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Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: Past developments and future research directions

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Abstract

Hydrocarbon seeps and hydrothermal vents are now known to be common at continental margins and oceanic spreading centers worldwide, exuding fluids rich in CH_4 and H_2S, and teeming with life based on chemosynthesis. These settings have been implicated as the crucibles for life's origin, and as locales for methane release to the atmosphere from hydrate destabilization during past climate change. Ancient vent and seep deposits are also increasingly recognized, and occur in various sizes, lithologies, biotic compositions, geotectonic settings and ages. Precambrian vents were populated with microbes, with the oldest metazoans in vent settings reported from possibly the Cambrian, but definitely by the Silurian. The oldest purported seep deposit with metazoan fossils is Silurian in age. A largely endemic and chemosymbiotic biota from modern vents and seeps appears distinct phylogenetically from those taxa in deposits older than Jurassic, with a shift from extant families of particular bivalves and gastropods to now-extinct family groups of brachiopods, monoplacophorans, bivalves and gastropods. An exception may be worm tubes of possible vestimentiferan origins, with a history in hydrothermal vent paleoenvironments extending back to the Early Paleozoic. Unfortunately their relatively simple morphology and particular style of preservation make comparisons with living groups a challenge. There may also be an ancient "lineage" of vent–seep restricted rhynchonellide brachiopods, which appears to have persisted in these settings from the Late Devonian through the Early Cretaceous. Because biotic components have changed in vent–seep settings through time, several lines of evidence must be marshaled to confirm the origin of suspected deposits in the geologic record. These include distinctive stable isotopic signatures of carbon, oxygen or sulfur in authigenic precipitates and/or tests of foraminiferans, certain mineral paragenetic sequences, and fluid-flow features. Lipid biomarkers also indicate biogeochemical cycling by Archaea and Bacteria, which performed sulfate-dependent, anaerobic oxidation of methane in ancient marine sediments.

The origin of an endemic modern vent–seep biota has been attributed to either enhanced accumulation of Paleozoic and Mesozoic relics, or migration of various invertebrate groups into vent and seep environments during the Phanerozoic. Current databases from fossils and molecular characterization of living groups suggest that adaptive radiations and extinctions have occurred, with a range of lineage-ages represented. Fossil and molecular data broadly coincide with respect to the Cretaceous origination of vesicomyid bivalves and neomphaline gastropods in vents and seeps, but the data sets appear discordant at

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present for vestimentiferan tubeworms and bathymodiolin bivalves. Paleobiogeographic patterns are just beginning to emerge from studies of vent and seep fossils, and are likely to reflect past plate tectonic configurations, sea-level change, as well as the history of organic matter accumulation, burial, hydrocarbon generation, and fluid migration with time. Thus far, ancient hydrocarbon seep deposits yield more diverse fossils than hydrothermal vent deposits, the opposite of the global diversity recently tabulated for modern vent–seep species. However, in the fossil record, taphonomic processes negatively impacted on ancient vent organisms, and the number of known ancient vent systems is still relatively small compared to regional occurrences of ancient seep deposits. Future research will likely investigate many new/suspected sites, inventory numerous additional taxa, decipher underlying causes of variability among settings, and mobilize biologists and geologists to work together to solve problems that cross both disciplines.

Keywords: Hydrocarbon seep; Hydrothermal vent; Chemosynthesis; Evolution; Paleoenvironments; Paleoecology

1. Introduction

Since communities based on chemosynthetic carbon-fixation were first discovered more than two decades ago at seafloor hydrothermal vents (Lonsdale, 1977; Corliss et al., 1979) and cold hydrocarbon seeps (Paull et al., 1984), further exploration of the deep-sea has revealed numerous modern vent–seep sites that sustain luxuriant populations of metazoans and microbes, in different geotectonic settings (Fig. 1). Today, hydrothermal vents and hydrocarbon seeps are known from the tropics to the poles, in shallow shelf to hadal depths (e.g., Miura et al., 1997; Bohrmann et al., 1999, 2002; Fujikura et al., 1999; Van Dover et al., 2001; Edmonds et al., 2003). “Classic” deposits formed at hydrothermal vents include the igneous rock-hosted, black smoker, volcanic massive sulfide (VMS) deposits. “Classic” hydrocarbon seeps comprise ^{13}C-depleted authigenic carbonates, commonly with cemented shelly biota, forming at or near the seafloor. Other types of fluid emissions in marine settings include sediment-hosted exhalative deposits (SEDEX, white smokers), filamentous ironstone pods in cherts, and barite-dominated seeps, to name a few. Today, vents and seeps are situated along plate boundaries (mid-oceanic ridges, subduction zones), in back-arc basins, and where faulting, diapirism, sediment compaction, or undersea landslides tap organic-rich porewaters (e.g., Van Dover, 2000; Kelley et al., 2001; Fujioka et al., 2002). Vent-type taxa also are found where reduced compounds seep from dead whale falls (Smith and Baco, 2003), attached to sunken wood (Distel et al., 2002), in reduced sediments (Van Dover, 2000), and in the rotting organic cargo of a shipwreck (Dando et al., 1992). Hence, chemosynthesis is now known to be widespread in the world’s oceans.

At the base of the chemosynthetic food chain, free-living and symbiotic prokaryotes oxidize the methane- and/or sulfide-rich fluids of vents and seeps to produce biomass utilized by the visually spectacular mega-invertebrates, many of which are chemosymbiotic (Fig. 2; Van Dover, 2000). Ecological distribution patterns at vent and seep sites are controlled by fluid flux rates and the availability of reduced chemical species in the water column or sedimentary pore waters (e.g., Van Dover, 2000; Sahling et al., 2002; Treude et al., 2003). Endemism of vent–seep species is high, with new families, orders and classes identified, and over 400 species named in the past two decades (Tunnicliffe, 1991, 1992; Tunnicliffe et al., 1998).

Recent developments in modern vent–seep research are myriad. Detailed site analyses at seeps and gas hydrate localities, for example, have verified the importance of sulfate-dependent, anaerobic oxidation of methane (AOM) in authigenic carbonate formation, and have revealed the microorganisms responsible for this major biogeochemical process (e.g., Elvert et al., 1999; Hinrichs et al., 1999; Thiel et al., 1999; Aharon, 2000; Boetius et al., 2000; Valentine, 2002; Treude et al., 2003). Furthermore, revelations pointing to the existence of a vast, virtually unexplored microbial biosphere (hot/cold, seafloor/subsurface) have opened up consideration of microbial worlds on other planets, and expanded views on the distribution and tolerances of life on Earth, including conditions at the time of its origin

