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Milestones in the discovery of hydrothermal-vent faunas

Seafloor Spreading and Hot Springs

Any account of the discovery of hydrothermal-vent faunas must begin with the geology of seafloor spreading centers. The symmetry of magnetic anomalies on either side of the mid-ocean ridges that girdle the globe and the correspondence of the anomaly patterns with the pattern of magnetic reversals on Earth confirmed the process of seafloor spreading and led to general acceptance of plate tectonic theory in the early 1960s (VINE & MATTHEWS 1963). The bathymetric relief of mid-ocean ridges was understood to be a consequence of the thermal buoyancy of hot rock in volcanic systems. Conductive heat loss was expected to be greatest at the axis of these linear volcanoes and to diminish along transects away from the ridge crest, but heat-flow measurements collected by placing a vertical array of thermistors into seafloor sediments consistently documented a heat-deficit near the ridge axis. This heat deficit suggested that conductive heat loss was not the only operative mode of cooling (STEIN et al. 1995). Geologists hypothesized that the convective heat driven by cells of seawater percolating into the crust and subsequent heating and buoyancy-driven flux of fluids out of the crust would account for the missing heat. Thus the presence of hot springs on the seafloor with temperatures as great as 300°C was anticipated (TALWANI et al. 1971; LISTER 1972; WOLERY & SLEEP 1976), and the first unequivocal evidence of warm-water, buoyant plumes was collected by May 1976 using the Scripps Institution of Oceanography Deep-Tow vehicle (WEISS et al. 1977). While systematic geophysical studies predicted the existence of hydrothermal vents on the seafloor, the discovery of their attendant chemosynthetic ecosystems was unimagined.

Strange Animals at Hydrothermal Vents on the Galapagos Spreading Center

The study of chemosynthetic ecosystems in the deep sea dates back to a Black and white photograph of large white clam shells lying within cracks in a pavement of Black basalt that was captured by the Deep-Tow camera system at 13:20:39 (GMT) on 29 May 1976 at 0°47'84"N, 86°09'18"W (Galapagos Spreading Center, eastern Pacific Ocean; LONSDALE 1977). Given that bivalves are generally suspension feeders, the diet of the clams was inferred to have been organic particulates concentrated by bottom-water currents (convection cells) induced by hydrothermal activity (LONSDALE 1977; ENRIGHT et al. 1981).

During Alvin dives at the Galapagos Spreading Center in 1977, geologist Jack Corliss first described vent mussels (although he erred in his initial identification). His difficulty in finding the words to describe what was before him, a vista no one had ever seen before, is evident:

"They are abalone shells. They are shells. They are big shells. They are living. … attached shellfish…."

The wonder in his voice is captured on the audio record of the dive.

Further into the dive series, geochemist John Edmond first sounds incredulous as he provided the first description of giant worms, and then frustrated as his observations were limited by the green light of the thallium iodide bulb on Alvin:

"There are big ones [worms] out there. Looks like an Indian [Native American] headdress. There are four of them in a row, right outside my view port. I wonder what color they are. You can't tell. They may be red."

Vent animals were useful as flux indicators of hydrothermal activity for geologists prospecting for vents, but geologists also appreciated the need for an explanation of the tremendous biomass of animals and of the means by which species could be maintained at vents in the face of inevitable local extinctions. Following the first Alvin dive series to Galapagos vents, microbiologist John Baross postulated that the millimolar concentrations of hydrogen sulfide in vent fluids were a source of reduced sulfur for free-living chemolithoautotrophic, sulfur-oxidizing bacteria (cited in CORLISS et al. 1979). Chemolithoautotrophs are primary producers that use the energy from the oxidation of reduced compounds like hydrogen sulfide to yield ATP. That ATP is then used to fix inorganic carbon (CO_2) into organic carbon. This contrasts with photosynthetic processes, where it is light energy that is harvested to produce ATP. Subsequent biochemical steps in the production of organic carbon can be identical in chemoautotrophs and photoautotrophs. Discovery of vents thus led us to understand for the first time that complex food webs could be dependent on microbial chemosynthetic primary production. The initial dives to deep-sea vents also sparked the hypothesis that life on Earth may have originated at submarine hot springs (CORLISS et al. 1980).

The triptych of charismatic vent organisms – clams (*Calyptogena magnifica*), mussels (*Bathymodiolus thermophilus*), and gi-

C.L. VAN DOVER, M. BISCOITO, A. GEBRUK, J. HASHIMOTO, V. TUNNICLIFFE,
P. TYLER & D. DESBRUYÈRES

Denisia **18** (2006) 13–25

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ant tubeworms (*Riftia pachyptila*) – has sustained scientific interest since their discovery (BALLARD 1977) and the first field investigations by biologists (GRASSLE et al. 1979). These organisms, together with "dandelions" (siphonophores: *Thermopalia taraxaca*), "spaghetti worms" (enteropneusts: *Saxipendium coronatum*), limpets, crabs, amphipods, polychaetes, and other animals collected from Galapagos vents in the earliest collections (HESSLER & SMITHEY 1983), established the existence of a fauna endemic to and specialized for life in chemosynthetic ecosystems. They provided a baseline against which all other vent faunas would be compared. Our understanding of species zonation, of food webs, and even of succession of megafaunal species at vents in the eastern Pacific dates back to reports from these first geological and biological expeditions to the Galapagos Spreading Center.

