.9% [576–base pair (bp) region of the gene coding for mitochondrial cytochrome oxidase subunit I (COI)], with no measured variation within populations from either of these biogeographic regions (*7*, *49*). In contrast, the Kairei *Chorocaris* shrimp species differs by 4.7% (560 bp of the COI gene) from *C. vandoverae*, a western Pacific species, and 9.2% from *C. chacei*, a Mid-Atlantic Ridge species. These data support a or western Pacific affinity for the Kairei *Chorocaris* species.

All other molecular comparisons also support affinities between Indian Ocean and

Table 1. Stable isotope compositions (mean ± SD) of tissues from potential invertebrate or bacterial symbioses. Snake Pit (Mid-Atlantic Ridge) *Rimicaris exoculata* data from (*39*); Mariana (western Pacific) data from (*63*); *Bathymodiolus thermophilus* data from (*64*). *N*, number of individuals analyzed.

Tissue and location	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	*N*
Rimicaris aff. *exoculata* abdominal muscle			
Kairei Field	−12.4 ± 0.2	6.8 ± 0.3	3
Snake Pit (*R. exoculata*)	−11.0 ± 0.7	7.3 ± 0.3	18
Bathymodiolus sp. gill			
Kairei Field (*B.* aff. *brevior*)	−31.3 ± 0.7	−8.1 ± 1.5	4
Mariana (*B. brevior*)	−34.8	−3.0	1
East Pacific Rise (*B. thermophilus*)	−30.5 to −37.3	−5 to +8	>100 for C, 9 for N
Alviniconcha spp. gill			
Kairei Field (*Alviniconcha* n. sp.)	−10.8 ± 0.3	6.4 ± 0.5	5
Mariana (*A. hessleri*)	−28.9 ± 0.9	4.2 ± 0.9	4
Scaly-foot gastropod gill			
Kairei Field	−17.7 ± 0.4	3.1 ± 0.5	5

Table 2. Geographic affinities of Kairei vent taxa. Pac., Pacific; Atl. Atlantic; P., phylum.

Taxon	Pac.	Atl.	Pac. and Atl.	Possible New Genera
P. Cnidaria				
Anemone	*Marianactis*			
P. Annelida				
Polychaetes	*Amphisamytha* *Branchinotogluma*		*Archinome* *Branchipolynoe* *Ophryotrocha* *Prionospio*	Capitellid sp. 1 Hesionid sp. 1 Hesionid sp. 2 cf. *Harmothoe* cf. *Levensteiniella*
P. Mollusca				
Aplacophoran				cf. *Helicoradomenia*
Limpets	*Eulepetopsis* *Lepetodrilus*		*Shinkailepas* *Pseudorimula* *Sutilizona*	Slit limpet sp. 1 Slit limpet sp. 2
Coiled Gastropods	*Alviniconcha* *Bruceiella* *Desbruyeresia*		*Phymorhynchus*	Scaly-foot gastropod
Bivalves			*Bathymodiolus*	
P. Arthropoda				
Barnacles	*Neolepas* *Eochionelasmus*			
Shrimp		*Rimicaris*	*Chorocaris*	
Anomuran			*Munidopsis*	
Brachyuran	*Austinograea*			
Other				Copepod
Other Phyla				Nematoda Nemertea Platyhelminthes

western Pacific taxa. This is most clearly demonstrated by the Kairei mussel, which, on the basis of 517 bp of the gene coding for mitochondrial NADH (the reduced form of nicotinamide adenine dinucleotide) dehydrogenase subunit 4, differs by 0.8% on average from *B. brevior*, a species found at western Pacific vents. More genetic markers are needed to estimate rates of gene flow and to assess taxonomic relationships between these regions. Mean sequence divergence between Kairei mussels, two Mid-Atlantic Ridge species (*B. puteoserpentis* and *B. azoricus*), and an East Pacific Rise species (*B. thermophilus*), ranges from 14.9 to 19.3%.

The Kairei polynoid scaleworm that lives as a commensal in the mantle cavity of vent mussels resembles most closely *Branchipolynoe pettiboneae* from the western Pacific (9% sequence divergence; 600 bp of the COI gene). The Kairei commensal worm differs by 17.2 to 19.6% from eastern Pacific, Atlantic, and Gulf of Mexico species of *Branchipolynoe* (*50*). Likewise, vent-endemic bythograeid crabs from Kairei resemble most closely *Austinograea* species from the western Pacific; mean sequence divergence (from 370 bp of the gene coding for mitochondrial cytochrome *b*) is 12.6%. Differences between Kairei crabs and eastern Pacific (*Bythograea*) and Atlantic (*Segonzacia*) species range from 16.5 to 27.0%. The large hairy gastropod from Kairei is genetically distinct from *Alviniconcha hessleri*, found only in the Mariana Trough (5.2% sequence divergence based on 650 bp of the mitochondrial 16S rDNA gene). Lastly, the *Lepetodrilus* limpet from Kairei may be a new species, but its affinities with known species from the western Pacific are poorly resolved using the region of mitochondrial 16S rDNA we have examined to date (*12*). Sequence divergence between Kairei specimens and seven known species of *Lepetodrilus* average 1.9%. Differences among other *Lepetodrilus* species range from 1.7 to 2.2%.

Kairei specimens belonging to the genera *Chorocaris*, *Branchipolynoe*, *Austinograea*, and *Alviniconcha* warrant consideration as new species on the basis of ongoing studies of within- and between-species levels of sequence divergence. For now, we consider the Kairei mussels as closely affiliated, and probably conspecific with *Bathymodiolus brevior*, and Kairei shrimp as closely affiliated with *Rimicaris exoculata*, despite morphological variations that distinguish the populations. More thorough morphological and genetic analyses are needed to resolve the specific status of Kairei *B.* aff. *brevior* and *R.* aff. *exoculata*.