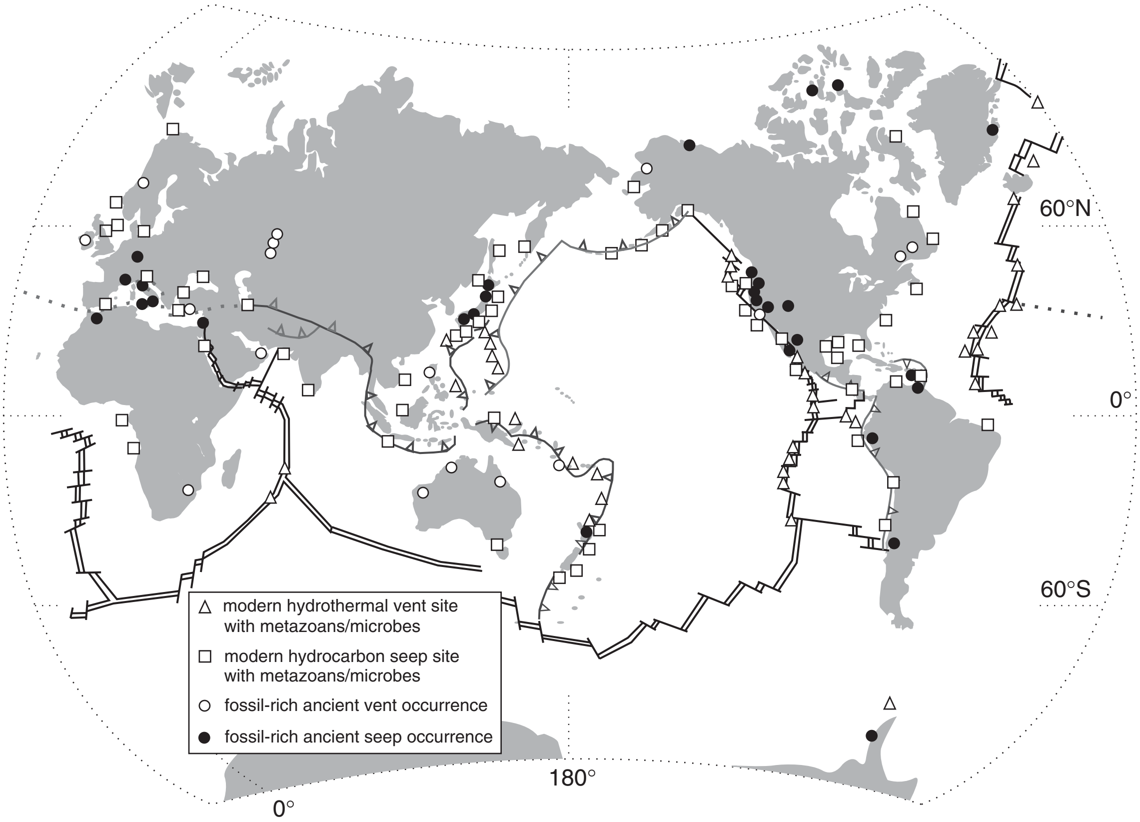

Fig. 1. Distribution map of chemosynthesis-based settings, illustrating those Archean to Recent hydrothermal vents and hydrocarbon seeps with associated metazoan and/or microbial signatures. Modern vent distributions are from Fricke et al. (1989), Kamenev et al. (1993), Van Dover (2000), Kelley et al., 2002, Kojima (2002), von Cosel and Marshall (2003), and Kojima et al. (2004). Modern seep locations were compiled from Hovland and Judd (1988), Hovland et al. (1987), Dando et al. (1991), Corselli and Basso (1996), Sibuet and Olu (1998), Greinert et al. (2000), Coleman and Ballard (2001), Bohrmann et al. (2002, 2003), Judd et al. (2002c), Kojima (2002), Kojima et al. (2002, 2004), Sahling et al. (2002), Salas and Woodside (2002), Stakes et al. (1999), Wiedicke et al. (2002), Hovland and Risk (2003), Han et al. (2004), MacDonald et al. (2004), Sassen et al. (2004), and Sellanes et al. (2004), Levin (in press). Ancient hydrothermal vent deposit locations are from Noll et al. (1984), Banks (1985), Moore et al. (1986), Duhig et al. (1992a), Little et al. (1998, 1999b), Rasmussen (2000), and Playford and Wallace (2001). Ancient hydrocarbon seep occurrences are from Druckman et al. (1994), Taviani (2001), Burhan et al. (2002), Campbell et al. (2002), Amano (2003), Goedert et al. (2003a, b), Gómez-Pérez (2003), Hikida et al. (2003), Kitazaki and Majima (2003), Majima et al. (2003, in press), Nobuhara (2003), Torres et al. (2003), and Barbieri et al. (2004).

(e.g., Gold, 1992; Nisbet and Fowler, 1996; Komatsu and Ori, 2000; Van Dover, 2000; Fujioka et al., 2002; Kelley et al., 2002; Reyensbach and Shock, 2002; Marion et al., 2003; Shapiro, 2004). Moreover, periodic, catastrophic release of stored methane in gas hydrates has been implicated in past, abrupt climate change scenarios (Dickens et al., 1995; Kennett et al., 2000). In addition, hydrothermal vents and hydrocarbon seeps are necessary components of climate models, because cycling of methane-derived carbon from the lithosphere to the hydrosphere and atmosphere includes emissions from the 75,000 km-long oceanic ridge system, and from seepages or gas hydrates released around the world's continental margins (e.g., Hovland and Judd, 1988; Judd et al., 2002a).

In addition to the advances made from studies of modern vent–seep settings, a multitude of ancient occurrences with metazoan fossils and/or microbial fabrics also have been recognized in the geologic record. They are now known from at least 59 regional groupings of Early Archean to Pleistocene age ore deposits and marine sedimentary sequences world-

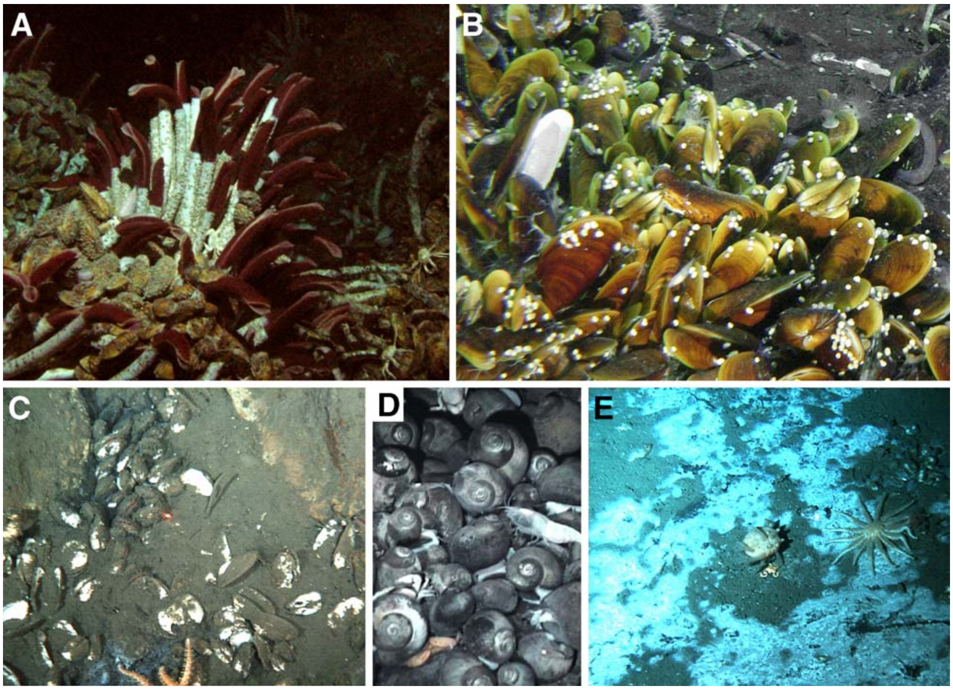

Fig. 2. Examples of typical biota from modern hydrothermal vents and hydrocarbon seeps, showing some of the groups generally represented at ancient vent–seep deposits, especially those of the Cenozoic and Mesozoic. (A) Tubeworm (*Riftia pachyptila*) and *Bathymodiolus thermophilus* mussel cluster at East Wall hydrothermal vent, East Pacific Rise. Photograph courtesy of C.L. Van Dover. (B) *Bathymodiolus heckerae* mussels at Florida Escarpment hydrocarbon seep. Photograph courtesy of I.R. MacDonald. (C) Vesicomyid clams at hydrocarbon seep offshore Eel River, California. Photograph courtesy of L.A. Levin. (D) *Alvinoconcha* gastropods at Indian Ocean hydrothermal vent. Photograph courtesy of C.L.Van Dover. (E) White bacterial mats at hydrocarbon seep offshore Eel River, California. Photograph courtesy of L.A. Levin.

wide (Fig. 1; Table 1). Not surprisingly, microbes were the dominant organisms in older purported hydrothermal vent deposits, such as from Australia's 3.25 Ga Pilbara craton (Rasmussen, 2000), and Ordovician Mount Windsor volcanic belt (Duhig et al., 1992a,b; Davison et al., 2001). Microbial fabrics and brachiopods also occur in the oldest purported hydrocarbon seep deposit (Silurian El Borj deposit, Morocco; Barbieri et al., 2004). Furthermore, mega-invertebrates have occupied seafloor hydrothermal vents since at least the Silurian (Little et al., 1997, 1999a; Little, 2002).

Ancient vent–seep paleoenvironments and fossils are important for several reasons. Their ubiquitous presence in the geologic record confirms that these chemosynthesis-based paleoenvironments have been diverse and variable, both in terms of geologic settings and taxonomic compositions, through more than 3 billion years of Earth's history. Consequently fluids circulating within the crust have influenced organism distributions and evolution for at least that same amount of time. In addition, the taxonomy and systematics of fossils in chemosynthesis-based settings provide ground-truth for evolutionary hypotheses on the origin(s) of the modern vent–seep fauna (cf. Little and Vrijenhoek, 2003). Paleobiogeographic data also help explain current distribution patterns of vent–seep taxa worldwide, driven largely by past plate tectonic configurations, sea-level change, and by the location, burial and exhumation history of sedimentary organic matter through time, including oceanic anoxia episodes. Finally, ancient vents and seeps reveal a window on the evolution of organisms living in extreme environments — despite broadly similar geochemical conditions compared to today, vent–seep community components have changed through geologic time.