Early Investigations on the East Pacific Rise

Early opportunities for ecological comparisons came with discovery and description of vent fields at 21°N [RISE Program in 1979 (Rise Project Group 1980); Oasis Expedition (HESSLER et al. 1985)] and 13°N [Biocyatherm (1982) and Biocyarise (1984) Expeditions; DESBRUYÈRES et al. 1982, LAUBIER & DESBRUYÈRES 1985] on the nearby northern East Pacific Rise (NEPR). Similarities between the invertebrate faunas at Galapagos and NEPR vent fields indicated that, despite the restricted, insular nature of the benthic vent communities, exchange between populations on the two ridge axes was sufficient to sustain relatively large species ranges (Rise Project Group 1980). The NEPR vent fields included a habitat – the warm-to-hot (20 to >110 °C), leaky surfaces of Black smoker chimneys – not present in Galapagos vent fields. At least some of the difference between Galapagos and NEPR species lists derives from the addition of species adapted to the warmer waters of the chimney habitat (DESBRUYÈRES & LAUBIER 1980, DESBRUYÈRES et al. 1982; FUSTEC et al. 1987), including the Pompeii worms (*Alvinella pompejana* and *A. caudata*) and a brachyuran crab (*Cyanagraea praedator*). Faunal similarities along the East Pacific Rise are now known to extend from the northern limit of the ridge system (Guaymas Basin) to 19°S (JUNIPER et al. 1990; BLACK et al. 1994; GEISTDOERFER et al. 1995). Vents in Guaymas Basin are exceptional in that they are one of the few localities along the mid-ocean ridge system where hydrothermal activity and volcanic eruptions take place in association with thick layers of pelagic and terrigenous sediment rather than bare basalt (EINSELE et al. 1980). The nominal transition of the southern East Pacific Rise to the Pacific Antarctic Ridge occurs south of the Easter and Juan Fernandez microplates, i.e., at ~37°S. This region lies at the boundary between the Indo-Pacific and Antarctic marine biogeographic provinces (VINOGRADOVA 1979); the region also appears to be a boundary region for some vent taxa (HURTADO et al. 2004). Bathymodiolid mussels and bythograeid crabs from 32°S, for example, are sister species to their northern counterparts (GUINOT & HURTADO 2003; WON et al. 2003b), but gene flow in alvinellid polychaetes (*Alvinella pompejana*) and commensal polynoid polychaetes (*Branchipolynoe symmytilida*) is unimpeded across the microplates (HURTADO et al. 2004).

Samples from American and French cruises to Galapagos, 21°N, and 13°N vent sites between 1979 and 1985 became the foundation for a noteworthy series of studies, in which the remarkable anatomy, physiology, and trophic ecology of many representative species of vent organisms was established (see JONES & BRIGHT 1985 for an exhaustive bibliography for this period). The important role of endosymbiotic, sulfur-oxidizing bacteria in the nutrition of tubeworms (*Riftia pachyptila*), for example, was established in 1981 through morphological (JONES 1981), ultra-structural (CAVANAUGH et al. 1981), and biochemical studies (FELBECK et al. 1981). The paradox of large animals living in waters with sulfide concentrations normally toxic to metazoans was also largely resolved by 1985, with descriptions of detoxification mechanisms, including symbiont consumption of sulfide, sulfide-binding proteins in tubeworms (ARP & CHILDRESS 1983; POWELL & SOMERO 1983) and clams (ARP et al. 1984), and high activities of sulfide-oxidizing enzymes in superficial cell layers (POWELL & SOMERO 1986).

Northeast Pacific Vents

The 1983 exploration of hydrothermal vents at Axial Seamount on the Juan de Fuca Ridge (CASM 1985; TUNNICLIFFE et al. 1985) and subsequent studies of vent faunas on the Explorer (TUNNICLIFFE et al. 1986) and Gorda Ridges (VAN DOVER et al. 1990) in the northeast Pacific provided the first evidence that the hydrothermal-vent fauna was not globally cosmopolitan at the species level (CASM 1985). Faunal alliances between the EPR and the NE Pacific vent systems are recognized at the level of genus and higher (TUNNICLIFFE 1988), although several major taxonomic groups commonly found at hydrothermal vents on the EPR are so far conspicuously absent (e.g., alvinocarid shrimp, lysianassid amphipods) at NE Pacific vents. Some alliances between the East Pacific Rise and NE Pacific vent faunas may reflect the paleotectonic history of the East Pacific Rise and NE Pacific ridge system, which were once part of a single continuous ridge system before the override of the North American Plate (TUNNICLIFFE 1988).