On the basis of their geographical proximity and faunal similarity, we expected Edmond and Kairei hydrothermal fields to support closely related populations of the shared species. In all cases examined, preliminary measurements of DNA sequence divergence are indicative of genetic exchange between the two areas (*51*), despite potential topographical barriers along the Central Indian Ridge between the two vent sites [two nontransform discontinuities and Knorr Seamount; see (Fig. 1B)]. No sequence differences were observed between Kairei and Edmond populations of the swarming shrimp (*Rimicaris* aff. *exoculata*, from mitochondrial COI) or the hairy gastropod (*Alviniconcha* n. sp., from mitochondrial 16S rDNA). Mean sequence (NADH dehydrogenase subunit 4) divergence between bathymodiolid mussels from Edmond and Kairei (*Bathymodiolus* aff. *brevior*) is 0.9%, the same as the mean divergence within the two populations. Similarly, vent-endemic bythograeid crabs (*Austinograea* n. sp.) from Kairei and Edmond differ on average by only 0.2% (from mitochondrial cytochrome *b*), comparable to the mean sequence divergence within the two populations (0.25%). These genetic similarities are consistent with intraspecific levels of diversification found in other vent-endemic species belonging to the same families (*8*, *12*, *49*, *50*).

If *Rimicaris* individuals at Kairei and Edmond are indeed conspecific with *R. exoculata* from the Mid-Atlantic Ridge, the species has an immense range (~17,000 km via the mid-ocean ridge system). Molecular studies suggest that *Rimicaris* is a young genus [~0.5 million years ago (Ma)] (*49*). Rapid development of such an extensive range is feasible for a species with good dispersal capability, as long as there are intervening vents to serve as stepping-stones between Mid-Atlantic and Indian Ocean Ridge systems (*52*). In addition to an adult stage that is a capable swimmer, *R. exoculata* has a free-swimming, planktotrophic, post-larval stage that feeds on photosynthetically derived organic material and can be found as far as 100 km from a known vent field (*53*, *54*). Mid-Atlantic Ridge vents also support two other shrimp genera, *Mirocaris* and *Chorocaris*. No *Mirocaris* species was observed at Indian Ocean vents; the Indian Ocean *Chorocaris* species is allied to a western Pacific member of the genus. Western Pacific and Atlantic shrimp genera have, thus, arrived at or dispersed from Indian Ocean vents by different routes and probably on different evolutionary time scales. If further studies corroborate that Indian Ocean mussels are the same species as western Pacific back-arc basin mussels, this genetic continuity must be accomplished without an interconnecting ridge and on an ecological time scale. *Bathymodiolus* species possess a planktotrophic larval shell and presumably have considerable dispersal potential (*6*, *55*), but little is known about duration of larval life, distribution of larvae in the water column, or timing of the acquisition and competency of their chemoautotrophic symbionts.

Morphological species shared between Atlantic and Pacific vents led to the hypothesis that Indian Ocean ridge systems serve as a conduit for contemporaneous dispersal between ocean basins (*3*, *4*). We present evidence that is more consistent with such connections on evolutionary time scales, based on the presence at Indian Ocean vents of genera shared with Atlantic and Pacific vents (Table 2). As yet, we have no molecular evidence for any Indian Ocean species shared with both Atlantic and Pacific vents. In general, the Indian Ocean vent community follows asymmetric assembly rules biased toward Pacific evolutionary alliances.

References and Notes

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A Four-Dimensional Generalization of the Quantum Hall Effect

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We construct a generalization of the quantum Hall effect, where particles move in four dimensional space under a *SU*(2) gauge field. This system has a macroscopic number of degenerate single particle states. At appropriate integer or fractional filling fractions the system forms an incompressible quantum liquid. Gapped elementary excitation in the bulk interior and gapless elementary excitations at the boundary are investigated.

Most strongly correlated systems develop long-range order in the ground state. Familiar ordered states include superfluidity, superconductivity, antiferromagnetism, and charge density wave (*1*). However, there are special quantum disordered ground states with fractionalized elementary excitations. In one-dimensional (1D) systems, Bethe's Ansatz (*2*) gives exact ground-state wave functions of a class of Hamiltonians, and the elementary excitations are fractionalized objects called spinons and holons. In the 2D quantum Hall effect (QHE) (*3*, *4*), Laughlin's wave function (*3*) describes an incompressible quantum fluid with fractionally charged elementary excitations. This incompressible liquid can also be described by a Chern-Simons-Landau-Ginzburg field theory (*5*), whose long-distance limit depends only on the topology but not on the metric of the underlying space (*6*). These two special quantum disordered ground states are the focus of much theoretical and experimental studies, because they give deep insights into the interplay between quantum correlations and dimensionality and into how this interplay can give rise to fractionalized elementary excitations.

In view of their importance, it is certainly desirable to generalize these quantum wave functions to higher dimensions. However, despite repeated efforts, the Bethe's Ansatz solutions have not yet been generalized to dimensions higher than one. Laughlin's wave function uses properties that seem to be special to the 2D space. In this work, we shall report the generalization of the quantum Hall system to four space dimensions, and this system shares many compelling similarities with the 2D counterpart. In the 2D QHE, the charge current is carried in a direction perpendicular to the applied electric field (and also perpendicular to the magnetic field, which

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