This paper reviews the character and evolution of vent–seep settings and fossils since the Precambrian. Hydrothermal vent and hydrocarbon seep paleoenvironments are defined, and criteria for their recognition

Table 1
Global data set of 59 regional groupings of ancient hydrothermal vent (shaded) and hydrocarbon seep occurrences (13 versus 46, respectively) — comprising onshore, Archean to Pleistocene age deposits that contain microbial or metazoan fossils, as reported from the literature

Location	Geotectonic/ stratigraphic context	Age	Deposit type, geometry	Fossil content	Inferred Paleo-depth/ setting	References
Be'eri sulfur mine, Israel	Coastal plain eolian, fluvial & paludal deposits	Upper Pleistocene (~30 kyr), Kurkar Group	Black sandstone with sulfur-rich horizon (to ~3 m thick)	Microbial mats with ^{13}C-depleted hopanoids, biphytane derivatives; extreme ^{13}C-depleted OM from AOM; H_2S from bacterial reduction of deep Messinian sulfates, migrated upward with CH_4, oxidized to S^0	Phreatic fresh to brackish, ~15 m below surface	Druckman et al., 1994; Burhan et al., 2002
Kimitsu City, Chiba Prefecture, Boso Peninsula, central Japan	Convergent/ forearc	Middle Pleistocene, Kakinokidai Fm., Kazusa Group	Cemented burrows/ shells+pipe-like concretions; micrite, acicular calcite	*Conchocele disjuncta, Lucinoma aokii, Acharax tokunagai, Yoldia similis, Portlandia lischkei, Limopsis tokaiensis, Neptunea kuroshio, Habevolutopsius hirasei, Fulgoraria prevostiana, Dentalium yokoyamai, Modiolus, Acila divaricata, Euspira pila*	Outer shelf, 100–150 m	Shibasaki & Majima, 1997; locality 73 in Majima et al., in press
Yokohama City, Kanagawa Prefecture, central Japan	Convergent/ forearc	Lower Pleistocene, Koshiba Fm., Kazusa Group	Micrite concretions, cemented breccia ("pockmark")	*Lucinoma, Conchocele bisecta, Acharax* cf. *tokunagai, Acila divaricata, Limopsis tokaiensis, Portlandia lischkei, Yoldia naganumana, Rosselia* isp.	Outer shelf, 100–200 m	Majima et al., 1996; Kitazaki & Majima, 2003; locality 71 in Majima et al., in press
Miura Peninsula, Kanagawa Prefecture, central Japan	Convergent/ Honshu Arc– Izu–Ogasawara Arc collision	Upper Pliocene Ikego, Urago & Nojima Fms.; & Miocene Misaki, Ochiai & Jike Fms.	Deep-sea fan tuffaceous sandstone & siltstone; faults, slump blocks, breccia & conglomerate	*Calyptogena nipponica, C.* cf. *kawamurai,* scattered to dense (90–130 individuals/m^2), *Venus, Conchocele bisecta, C. disjuncta, Acharax tokunagai, A. yokosukensis, Ennucula, Yoldia, Lucinoma spectabilis, L. annulata, Adulomya azarie, Bathymodiolus?, Thracidoragigantea, Thracia kakumana, Lunatica, Calliostoma, Neptunea, Buccinum,* worm tubes	Lower–upper bathyal	Niitsuma et al., 1989; Kanie et al., 1992a,b, 1995; Naganuma et al., 1995; Watanabe & Karamochi, 1995; Kanie, 1996; localities 26, 33, 40, 42, 52-62 in Majima et al., in press
Kuge Shrine, Shintomi, Miyazaki Prefecture, Kyushu Is., SE Japan	Convergent/ forearc	Upper Pliocene, Takanabe Fm.	Carbonate concretions in muddy tuffaceous sandstone	*Lucinoma, Glycymeris, Natica, Modiolus, Nemocardium,* Brachiopoda, *Turcica, Xenophora, Paphia, Venericardia*	Outer shelf, 50–150 m	Majima et al., 2003; locality 68 in Majima et al., in press
Quinault coast, Washington, USA	Convergent/ Cascadia forearc	Pliocene, Quinault Fm.	Micrite as burrow/shell–fill & blebs in sandy siltstone	*Acharax ventricosa, Lucinoma annulata, Modiolus modiolus, Yoldia*	Mid-shelf	Campbell, 1992; Campbell & Nesbitt, 2004; Nesbitt & Campbell, 2004a,b

Sagara–Kakegawa, Shizuoka Prefecture, central Honshu, Japan	Convergent/ forearc	Pliocene, Tamari, Horinouchi & Hijikata Fms.; Miocene, Setogawa Group	Lenticular to barrel–shaped carbonate concretions in siltstone	*Vesicomya (Calyptogena) kawamurai, Lucinoma* aff. *aculineata, Conchocele bisecta, Acharax johnsonii, Thyasira nakazawai, Saxolucina (Magaxinus) matsushitai, Bathymodiolus?,* patellogastropod	Upper-middle slope, 300–1000 m	Nobuhara, 2003; localities 18, 19, 65–67, 69, 70 in Majima et al., in press
Chiba Prefecture, central Honshu, Japan	Convergent/ forearc	Pliocene Naarai, Shiramazu & Kurotakai Fms.; Lower Miocene Aokiyama Fm.	Tuffaceous sandstone & mass movement deposits; shells allochthonous	*Calyptogena bosoensis, C.* cf. *nipponica, C. (Ectenagena)* sp., *Vesicomya ellipsoidea, Lucinoma acutilineata, Akebiconcha kawamurai, Conchele disjuncta, Acharax* aff. *tokunagai*	Shelf to slope	Localities 16, 17, 48–51, 63, 64 in Majima et al., in press
Niigata Prefecture, western Honshu, Japan	Convergent/ backarc	Pliocene–Miocene, Nadachi, Kawazume, Nôdani, Nanbayama, Kurokura, Teradomari & Ogaya Fms.	Sandstone and mudstone turbidites with calcareous concretions	*Calyptogena pacifica, C. nipponica, C. (Adulomya)* sp., *Lucinoma acutilineata, Conchocele disjuncta, C. bisecta, Acharax tokunagai, Delectopecten peckhami, Acila insignis, Nuculana onoyamai, N. pernula, Portlandia lischkei, Macoma, Neptunea* cf. *modesta, Limatula*	Shelf to slope	Kanno et al., 1989; localities 29, 35, 38, 39, 41, 43, 45, 46 in Majima et al., in press
Morai, western Hokkaido, north Japan	Convergent/ backarc	Upper Miocene, Morai Fm.	Indurated mudstone with numerous concretions	*Calyptogena pacifica, Lucinoma acutilineata, Conchocele bisecta, Acharax tokunagai, Acilavigilia, A. insignis, Macoma, Fissidentalium* cf. *horikoshii, Euspira pallida, Cryptonatica, Clinopegma* aff. *borealis, Neptunea, Buccinum*	Outer shelf, 120–250 m	Amano, 2003; locality 36 in Majima et al., in press
Northern East Coast Basin, North Island, New Zealand	Convergent/ Hikurangi forearc	Lower to Upper Miocene, "Moonlight Limestone"	Micrite and fibrous aragonite lenses, pipes & nodules in siltstone	*Bathymodiolus, Lucinoma* cf. *taylori, Thyasira* cf. *motutaraensis, Lepetella,* worm tubes, *Xenostrobus* cf. *altijugatus, Modiolus* cf. *areolatus, Diplodonta?, Polinices, Friginatica?, Miltha, Calyptogena, Vesicomya,* venerid, decapods, *Parvamussium,* turrids, buccinids, mitrids, trochids, *Liothyrella?* terebratulid, *Goniocorella?,* thrombolites	?Bathyal	Collins, 1998; Campbell & Francis, 1998; Campbell et al., 1999; unpublished data
Appenines, Italy	Subduction & thrusting – foredeep, episutural, foreland peripheral & interfrontal satellite basins	Lower-Upper Miocene, calcari a *Lucina* limestone	Micrite nodules, doughnuts & breccia, aragonite veins, in siltstone turbidites & olistostromes	*Lucina hoernea, Thalassonerita megastoma Bathymodiolus? exbrocchi,* vesicomyids, solemyids, *Homalopoma domeniconii, Xenophora borsonii, Galeodea delibrata, Neptunea hoernesi subdilatata, Phasianema taurocrassum, Hinia ruggierii,* columbellids?, turrids		Terzi et al., 1994; Conti & Fontana, 1999; Taviani, 1994, 2001; Conti et al., 2004; Peckmann et al., 2004

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Table 1 (*continued*)