Subsequent explorations along the Juan de Fuca Ridge revealed vent assemblages in a wide variety of venting conditions: extensive Black smoker fields at Endeavour (e.g., SARRAZIN et al. 1997), sedimented sulfide mounds at Middle Valley (e.g., JUNIPER et al. 1992), and recent eruptive lavas of the Cleft Segment (e.g., TSURAMI & TUNNICLIFFE 2001). From Explorer Ridge to Gorda Ridge, eight major vent fields provide biologists with settings that vary in depth, age, substratum and the relative importance of volcanism versus tectonism. In recent years, studies of community dynamics on sulfide edifices of Juan de Fuca vents have given us a view of temporally and spatially shifting species populations in response to physical and chemi-

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cal changes in the environment and to biological interactions (e.g., SARRAZIN & JUNIPER 1999). The proximity of NE Pacific vent sites to coastal ports has fostered studies that examine temporal change and community comparisons.

Discoveries in the Atlantic

Discovery of shrimp- (*Rimicaris exoculata*) dominated vent fields at TAG (36°N; RONA et al. 1986) and Snake Pit in 1985 (23°N; ODP Leg 106 Scientific Party 1986; MEVEL et al. 1989) on the Mid-Atlantic Ridge (MAR) highlighted the fact that similar types of organisms might be found at hydrothermal vents throughout the world's oceans (e.g., alvinocarid shrimp, bathymodioliform mussels, siphonostome copepods), but that the species, and even many genera, are different from one ocean basin to another. Major taxonomic groups familiar from EPR vents (e.g., vestimentiferan tubeworms, alvinellid polychaetes, stalked barnacles) are so far unknown at the MAR vents. In contrast to the dynamic succession of macrofaunal species observed in some NE Pacific vent habitats (e.g., SARRAZIN & JUNIPER 1999) and of megafaunal invertebrates at EPR vents (e.g., SHANK et al. 1998), communities at MAR vent fields are remarkably stable on decadal time scales (COPLEY et al. 1997, 1999).

The visual impact of vent megafauna is different between MAR and eastern Pacific vents: motile shrimp at MAR vents were described by John Edmond as looking "like maggots swarming on a hunk of rotten meat"; sessile worms and bivalves at EPR and NE Pacific vents lend the sites a more garden-like serenity, as evoked by names like Rose Garden and Garden of Eden. There are differences as well in the details of the bacterial-invertebrate symbioses implicated in the nourishment of the dominant megafauna between the two ocean basins. Episymbionts likely contribute to the nutrition of rimicarid shrimp on the MAR (VAN DOVER et al. 1988; GAL'CHENKO 1989; GEBRUK et al. 1992; SEGONZAC et al. 1993), whereas tubeworms, clams, and mussels that dominate EPR vents rely on endosymbionts. MAR mussels have dual endosymbionts (methanotrophs and thiotrophs), while EPR mussels have only thiotrophic endosymbionts in their gills (FIALA-MEDIONI 1984; LE PENNEC & HILY 1984). Discovery of shrimp swarms at Mid-Atlantic Ridge vents ultimately led to the description of modified eyes in *Rimicaris exoculata* and other alvinocarid shrimp, eyes that are adapted for detecting dim sources of light (VAN DOVER et al. 1989; WHITE et al. 2002).

Western Pacific Explorations

Hydrothermal vents in Manus Basin were discovered in 1985 (BOTH et al. 1986), the same year that vents on the Mid-Atlantic Ridge were reported (RONA et al. 1986). Further attention was brought to the southwestern Pacific in 1987 with the first description of vent faunas from the Mariana back-arc spreading center (HESSLER et al. 1988, HESSLER & LONSDALE 1991). Back-arc spreading centers are zones of extension of oceanic crust between active and remnant volcanic arcs associated with subduction zones. Because back-arc systems tend to be short, relatively young, and isolated (i.e., separated by large distances from the nearly continuous mid-ocean ridge systems), fauna distinct from that of EPR vents, but evolved to occupy similar niches was postulated (HESSLER & LONSDALE 1988). Dense clusters of large, "hairy gastropods" (*Alviniconcha hessleri*) with chemoautotrophic endosymbionts in their gills (STEIN et al. 1988) proved to be one of the most distinctive species, belonging to a new genus and having trophic attributes not previously known within the Gastropoda.

Although Mariana vent organisms belonged to undescribed species, more than half of the genera found there were already known from vent fields in the eastern Pacific. A mussel in the genus *Bathymodiolus* dominated the biomass; other familiar animal types included polychaete worms in the genus *Paralvinella* and limpets in the genus *Lepetodrilus*. Affinities of some Mariana taxa were shared with species known from Atlantic hydrothermal vents – for example, shrimp in the genus *Chorocaris*. There were no surprises in terms of fidelity to a particular niche or microhabitat in genera shared between Mariana and other mid-ocean ridge vents; the implication is that speciation has largely been passive within these genera, a consequence of isolation by distance and barriers to dispersal, rather than of adaptive radiations into new niches. The Mariana studies provided the first incontestable evidence for faunal interchange and for barriers or filters to dispersal of species between Pacific back-arc basins and the mid-ocean ridge system (HESSLER & LONSDALE 1988). They also provided compelling evidence for the potential for discovery of unanticipated taxa (in this case, the hairy gastropods) as new geographic regions are explored.