Location	Geotectonic/ stratigraphic context	Age	Deposit type, geometry	Fossil content	Inferred Paleo-depth/ setting	References
Monferrato, Marmorito, northwest Italy	Transpressional	Miocene	Micrite cements, veins, fibrous aragonite	Microbial mats (cf. *Beggiatoa*) yielding hopanoids & short-chain n-fatty acids, worm tubes, *Lucina*		Clari et al., 1988, 1994; Cavagna et al., 1999; Peckmann et al., 1999a, 2004;Clari & Martire, 2000
Southwestern Trinidad & northern Venezuela	Convergent foredeep	Miocene, Freeman's Bay Limestone Mbr., Lengua Fm. & Huso Mbr., Pozon Fm.	Calcareous mudstone & asphalt; white limestone	Vesicomyid, thyasirid, solemyid, lucinid, bathymodiolin & nuculanid bivalves, *Cataegis meroglypta*, provannids & trochids	Deep offshore	Van Winkle, 1919; Gill et al., in press
Fukushima Prefecture, SE Honshu, Japan	Convergent/ forearc	Lower Miocene, Honya & Kabeya Fms.	Sandy, pumiceous mudstone	*Adulomya chitanii, Vesicomya kawadai, Lucinoma otukai, L. otsukai, L. acutilineata, Conchocele nipponica, Acharax tokunagai*	Bathyal	Localities 10–13 in Majima et al., in press
North Slope, Alaska, USA	Foreland/ anticline	Miocene or Oligocene, Nuwok Mbr., Sagavanirktok Fm.	Micrite beds & nodules in mudstone, associated glendonites	*Thyasira, Solemya, Calyptogena, Teredo*-bored wood	Shallow shelf	Campbell et al., 2000; unpublished data
Shipwreck Pt., Strait of Juan de Fuca, Washington, USA	Convergent	Lower Oligocene, Makah Fm.	Allochthonous carbonate blocks of micrite, fibrous cement & spar, in siltstone	*Bathymodiolus, Calyptogena chinookensis, Acharax, Anodontia? inflata, Lucinoma hannibali, Nuculana, Macoma?, Vesicomya?, Provanna antiqua, Retiskenea statura, Turrinosyrinx, Margarites (Pupillaria) columbiana, limpet, Solariella?, Aforia*, naticids, marginellids, turrids, schaphandrids, buccinids, *Leptochiton alveolus*, scaphopods, vestimentiferan? worm tubes	?slope olistostrome	Goedert & Campbell, 1995; Squires, 1995; Goedert & Benham, 1999; Kiel, in press
Vernonia-Timber Road, northwest Oregon, USA	Convergent	Lower Oligocene, Keasey Fm.	Carbonate lenses & nodules, chimney, in siltstone	*Conchocele disjuncta, Acharax dalli*, lucinids, anomuran fecal pellets	Deep offshore	Campbell & Bottjer, 1993; Campbell, unpublished data
Knappton, Canyon & Satsop	Convergent	Oligocene, Lincoln Creek Fm.	Micrite nodules, allochthonous	*Calyptogena chinookensis, Bathymodiolus willapaensis,* vestimentiferan? worm tubes,	Deep offshore	Goedert & Squires, 1990, 1993; Squires,

Rivers, southwestern Washington, USA			blocks in siltstone	*Isocrinus?, Vesicomya (Calyptogena), Provanna antiqua, Ennucula, Leptochiton alveolus, Eurete, Aphrocallistes polytretos, Hexactinella? conica, H.? tubula, Farrea?, Acharax, Lucinoma, Natica, Nuculana, Conchocele bisecta, Retiskenea statura, Liracassis, Acteon, Trophonopsis?, Cylichna, Granula?, Pyropelta?, Xanthodaphne?, Niso, Depressigyra?, Homalopoma?, Margarites (Pupillaria) columbiana*, solariellinid, cerithopsid, eulimid?, *Benthomangelia?, Lurifax, Hyalogyrina?, Nuculana?* aff. *grasslei, Ledella, Tindaria?, Catillopecten?, Delectopecten, Flabellum (Ulocyathus), Archohelia ?, Caryophyllia wynoocheensis, Dendrophyllia hannibali, Deltocyathus insperatos*		1995; Squires & Goedert, 1995; Goedert & Benham, 1999; Rigby & Goedert, 1996; Goedert et al., 2000; Peckmann et al., 2002; Goedert & Peckmann, 2005; Kiel, in press
Scotland district, northeast Barbados	Convergent	Eocene-Miocene, diapiric mélange & Sub-Oceanic Fault Zone	Micritic carbonate blocks	*Abyssochrysos, Cataegis meroglypta,* neritids, fissurellids, acmaeids, zygopleurids, trochids, vesicomyids, lucinids, thyasirids, solemyids, nuculanids, vestimentiferan worm tubes	Deep offshore	Gill et al., in press
Barlo, Luzon, Philippines	Supra-subduction zone	Upper Eocene, Zambales Ophiolite	VMS deposit	Vestimentiferan? worm tubes, filaments in jasper	Deep offshore	Boirat & Fouquet, 1986; Little et al., 2004a
Central Hokkaido, northern Japan	Convergent/ forearc	Upper Eocene, Poronai Fm.	Shelly limestone, in places brecciated, in mudstone	*Conchocele disjuncta*, *Hubertschenkia ezoensis*	Upper bathyal	Localities 6, 7 in Majima et al., in press
Whiskey Creek, Strait of Juan de Fuca, Washington, USA	Convergent	Upper Eocene, Pysht Fm.	Micrite, fibrous cement in boulders - bioturbated, brecciated; pyrite	*Acharax dalli, 'Nuculana' aff. grasslei, Bathymodiolus, Cryptolucina megadyseides, Conchocele bisecta, Vesicomya* (*Calyptogena*), serpulid? worm tubes; biomarkers: n-Alkanes, isoprenoid & cyclic terpenoid hydrocarbons, carboxylic acids	Deep offshore	Goedert et al., 2003a; Peckmann et al., 2003; Kiel, in press
Wagonwheel Mountain,	Convergent	Upper Eocene, Wagonwheel Fm.	Calcareous sandstone lenses	*Epilucina washingtoniana, Vesicomya* (*Vesicomya*) aff. *tschudi, Conchocele*	Deep offshore	Squires & Gring, 1996

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Table 1 (*continued*)

Location	Geotectonic/ stratigraphic context	Age	Deposit type, geometry	Fossil content	Inferred Paleo-depth/ setting	References
central California, USA			in silty mudstone	*bisecta*, oyster fragments, naticid, buccinid?, serpulid worm tubes		
Humptulips, Holcomb, W. Fork Satsop River, Menlo & Bear River sites, SW Washington, USA	Convergent	Upper Middle-Upper Eocene, Humptulips Fm., Lincoln Creek Fm., Cliff Pt. siltstone	Lenses of micrite, fibrous cement & spar, in siltstone	*Conchocele folgeri*, serpulid & vestimentiferan? worm tubes, *Pyropelta, Retiskenea statura, Hyalogyrina?, Homalopoma, Lurifax, Dentalium, Cryptolucina megadyseides, C. elassodyseides, Leptochiton alveolus, Margarites (Pupillaria) columbiana, Sahlingia eocenica, Bathymodiolus, Calyptogena chinookensis, Aphrocallistes polytretos, Abyssochrysos raui, Acharax dalli, Flabellum hertleini, Stephanocyathus holcombensis*, lucinids, decapods	Bathyal	Goedert & Squires, 1990; Squires & Goedert, 1991; 1996; Campbell, 1995; Squires, 1995; Goedert & Kaler, 1996; Goedert & Benham, 1999; Saul et al., 1996; Goedert & Peckmann, 2005; Kiel, in press
Lomitos Cherts, northwestern Peru	Convergent	Middle Eocene, Talara Fm.	Yellow, chert-rich limestones in shales	*Calyptogena peruviana, Thyasira peruviana, T. staufti, Myrtea?, Vesicomya (Vesicomya)* aff. *tschudi, Solemya lomitensis, Cytherea?, Nerita?*	Deep offshore	Olsson, 1931; cf. Squires & Gring, 1996
Panoche Hills, central California, USA	Convergent/ forearc	Paleocene, Moreno Fm.	Carbonate pavements, pipes; associated sandstone intrusions	Worm tubes, *Teredolites*, lucinids, solemyids, naticids, provannids, *Flabellum*, microbial laminites	Shelf edge, 100–200 m	Schwartz et al., 2003
Azema, New Caledonia	Oceanic spreading center	Paleocene or Upper Cretaceous; ophiolite	VMS deposit	Worm tubes	Deep offshore	Oudin et al., 1985; Little et al., 1998
Guenoc Ranch & Romero Creek, northern California	Convergent/ forearc	Upper Cretaceous; Campanian	Carbonate lenses & nodules in siltstone turbidites	*Thyasira cretacea*, solemyid & vesicomyid bivalves, high-spired abyssochrysid	Slope	Elder & Miller, 1993; Hepper, 2004
Tepee Buttes, Colorado, South Dakota,	Epeiric seaway/ basement faults, early Laramide	Upper Cretaceous, late	Micrites in pipe-like core; irregular nodules	*Nymphalucina occidentalis*, thrombolitic microbialite, *Inoceramus, Tellina, Phelopteria, Cymbophora, Euspira*,	Deep offshore	Arthur et al., 1982; Kauffman et al., 1996; Bishop &