Subsequent explorations of other southwestern Pacific back-arc systems [Manus (AUZENDE et al. 1997; HASHIMOTO et al. 1999); North Fiji and Lau Basins (HASHIMOTO et al. 1989; DESBRUYÈRES et al. 1994); New Ireland Basin (HERZIG et al. 1994)] demonstrated that some species have restricted distributions while other species, such as provannid gastropods, are shared among basins. Molecular techniques have now distinguished four species of alviniconchid snails: *Alviniconcha hessleri* at Mariana vents, two *Alviniconcha* species in the Manus and North Fiji Basins, and a fourth *Alviniconcha* species at Indian Ocean vents (KOJIMA et al. 2003; OKUTANI et al. 2004). In contrast to the basin-scale differentiation of alviniconchid gastropods in the southwestern Pacific, *Ifremeria nautilei* (synonymous with *Olgaconcha tufari*) so far is only known to inhabit vent sites in the Manus, North Fiji, and Lau Basin region (DESBRUYÈRES et al. 1994; HASHIMOTO et al. 1999). The relatively narrow distributional range of *Ifremeria nautilei* might be attributed its lower dispersal ability compared to that of *Alviniconcha* species (KOJIMA et al. 2000, 2001). *Ifremeria nautilei* is also the only known gastropod that supports dual symbioses, with methane- and sulfur-oxidizing bacteria in gill bacteriocytes (GAL'CHENKO et al. 1992).

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Japanese biological explorations of deep-sea hydrothermal systems in the northwestern Pacific began in 1988 with the discovery of active hydrothermal vents at Izena Hole (Okinawa Trough; TANAKA et al. 1990) by scientists using Shinkai 2000. Subsequent work discovered venting in yet another setting on the arc volcanos of the Izu-Bonin seamount chain south of Japan (KOJIMA 2002). Recent exploration of the Mariana Arc reveals variability in venting conditions and associated communities (EMBLEY et al. 2004). Together, the southwestern and northwestern Pacific hydrothermal fields represent a fertile region for the study of population genetics and the biogeography and evolution of vent taxa (DESBRUYÈRES et al. 2006).

Discovery of Seeps and Other Chemosynthetic Settings

The 1980s included other milestones: Seep communities discovered first in 1984 at the base of the Florida Escarpment in the Gulf of Mexico (PAULL et al. 1984; HECKER 1985) and in Sagami Bay (OKUTANI & EGAWA 1985; HASHIMOTO et al. 1989), and then in association with subduction zone settings off Oregon (SUESS et al. 1985), in the northwestern Pacific (LAUBIER et al. 1986; OHTA & LAUBIER 1987), and off Barbados (FAUGERES et al. 1987), taught us that vent-like taxa and trophically complex, chemosynthetically based ecosystems are not restricted to hydrothermal settings. Discovery of chemosynthetic ecosystems and of vent- and seep-like taxa associated with whale skeletons on the seafloor (SMITH et al. 1989; reviewed in SMITH & BACO 2003) underscored the need to adopt a broad view of chemosynthetic faunas. Vent taxa were also discovered in diverse volcanic and hydrothermal settings, including alvinocarid shrimp at a mid-plate, hot-spot volcano (Loihi seamount; KARL et al. 1989; WILLIAMS & DOBBS 1995), alvinellids, mussels, crabs, and alvinocarid shrimp at Pito Seamount (NAAR et al. 2004), and relatively shallow (489 m) populations of vesicomyid clams at Piips volcano (SELIVERSTOV et al. 1986; SAGALEVITCH et al. 1992). Thus we learn that vent and vent-like taxa and trophically complex, chemosynthetically based ecosystems are not restricted to mid-ocean ridge hydrothermal settings, and that an understanding of the evolution and biogeography of vent taxa can only be understood in the broader context of the evolution and biogeography of allied taxa at other reducing environments (SIBUET & OLU 1998; VAN DOVER et al. 2002; TUNNICLIFFE et al. 2003a).

Other shallow hydrothermal settings were found to lack endemic invertebrate species and do not support invertebrates with endosymbiotic chemoautotrophic bacteria [e.g., subtidal vents off the coast of Southern California (KLEINSCHMIDT & TSCHAUDER 1985); vents of the volcanic arc in the Mediterranean (reviewed in DANDO et al. 1999); vents on the Kolbeinsy (Olafsson et al. 1989) and Jan Mayen ridges (FRICKE et al. 1989) north of Iceland; vents in the crater of Ushishir volcano of the Kamchatka region (TARASOV et al. 1990, TARASOV 2006)].

Hydrothermal vents also occur in fresh-water lakes. Fresh-water hydrothermal systems, similar to those in the ocean, are related either to rift zones, like lakes Baikal (CRANE et al. 1991) and Tanganyika (TIERCELIN et al. 1993), or volcanic activity in subduction zones, e.g. Crater Lake in Oregon (Anonymous 1989). No examples of fresh-water, vent-specific metazoa are known. Bacterial mats are common at all known fresh-water vents. Mineral structures analogous to Black smoker chimneys, reaching up to 10 m in height, can also develop (e.g., in Crater Lake). The Russian-operated Pisces submersible studies in Lake Baikal documented aggregations of non-vent fauna in association with bacterial mats; carbon derived from bacterial methane oxidation is incorporated into local food web of the benthic fauna (GEBRUK et al. 1993).

Eruptions and the Hydrothermal Cycle

1991 was the year of the eruption at 9°50'N on the East Pacific Rise (HAYMON et al. 1993) and the beginning of a long-term study of hydrothermal cycles in this region (SHANK et al. 1998). The bloom of bacteria that marked the commencement of the cycle (NELSON et al. 1991; HAYMON et al. 1993) and other biological indications of recent volcanic activity were subsequently observed at other locales, including the NE Pacific Ridges (e.g., TUNNICLIFFE et al. 1997; JUNIPER et al. 1998) and at 17°S on the East Pacific Rise (EMBLEY et al. 1998). Repeated visits to developing vent communities documented the rapidity with which colonization of new sites of venting takes place (e.g., well-established colonies of tubeworms within one year; TUNNICLIFFE et al. 1997; SHANK et al. 1998) and confirmed earlier reports of rapid growth rates in vent species (LUTZ et al. 1994). Careful re-sampling of evolving vents allows insights into trophic strategies and the role of biological interactions such as competition (LEVESQUE et al. 2003).

The 9°50N vent field became a favored field site for ecological studies for several reasons: (1) the eruption took place there, (2) its relatively simple topography has been thoroughly mapped, (3) its vents support a variety of foundation species with different habitat preferences (e.g., tubeworm clumps, mussel beds, alvinellid galleries, serpulid and anemone fields), (4) there is a long record of contemporaneous and complementary geological and geochemical studies, and (5) the transit time from major ports in Mexico is relatively short. The 15+ years of research at 9°50'N since the eruption have resulted in important new insights into successional sequences (SHANK et al. 1998), physiological adaptations to the vent environment (e.g., GOFFREDI et al. 1997; SHILLITO et al. 2001), reproductive attributes of vent invertebrates (e.g., MARSH et al. 2000; PRADILLON et al. 2001), biological interactions among species (e.g., MULLINEAUX et al. 2000; MICHELI et al. 2002; MULLINEAUX et al. 2003), animal-chemical relationships (e.g., LUTHER et al. 2001; LE BRIS et al. 2006), population genetics (reviewed in VRIJENHOEK 1997), and community structure (e.g., VAN DOVER 2003; GOVENAR et al. 2004).

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One of the longest records of time-series studies at vents is that for 13°N on the East Pacific Rise, where French and American scientists have made intermittent observations since 1982 (reviewed by DESBRUYÈRES 1995). At this site, a previously "dead" vent area with relic populations resumed activity in 1987, and followed the successional pattern described for 9°N by SHANK et al. (1998). The presumption is that there was a subsurface dyking event (i.e., an upward migration of molten rock through a fissure, but without overflow onto the seabed) in 1987 that delivered heat to the system and restored the hydrothermal circulation at this site.

More Atlantic Discoveries

Attention returned to the Mid-Atlantic Ridge in 1992 with the chance collection of vent animals in a rock-dredge haul, and in 1993 during dives at the site that came to be known as Lucky Strike at 37°N (VAN DOVER et al. 1996; LANGMUIR et al. 1997). Although Lucky Strike shares a few species with the TAG and Snake Pit vent sites, most species at Lucky Strike were new to science. This site and the nearby Menez Gwen vents explored in 1993 (FOUQUET et al. 1995; DESBRUYÈRES et al. 2001) appear to belong to a biogeographic province different from that of the more southerly TAG and Snake Pit faunas. Variables associated with the depth differential between the two provinces (<1700 m at Lucky Strike and Menez Gwen vs. >3000 m at TAG, Snake Pit) have been implicated in the biogeographic differentiation of the two vent faunas (VAN DOVER et al. 1996; DESBRUYÈRES et al. 2000, 2001).

Continuing geological and geochemical exploration for hydrothermal activity on the Mid-Atlantic Ridge between the Vema transform fault at 11°N and the Azores hotspot (38°N) resulted in the first submersible dives to hydrothermal sites at Logatchev in 1993 (BOGDANOV et al. 1995; GEBRUK et al. 2000), Broken Spur in 1993 (MURTON et al. 1995), and Rainbow in 1997 (FOUQUET et al. 1997). The Logatchev site at 14°45'N was the first vent discovery where the host rock was ultramafic (i.e., of mantle rather than crustal origin; BOGDANOV et al. 1997; FOUQUET et al. 2006). Logatchev represents the current southern limit of published information on vent faunas along the Mid-Atlantic Ridge, although a new active vent field known as Ashadze at 12°38'N has been reported (BELTENEV et al. 2004), as have vent fields south of the equator (C. German, pers. comm). Logatchev is notable as the only known site on the Mid-Atlantic Ridge that supports large populations of vesicomyid clams; in other aspects, it has a species list similar to that found at Snake Pit (e.g., TURNIPSEED et al. 2004). Broken Spur (29°10'N) is a hybrid zone for mussels, where two species of mussels (*Bathymodiolus puteoserpentis*, dominant at southern locales, and *B. azoricus*, known from the northern vent sites) co-occur and inter-breed (WON et al. 2003a). Rainbow (FOUQUET et al. 1997), Saldanha (BARRIGA et al. 1998), and Lost City (KELLEY et al. 2001) vent fields, like Logatchev, are hosted by ultramafic rocks. Their megafaunal and macrofaunal communities are generally meager [except for dense shrimp *Rimicaris exoculata* populations at Rainbow], possibly due to the distinctive fluid chemistries associated with these sites (KELLEY et al. 2001).