Montana Wyoming, USA	orogeny	Campanian		*Raninella manningi*, *Plagiophthalmus bjorki*, *Hoplitocarinus*? *punctatus*, *Hues foersteri*, *Didymoceras nebrascense, Baculites*, *Teredolites*, worm tubes		Williams, 2000; Shapiro & Fricke, 2002
Nakagawa-cho region, NW Hokkaido, north Japan	Convergent/ Yezo forearc	Upper Cretaceous, Cenomanian-Santonian, Oomagari Fm., Yezo Supergroup	Upper worm tube boundstone & lower carbonate breccia, in muddy turbidite	*Calyptogena*, *Miltha*, *Thyasira*, vestimentiferan worm tubes, *Margarites*, *Nipponothracia* cf. *ponbetsensis*, *Serradonta* cf. *vestimentifericola*, *Gaudryceras tenuiliratum*, *Bathyacmaea* cf. *nipponica*, terebratulids, nuculaceans	Slope	Hikida et al., 2003; locality 4 in Majima et al., in press
Persterka, Kapedhes, Kinousa, Kambia, Memi, Sha sites, Cyprus	Supra-subduction zone	Upper Cretaceous, Turonian, Troodos ophiolite	VMS deposits	Vestimentiferan & serpulid? worm tubes, cerithids or provannids, epitoniids, filaments in jaspers	Deep offshore	Oudin & Constatinou, 1984; Little et al., 1998, 1999c, 2004a; Little, 2002
Bayda, Oman	Oceanic spreading center/ ?marginal basin	Upper Cretaceous, Cenomanian, Samail ophiolite	VMS deposit	Vestimentiferan? worm tubes	Deep offshore	Haymon et al., 1984; Haymon & Koski, 1985
Obira-machi, northwestern Hokkaido, north Japan	Convergent/ Yezo forearc	Upper Cretaceous, Lower Cenomanian, Yezo Supergroup	Calcareous concretions in mudstone	*Thracia yezoensis*, *Miltha*, *Nipponothracia*?	Slope	Kanie & Karamouchi, 1996; locality 2 in Majima et al., in press
Horokanai-cho, northwestern Hokkaido, north Japan	Convergent/ Yezo forearc	Upper Cretaceous, Lower Cenomanian, Yezo Supergroup	Large round concretions in mudstone	*Miltha*, *Vesicomya inflata*, *Acharax cretacea*	?Slope	Kanie & Nishida, 2000; Kanie et al., 2000; locality 3 in Majima et al., in press
Kuhnpasset Beds,Wollaston Forland, NE Greenland	Passive margin/ post-rift mudstone succession	Lower Cretaceous, Barremian, Wollaston Forland Group	Large carbonate lenses & mounds in sandy shale	*Cryptolucina kuhnpassetensis*, *Caspiconcha whithami*, *Solemya*, *Propeamussium*, nuculanacean, *Turnus*, *Lytoceras*, *Cymatoceras*, *Oxyteuthis*, *Teredolites clavus*, bathrotomariid, limpet	Mid-outer shelf	Kelly et al., 2000
Rocky & Bear Creeks, northern California, USA	Convergent/ forearc	Lower Cretaceous, Valanginian, Great Valley Group	Carbonate lenses & nodules in siltstone turbidites	*Lithomphalus enderlini, Pecten complexicosta, Astarte? trapezoidalis*, provannids, serpulid worm tubes, buchiids, *Dentalium?*	Upper slope	Kiel & Campbell, in press; Campbell, 1996, unpublished data

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Table 1 (*continued*)

Location	Geotectonic/ stratigraphic context	Age	Deposit type, geometry	Fossil content	Inferred Paleo-depth/ setting	References
Mikasa City, central Hokkaido, north Japan	Convergent/ Yezo forearc	Lower Cretaceous, Upper Albian, Yezo Supergroup	Carbonate concretions in siltstone	*Acharax yokosukensis, Calyptogena (Ectenagena)* sp., *Conchocele, Yoldia (Megayoldia), Nipponthracia ponbetsuensis Solemya* cf. *angusticaudata*	Subneritic	Kanie et al., 1993; locality 1 in Majima et al., in press
Canadian Arctic Islands	Sverdrup Basin/ faults associated with salt diapir or half-graben	Lower Cretaceous, Aptian-Albian, Christopher Fm.	Carbonate mounds with complex cement sequence	Serpulid worm tubes, *Grammatodon, Nucula, Taimyrothyris, Spirorbis*	~400 m	Beauchamp & Savard, 1992
Cold Fork of Cottonwood Creek, northern California, USA	Convergent/ syn-sedimentary faults in forearc basin	Lower Cretaceous, Aptian-Albian, Great Valley Group	Carbonate lenses & nodules with complex cement sequence	*Modiola major,* worm tubes, *Lucina?, Rhynchonella, Terebratula californica, Fissurella bipunctata, Retiskenea?,* provannids	Upper slope	Stanton, 1895; W. Elder, pers. comm., 1990; Campbell, 1996; Campbell & Bottjer, 1993; Campbell et al., 1993, 2002; unpublished
Wilbur Springs & Rice Valley, northern California, USA	Convergent/ atop serpentinite diapirs in forearc basin	Lower Cretaceous, Hauterivian, Great Valley Group	Carbonate lenses in serpentinites and siltstone turbidites	*Peregrinella whitneyi, Modiola major, Solemya stantoni, Retiskenea?,* worm tubes, micritic thrombolites	Upper slope	Stanton, 1895; Campbell, 1995; Campbell & Bottjer, 1993; Campbell et al., 1993, 2002, unpublished
Paskenta, northern California, USA	Convergent/ syn-sedimentary faults in forearc basin	Upper Jurassic, Tithonian, Great Valley Group	Carbonate lenses in siltstone turbidites	*Solemya stantoni, Modiola major, Lucina ovalis, L. colusaensis, Cooperrhynchia schucherti,* provannids, abyssochrysids, microbial laminites, *Buchia piochii, Nucula gabbi, Cardinopsis unioides, Corbula persuleata, Hypsipleura occidentalis*	Upper slope	Stanton, 1895; W. Elder, pers. comm., 1990; Sandy & Campbell, 1994; Campbell, 1996; Campbell & Bottjer, 1993; Campbell et al., 1993, 2002
Gateway Pass Limestone Bed, Alexander Is., Antarctica	Convergent/ forearc basin fault	Upper Jurassic, Tithonian, Fossil Bluff Group	Carboante crusts, cemented sediments in turbidites	Lucinaceans, cerithiform & neritiform gastropods, crinoids, protobranch bivalves, *Trypanites, Lytoceras, Belemnopsis*	Deep offshore	Kelly et al., 1995
Beauvoisin,	Extensional/	Upper	Carbonate lenses,	Lucinids, echinoids (*Tithonia*), gastropods,	Deep basin	Gaillard et al., 1992;

southeastern France	subsiding basin marginal to extensional Ligurian Tethys/ fault associated	Jurassic, Oxfordian, Terres Noire Fm.	nodules, concretions	ammonites, anomuran decapods, holothuroid sclerites, crinoid ossicles, lyssacid & lychniscid hexactinellids, demosponges; biomarkers: *n*-Alkanes, acyclic isoprenoid hydrocarbons (PME)		Peckmann et al., 1999a
Neuquén, Argentina	Fault-controlled rift depo-centers, early post-rift subsidence	Lower Jurassic, Lower Toarcian, Los Molles Fm.	Carbonate bioherm in shales & turbidite sandstones	Microbial stromatolites (tabular & columnar), *Frutexites* (nonphototrophic cyanobacterium), worm tubes	Offshore, 50–100 m	Gómez-Pérez, 2003
Figueroa, San Rafael Mountains, southern California	Mid-ocean ridge or seamount	Lower Jurassic, Pleinsbachian, Franciscan Complex	VMS deposit	Vestimentiferan worm tubes, *Anarhynchia* cf. *gabbi, Francisciconcha maslennikovi,* filaments in jasper	Deep offshore	Little, 2002; Little et al., 1999b, 2004a,b
Drowned Iberg reef, Harz Mountains, Germany	Passive/ Seamount drowning in siliciclastics	Lower Carboniferous, Upper Visean	Carbonates in neptunian dikes, breccia; impsonite (metamorphosed petroleum)	*Ibergirhynchia contraria,* solemyids, pleurotamariids?, large and small bivalves, *Fuxtexites, Achaeolithophyllum* (red alga), stromatolitic & thrombolitic boundstones	Water depth <250 m	Peckmann et al., 2001; Gischler et al., 2003
Tynagh lead-zinc deposit, Ireland	Intracontinental basin adjacent to active fault/ exhalative	Lower Carboniferous, Upper Tournaisian-Lower Visean	Sediment-hosted Pb-Zn-barite deposit; pyrite chimneys	Pyritized worm tubes	Water depth <100 m	Banks, 1985
Red Dog Zn-Pb-Ag deposit, western Brooks Range, Alaska, USA	Active horst & graben / long-lived starved sedimentary basin	Carboniferous, Kuna Formation	Barites and sulfides hosted in siliceous black shale and chert; seep-related	Worm tubes, peloids	Offshore	Moore et al., 1986; Johnson et al., 2004
Sonora, Mexico & Roberts Mountain Allochthon, Nevada, USA	Extensional basins	Upper Devonian, Famennian	Stratiform barite deposits, associated with methane-seeps on continental margin	*Dzieduszyckia,* worm tubes	Deep offshore	Noll et al., 1984; Dubé, 1988; Torres et al., 2003
Canning Basin reefs, Western Australia	Platform margin to basinal/ post-depositional compaction, faulting	Upper Devonian, Frasnian, basinal facies, Gogo Fm.	Cool, early exhalative phase, stromatolite-barite-sulfide buildups	Intergrown stromatolites & barite	Deep basin	Playford & Wallace, 2001