The Indian Ocean

By 2000, a basic understanding of vent faunas of the northern Mid-Atlantic Ridge, the East Pacific Rise, the Northeast Pacific, and back-arc basins in the western Pacific was established. One of the biggest missing pieces of the biogeographic jigsaw puzzle was the ridge system in the Indian Ocean. Cyana dives in the Gulf of Aden in 1984 (1400-1600 m) had documented low-temperature flow dominated by shrimp, anemones, and galatheid squat lobsters, but specimens were not collected (JUNIPER et al. 1990). Japanese scientists brought attention to the Indian Ocean in 2000, using the ROV Kaiko to explore the Kairei hydrothermal field on the Central Indian Ridge, just north of the Rodriguez Triple Junction (HASHIMOTO et al. 2001). Shrimp closely related to *Rimicaris exoculata* of Atlantic vents dominate the biomass of the Kairei field so that the site resembles TAG and Snake Pit, but other taxa, including hairy gastropods and mussels, are more closely allied with Pacific vent faunas. These observations supported the hypothesis that the Indian Ocean ridges serve as a link between Atlantic and Pacific vent faunas (HASHIMOTO et al. 2001). Further explorations of the Kairei Field (VAN DOVER et al. 2001) led to the discovery of a remarkable scaly-footed gastropod with no close alliance to any known Pacific or Atlantic vent genera (Waren et al. 2003). Unlike other mollusks at vents that house autotrophic endosymbionts in epithelial bacteriocytes of their gills, the scaly-footed gastropod hosts its symbionts in a hypertrophied esophageal gland (GOFFREDI et al. 2004).

Fossil Records

The first accounts of fossil vent invertebrates comes from studies of Cretaceous Oman and Cyprus ophiolites that yielded well-preserved tubes of worms, including what might be a vestimentiferan (HAYMON et al. 1984; OUDIN & CONSTANTINOU 1984; HAYMON & KOSKI 1985). Invertebrates have occupied vents (KUZNETSOV 1993; LITTLE et al. 1997) and seeps (BARBIERI et al. 2004) at least since the Silurian, but the ancient (older than the early Cretaceous) assemblages described so far were dominated by now-extinct families of brachiopods, monoplacophorans, bivalves, and gastropods (reviewed in CAMPBELL 2006). There is little evidence to support the view that vents (or seeps) have served as a refuge during global extinction events for most taxa (reviewed in WARÉN & BOUCHET 2001; LITTLE & VRIJENHOEK 2003), although there may be exceptions (YAMAGUCHI et al. 2004). As in extant chemosynthetic communities, fossil records include indications of successional responses to changing conditions at a given site (CAMPBELL et al. 2002), and paleobiogeographic patterns that are likely to reflect past plate tectonic configurations (CAMPBELL 2006).

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Prospects for Exploration and Discovery

There remain a number of oceanic regions where we can anticipate discovery of entire communities of new species at hydrothermal vents (VAN DOVER et al. 2002; TYLER et al. 2003). Of these, the Arctic Ocean has long been of great interest: its relative youth and degree of bathymetric isolation from the rest of the deep waters of the world's oceans suggest that the vent fauna of the region might provide insight into the invasibility of vent environments by metazoans. Hydrothermal vents on the Gakkel Ridge in the Arctic Ocean have been localized (EDMONDS et al. 2003), but their faunas remain to be photo-documented and sampled. Shells of vesicomyid clams (*Archivesica* sp.), indicative of reducing environments, occur in dredge samples from depths of ~2000 m near the Gakkel Ridge and seem likely to have been associated with a hydrothermal site when the animals were alive (SIRENKO et al. 1995).

Other sites of considerable biogeographic and taxonomic interest are isolated ridge systems, such as the Scotia Ridge in the southwest Atlantic, the Cayman Rise in the Caribbean, and the Andaman back-arc ridge in the northeast Indian Ocean. Even on the mid-ocean ridge system, there remain large stretches of unexplored ridge axis. One of the most compelling ridge segments is the Mid-Atlantic Ridge north of the Azores – here the ridge axis dives from shallowest depths back down to more than 2500 m – has the Azores hot spot served as a faunal break to north and south? The deep, greatly offset fracture zones of the Mid-Atlantic Ridge north of the Azores and south of the equator (i.e., south of the Romanche Fracture Zone) beg for studies of gene flow and the role of these fracture zones as barriers or filters to species dispersal. The Chile Rise in the southeast Pacific and the Antarctic ridges are also certain to be of interest in comparative studies of taxonomy, diversity, and gene flow. Phylogeographic studies of the vent fauna of the triple ridge system of the Indian Ocean, in comparison to faunas of the Atlantic and western Pacific, should allow us to determine the direction of dispersal of species between the Atlantic and Pacific.

Even within extremely well-explored vent fields, the potential for discovery of previously unknown adaptations exists, as in the recent documentation of a blood-sucking polychaete (*Galapagomystides aristata*; JENKINS et al. 2002) that had been described from some of the earliest collections at the Galapagos Spreading Center (BLAKE 1985). Little is known of the biology of most vent species. There is great potential in careful studies of populations, life history traits and behavior of individual species to learn more of the range of adaptations present in these unusual habitats. Investigation of relationships of biomass-dominant metazoans to microbial communities and chemical settings will yield better insight into the complex processes that control vent community structure and function (TUNNICLIFFE et al. 2003b).

The ChEss program (a component of the Census of Marine Life) was conceived to promote international efforts to improve our understanding of the identity and biogeography of the fauna of these reducing environments (TYLER et al. 2003). ChEss also promotes tests of hypotheses regarding potential barriers and filters to dispersal of species whose adults are restricted to these environments. Through ChEss and other ocean exploration activities, we look forward to the next decade of discovery that will undoubtedly add many new species, genera, and families to the compendium of taxa so carefully compiled here.

Acknowledgements

We thank our many shipboard colleagues – Captains, pilots, ships' crews, scientists, technicians, and students – who have contributed to the discovery of deep-sea hot springs and of the strange animals that live at them. There are too many individuals to cite by name; we honor their efforts with images of some of the many vehicles that have given us such remarkable access to the seafloor (Fig. 1, 2).

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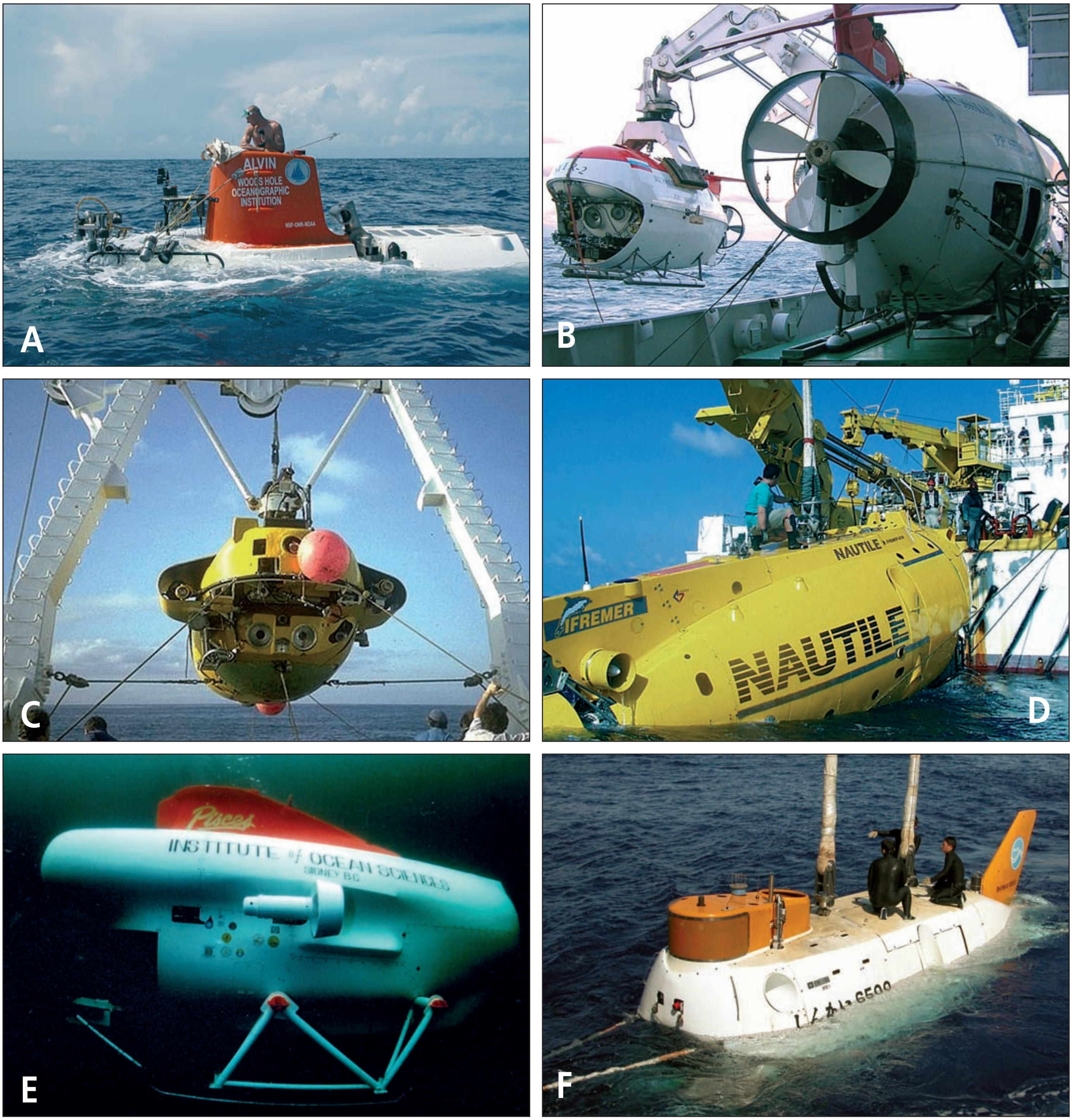

Fig. 1: Human-occupied vehicles (and maximum depth rating) in which many of the observations reported here were made. A: Alvin (4500 m), operated by the Woods Hole Oceanographic Institution, U.S.A.; B: Mir I and Mir II (6000 m), operated by the Shirshov Institute, Russia (by courtesy of Prof. A.M. Sagalevitch); C: Cyana (3000 m), operated by Ifremer, France; D: Nautile (6000 m), operated by Ifremer, France; E: Pisces IV (2000 m), formerly operated by the Department of Fisheries and Oceans, Canada, currently operated by the Hawaii Undersea Research Laboratory, U.S.A.; F: Shinkai 6500 (6500 m), operated by JAMSTEC, Japan.