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Table 1 (*continued*)

Location	Geotectonic/ stratigraphic context	Age	Deposit type, geometry	Fossil content	Inferred Paleo-depth/ setting	References
Hollard Mound, Hamar Laghdad, Antiatlas, Morocco	Epeiric/ submarine rise and associated neptunian dikes	Middle Devonian, Eifelian-Givetian	Carbonate lenses with complex cement sequence	Modiomorphids, vestimentiferan worm tubes, solemyids, phacopid trilobites, small gastropods, orthocone cephalopods, microbialites	Offshore	Peckmann et al., 1999b, in press
Sibay, Uzelga Safyanovka, Oktyabrsk, Buribay, Yubileinoe sites, Ural Mountains, Russia	Inter-arc basin	Middle-Lower Devonian	VMS deposits	Annelid? worm tubes, *Tevidestus serriformis* (vestimentiferan? worm tube), *Sibaya ivanovi* (modiomorphid), indeterminate bivalves or brachiopods	Deep offshore	Little et al., 1998, 1999a; Little, 2002
Yaman Kasay, Ljeviha, Krasnogvardeyski sites, Ural Mountains, Russia	Back arc basin	Silurian	VMS deposits	*Eoalvinellodes annulatus* (polychaete? worm tube), *Yamankasia riftia* (vestimentiferan? worm tube), *Pyrodiscus lorrainae* (lingulid brachiopod), *Mytilarca* (ambonychiid bivalve) *Thermoconus shadlunae*, indeterminate vetigastropod	Deep offshore	Little et al., 1997, 1998, 1999a; Little, 2002
El Borj unit, Middle Atlas, Morocco	– –	Upper Silurian, Sèrie à faciés flysch, Meseta domain	Carbonate & hematite body in shales	*Dubaria lantenoisi*, stromatolites	Offshore photic zone?	Barbieri et al., 2004

Thalanga, Mt. Windsor volcanic belt, northern Queensland, Australia	Back arc basin/ fault-associated brine-rich fluid flow	Ordovician, Trooper Creek Fm.	Silica-iron exhalites in quartz-magnetiteor hematite pods	Hematitic filament networks	Deep offshore, > 1000 m	Duhig et al., 1992a,b; Davison et al., 2001
Løkken area, Trondheim region, Norway	Back arc basin	Lower Ordovician	Jaspers associated with VMS deposits	Hematitic filament networks	Deep offshore	Little et al., 2004a
Lady Loretta, HYC/Mt. Isa/ McArthur River, northern Australia	Intracratonic basin/ syn-depositional faulting	Proterozoic, 1640 Ma	SEDEX Zn-Pb-Ag deposits	Stromatolitic textures in pyrite: crinkly laminated, filaments; biomarkers: *b*-Alkanes, squalane, isoprenoids	Shallow to deep water	Logan et al., 2001; McGoldrick, 2004
Sulphur Springs, Pilbara craton, Australia	Oceanic spreading center	Archean, 3235 Ma	VMS deposit	Pyritic filaments	Deep offshore, > 1000 m	Rasmussen, 2000

OM, organic matter; AOM, anaerobic oxidation of methane by Archaea; Fm., Formation; Mbr., Member; VMS, volcanic massive sulfide; SEDEX, sedimentary exhalative. Includes 2 Precambrian, 30 Mesozoic–Paleozoic, and 27 Cenozoic regional occurrences (grouped by geographic region and age/stratigraphy). Each regional grouping consists of 1 to thousands of individual deposits. Not shown are offshore (Holocene–Pleistocene) or controversial sites (see text for details). Faunal lists exclude shelly microfossils; megafaunal taxonomy not checked for validity but nomenclatural updates made where possible. Data compiled from references as indicated, and from summaries in Campbell and Bottjer (1993); Naganuma et al. (1995); Kanie (1996); Little (2002); Little et al. (2004a); Peckmann and Thiel (2004); Majima et al. (in press). For Japan, only broad, regional seepage areas shown; see Majima et al. (in press) for further details and additional scattered localities.

in the geologic record are outlined. The significance of variability is explored, which is found at all scales and guises in modern and ancient vent–seep settings. The evolution and (paleo)biogeography of the vent–seep biota through time are also evaluated. Nonetheless, this review is necessarily limited in its scope because of the enormity of the discipline, spanning plate tectonics to microbiology, astrobiology to life's origins on Earth, and the Archean to the present. There also has been explosive growth in the literature on modern and ancient vents and seeps over the past five years. Thus, modern vent–seep settings and taxa are selectively covered herein, with a focus on subjects most directly relevant to ancient occurrences and research developments. This paper also is biased toward evaluating hydrocarbon seep paleoenvironments and fossils, because of the greater number known in the stratigraphic record (46 versus 13 ancient vent systems; Table 1), and the many new developments emerging from modern hydrocarbon seep studies.