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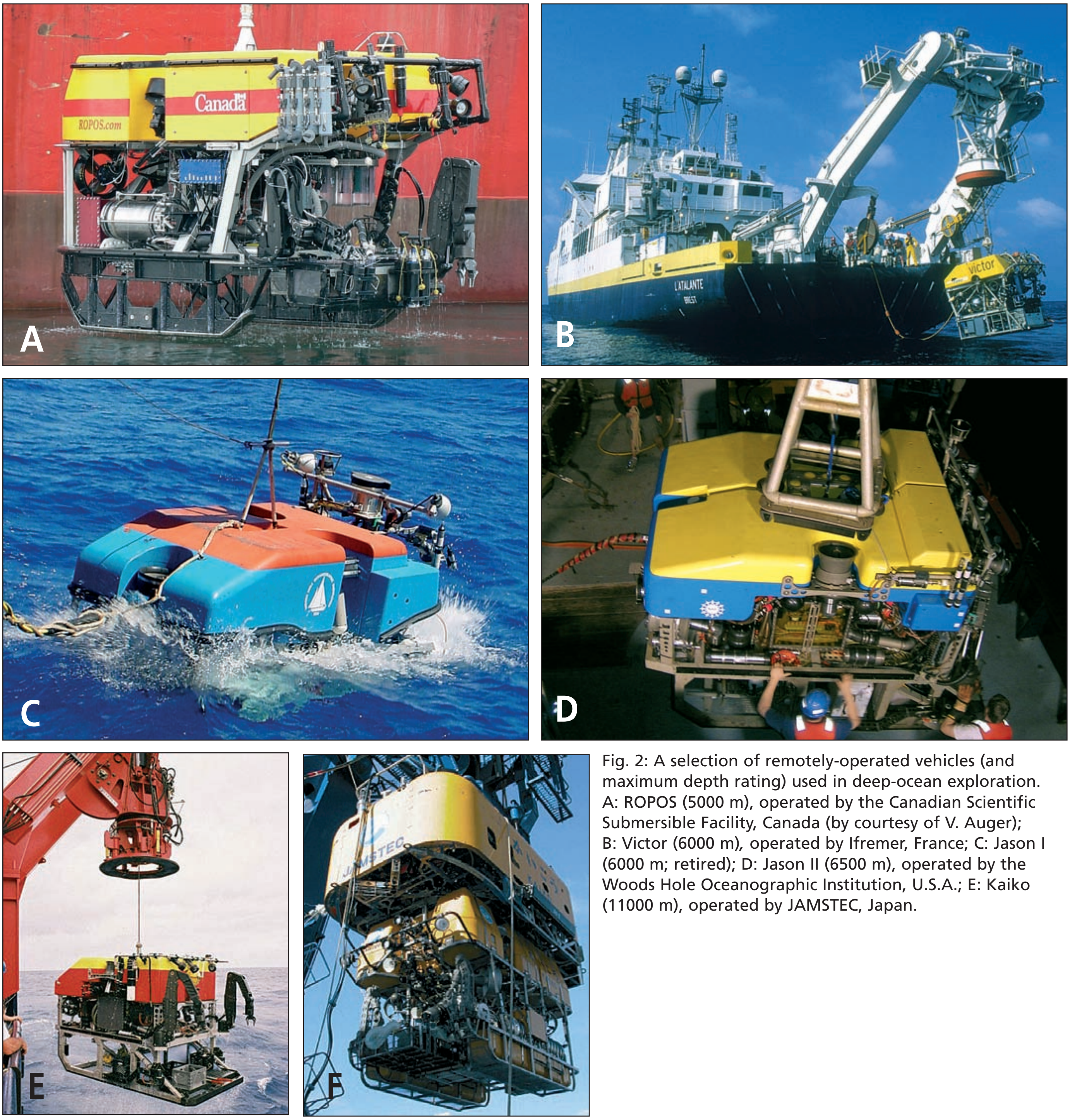

Fig. 2: A selection of remotely-operated vehicles (and maximum depth rating) used in deep-ocean exploration. A: ROPOS (5000 m), operated by the Canadian Scientific Submersible Facility, Canada (by courtesy of V. Auger); B: Victor (6000 m), operated by Ifremer, France; C: Jason I (6000 m; retired); D: Jason II (6500 m), operated by the Woods Hole Oceanographic Institution, U.S.A.; E: Kaiko (11000 m), operated by JAMSTEC, Japan.

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Zeitschrift/Journal: Denisia

Jahr/Year: 2006

Band/Volume: 0018

Autor(en)/Author(s): Bright Monika

Artikel/Article: Milestones in the discovery of hydrothermal-vent faunas 13-25