2. Identifying vent–seep paleoenvironments

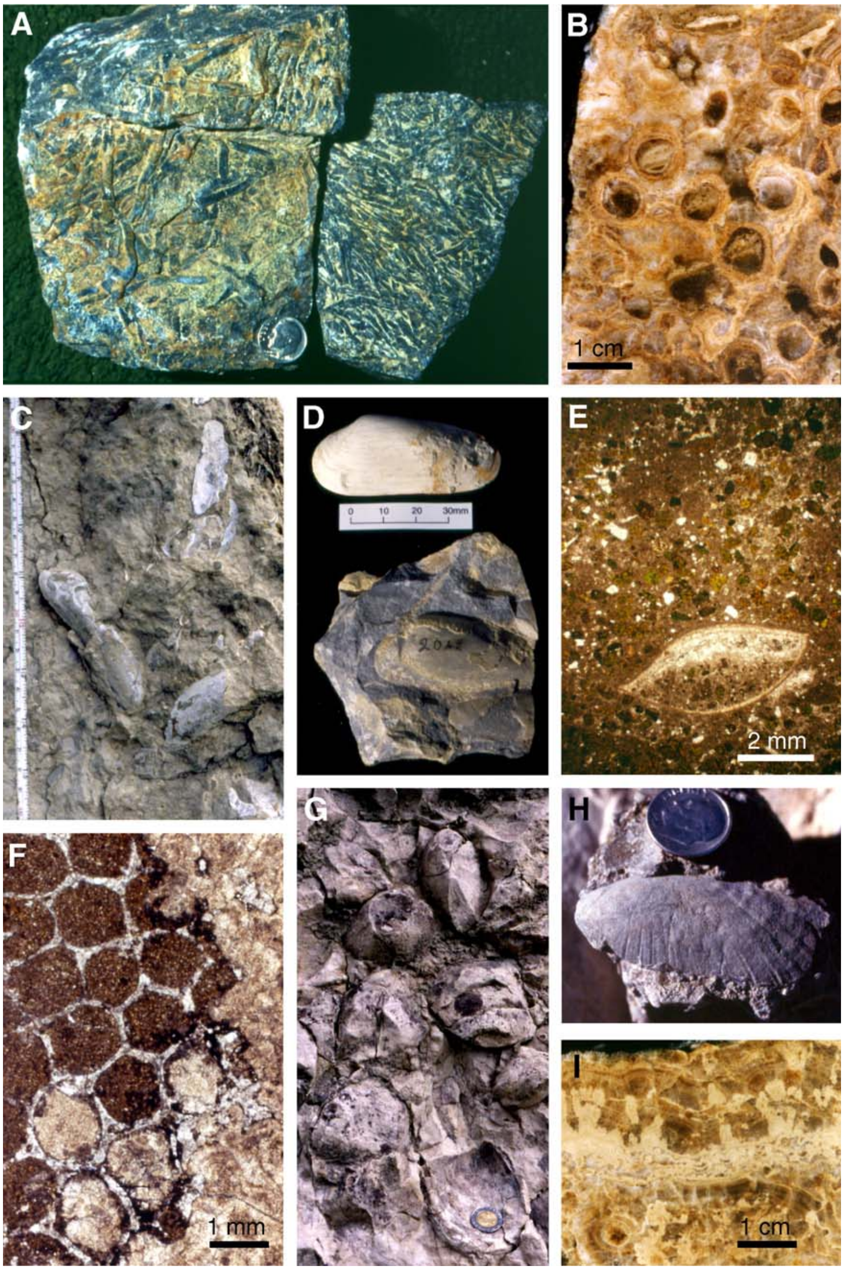
2.1. Biotic components

Distinctive biotic associations of classic, modern hydrothermal vents and hydrocarbon seeps can also be recognized in their ancient counterparts (Fig. 3). These deposits contain several familiar, family-level groups of mega-invertebrates that date back until at least the Late Jurassic or Early Cretaceous (~150–110 Ma; Campbell and Bottjer, 1995a). Typical taxa include siboglinid (vestimentiferan and frenulate) tubeworms, solemyid, vesicomyid, lucinid, thyasirid and bathymodiolin bivalves, and distinctive chemosymbiotic and/or grazing gastropods such as provannids, neomphalids, and certain limpets (cf. Lutz and Kennish, 1993; Campbell and Bottjer, 1995a; Sibuet and Olu, 1998; Rouse, 2001). Many vent–seep taxa today contain chemoautotrophic symbionts that oxidize sulfide and/or methane in the discharging fluids to generate biomass in a chemosynthetic food chain (Van Dover, 2000). Other common taxa, either endemic or opportunistic, include certain fish, galatheid lobsters, polychaetes, barnacles, holothurians, sponges and trochid and turrid gastropods (e.g., Vacelet et al., 1995; Sibuet and Olu, 1998; Yamaguchi et al., 2004). Of the living vent–seep associated taxa, decapods, sponges, chitons and gastropods have a fossil record in ancient vent–seep settings.

By contrast, vent–seep deposits older than Early Cretaceous tend to be populated or even dominated by other types of apparently endemic metazoans. In particular, certain extinct rhynchonellide, terebratulide and lingulide brachiopods (Sandy and Campbell, 1994; Campbell and Bottjer, 1995a; Gischler et al., 2003; Little and Vrijenhoek, 2003) are currently known, as well as worm tubes with uncertain affinities to modern vestimentiferans, extinct ambonychiid and modiomorphid bivalves, and an Early Paleozoic family of monoplacophorans (Little and Vrijenhoek, 2003). These fossils have either controversial or no direct taxonomic connections to living groups (discussed further in Section 4). Therefore, it is important to assess other criteria for recognition of hydrothermal vent and hydrocarbon seep deposits in the geologic record, since mega-faunal components have changed through time (cf. Little et al., 2002).

Fig. 3. Examples of fossils from ancient hydrothermal vent and hydrocarbon deposits. (A) Worm tube concentration in barite, on bedding plane surface. Devonian cold seep deposit, Queen Lode mine, Tuscaroa Range, Nevada, U.S.A. Coin = 2 cm diameter. Photograph courtesy of T.E. Dubé. (B) Worm tubes in cross-section with encrusting microbial laminites (beige-colored coatings). Miocene seep-carbonate, Rocky Knob deposit, East Coast North Island, New Zealand. (C) Large bathymodiolin mussels from same locality as (B). (D) Vesicomyids from hydrocarbon seeps on the Hikurangi convergent margin, East Coast, North Island, New Zealand. Recent to Sub-Recent individual (upper, white), dredged from 1000–1202 m water depth on Ritchie Bank; sample courtesy of B.A. Marshall. Miocene specimen (lower, in blue-grey carbonate) from Manley Stream site. (E) Cross-section of juvenile thyasirid bivalve, *Conchocele*, in glauconite/detrital-rich micrite, Eocene Keasey Formation, Vernonia–Timber seep, NW Oregon, U.S.A. (F) *Aphrocallistes* sponge in typical seep-carbonate paragenetic sequence: chambers filled with brown micrite; then margin irregularly corroded by H_2S and coated with pyrite (black); followed by precipitation of buff fibrous calcite. Eocene Bear River deposit, southwestern Washington, U.S.A. (G) Large lucinid bivalve coquina, Miocene "calcari a *Lucina*" seep-carbonate, Italian Appenines. Coin = 2.5 cm diameter. (H) *Solemya stantoni* Vokes 1955, from Upper Jurassic seep-carbonate, Paskenta, Great Valley Group, California, U.S.A. Coin = 2 cm diameter. (I) Detail of early diagenetic microbial textures (i.e., buff-colored thrombolites) enclosed in fibrous aragonite, from same locality as (B).

Vent–seep deposits are also recognized by their microbiological content. For example, microbial fabrics are common in many vent–seep deposits, past and present, where they occur as stromatolites, thrombolites, laminated micritic crusts and clotted peloids (e.g., Cavagna et al., 1999; Campbell et al., 2002; Greinert et al., 2002; Gómez-Pérez, 2003; McGoldrick, 2004; Peckmann and Thiel, 2004; Shapiro, 2004). Moreover, characteristic biomarker compounds (e.g., isoprene-based archaeal lipids, acetate-based lipids carrying non-isoprenoid carbon chains, hopanoids) in modern and ancient hydrocarbon seeps, and their depleted ^{13}C signatures, preserve a robust record of microbial methane utilization far back into Earth's



history (Peckmann and Thiel, 2004). Finally, some fine-grained iron oxides associated with VMS and SEDEX deposits contain hematitic filamentous microfossils as old as Ordovician (Little et al., 2004a), and pyritic filaments are recorded in VMS deposits back to the Archean (Rasmussen, 2000).

2.2. Authigenic mineralization and fluid-flow features

Particular types of precipitates and their isotopic signatures serve as robust signals of hydrothermal vent and hydrocarbon seep (paleo)environments. Authigenic carbonate or barium sulfate minerals in seep settings form by the microbially mediated process of AOM, or as a consequence of it (cf. Ritger et al., 1987; Ferrell and Aharon, 1994; Fu et al., 1994; Aquilina et al., 1997; Nähr et al., 2000; Greinert et al., 2001). Authigenic minerals at hydrothermal vents form by mixing of hot, metal-rich, reduced fluids with seawater (e.g., vent sulfides in black smokers, >300–~ 400 °C; white smokers, 100–300 °C; Hannington et al., 1995).

Recently other types of deposits have been discovered, such as hydrothermal carbonates from off-axis sites of low-temperature hydrothermal venting through old oceanic crust (Kelley et al., 2001, 2005). This finding substantially extends the known areas of seafloor that support hydrothermal activity and microbial life. Furthermore, numerous classic, seafloor seep-carbonates exhibit ^{13}C-depleted signatures indicative of methane oxidation ($\delta^{13}C < -30$‰ PDB), the values of which serve as a "litmus test" for identification of many modern and ancient examples (cf. Campbell et al., 2002). However, a wide spectrum of carbonate–carbon values is recorded across all Phanerozoic seep deposits ($\delta^{13}C + 24$ to -76 ‰ PDB; cf. Roberts and Aharon, 1994; Greinert et al., 2001; Campbell et al., 2002), driven by biogeochemical activity and other processes (e.g., Fig. 13 in Sassen et al., 2004), discussed further below (see Section 3). Sulfur isotopes in sulfides or sulfates also leave robust fingerprints of hydrothermal vent or hydrocarbon seep activity. The values reflect variations in sedimentation rate, oxidation of ferrous minerals in seafloor basalts, seawater–hydrothermal circulation/recharge, or bacterial (hydrocarbon seeps) or thermochemical (hydrothermal vents) sulfate reduction (e.g., Boyce et al., 1983; Duckworth et al., 1995; Knott et al., 1995; Shanks et al., 1995; Kohn et al., 1998; Peckmann and Thiel, 2004). Hence, multiple lines of evidence must be evaluated before a hydrothermal vent or hydrocarbon seep origin can be attributed to a particular deposit in the geologic record.

The physical character and setting of ancient hydrothermal vent and hydrocarbon seep deposits also may provide clues to their origins. In particular, many authigenic precipitates are: (1) isolated stratigraphically; (2) in places affiliated with syn-sedimentary faults or diapirs (mud, serpentinite); and (3) situated in geologic settings analogous to those of vent–seep environments today, such as forearc, rift or backarc basins, or accretionary complexes (e.g., Moore et al., 1986; Dubé, 1988; Campbell, 1992, 1995; Campbell et al., 1993, 2002; Little et al., 1998, 1999b; Majima et al., in press). At the outcrop scale, fluid migration features are common, including chimneys, doughnuts, pipes, cemented or open conduits, injection sandstones, and breccia (e.g., Fig. 4; cf. Oudin and Constantinou, 1984; Banks, 1985; Campbell and Bottjer, 1993; Herrington et al., 1998; Aiello et al., 2001; Schwartz et al., 2003; Conti et al., 2004; Majima et al., in press).

2.3. Global distribution of hydrothermal vents and hydrocarbon seeps

A global distribution map of hydrothermal vent and hydrocarbon seep systems, past and present, is shown in Fig. 1. The marked localities include only those sites where metazoans and/or microbial fabrics have been reported in association with venting or seepage. Nonetheless, there are many ore bodies, gas, petroleum and groundwater seeps, methane clathrates, pockmarks, and collapse depressions present worldwide that appear to have no discernable organism activity associated with their fluid emissions, or which have yet to be studied for their potential biological and biogeochemical content. These sites are omitted from Fig. 1, but can be evaluated in other published reports (e.g., Franklin et al., 1981; Hovland and Judd, 1988; Judd et al., 2002b; Díaz-del-Río et al., 2003; Judd, 2003; Mazurenko and Soloviev, 2003; Zhang and Lanoil, 2004).

Geologic mapping of ancient seep systems indicates that each comprises from a few to thousands of indi-

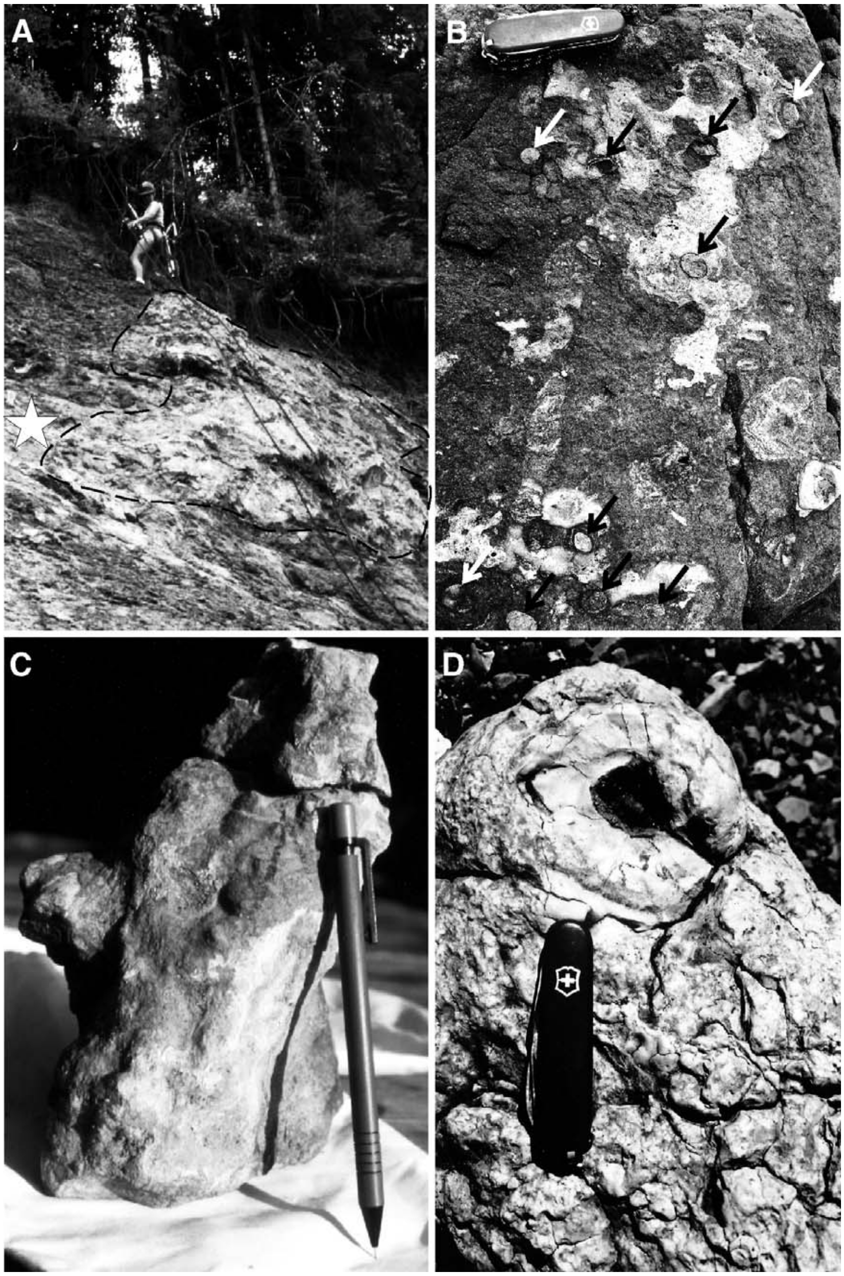


Fig. 4. Examples of carbonate deposits and fluid-flow structures associated with ancient hydrocarbon seepage. (A) Typical seep-carbonate deposit (dashed symbols) surrounded by glauconite-rich sandy siltstone. Eocene Vernonia–Timber locality, Keasey Formation, NW Oregon, U.S.A. Star indicates position of chimney structure of (C). (B) Authigenic micrite (white) of "diffuse" seep formed at shelf depths in bioturbated sandy siltstone, Pliocene Quinault Formation, Washington, U.S.A. Arrows show locations of *Acharax ventricosa* burrows. (C) Carbonate chimney, Eocene Keasey Formation, Vernonia–Timber Road, Oregon, U.S.A. (D) Carbonate doughnut, Oligocene Lincoln Creek Formation, West Fork Satsop River, Washington, U.S.A.

vidual features, which collectively represent the products of ancient fluid over-pressuring/expulsion through time. For seep settings, some of these carbonate/barite deposits, tubular/tabular concretions, cemented breccias and pavements, and fossil mud volcanoes were geographically and/or temporally extensive. In comparison, only a fraction of modern seep regions (e.g., Gulf of Mexico, North Sea) have been mapped in enough detail to estimate the geographic spread for a given hydrocarbon seepage province. In the stratigraphic record, there are certain paleogeographic locales and intervals that were typified by relatively voluminous hydrocarbon seepage. These include: (1) Jurassic–Cretaceous seeps of California (Campbell et al., 2002); (2) Cretaceous Tepee Buttes seeps of Colorado, South Dakota, Montana and Wyoming (Kauffman et al., 1996; Bishop and Williams, 2003); (3) Cretaceous–Recent seeps of Japan (e.g., Kojima, 2002; Majima et al., in press); (4) Paleocene seeps of the Panoche Hills, California (Schwartz et al., 2003); (5) Eocene–Oligocene seeps of Oregon and Washington (e.g., Goedert and Squires, 1990; Goedert and Campbell, 1995; Goedert et al., 2000, 2003a; Peckmann et al., 2002); (6) Miocene seeps of the Italian Appenines (e.g., Clari et al., 1988; Conti et al., 2004); and (7) Neogene–Recent seeps of the East Coast Basin and offshore Hikurangi Margin, New Zealand (Lewis and Marshall, 1996; Campbell and Francis, 1998; Collins, 1998; Campbell et al., 1999). For clarity, each regional grouping (in time and space) is generally illustrated on the global map as one "occurrence" (Fig. 1). However, in detail, many additional sites can be encompassed by the individual symbols shown in Fig. 1. For instance, Majima et al. (in press) have recently reported 75 known chemosynthesis-based fossil assemblages of Cretaceous to Holocene age in Japan, and individual Miocene seep deposits in the Appenines number at least 100 (S. Conti and D. Fontana, pers. comm. 2005). In another example, a detailed evaluation of an ancient continental margin seep system in western California has revealed 22 major seepage areas, shown in Fig. 5, which spanned >700 km geographically over ~140 m.y. of sedimentary basin history. Most of the Californian sites require further taxonomic and geochemical study. Their abundant seep-related gastropods (e.g., Fig. 6), for example, already suggest diverse fossil species and distinctive distribution patterns among sites (Stanton, 1895; Campbell, 1996, and unpublished data; Kiel and Campbell, in press), awaiting comparisons with modern biogeographic data.

2.4. Unusual or controversial vent–seep deposits

Controversy surrounds some deposits proposed as vent–seep paleoenvironments in the geologic record. For instance, the hydrothermal origin of the Early Devonian Kess Kess mounds, Morocco, is in dispute owing to alternative interpretations of low $\delta^{18}O$ values (hydrothermal carbonate versus meteoric alteration; Belka, 1998; Mounji et al., 1998; Joachimski et al., 1999). In another example, the setting of Early Carboniferous microbialites, brachiopods, and worm tubes from Newfoundland is debated with respect to timing of metal-rich hydrothermal mineralization, specifically early seafloor (von Bitter et al., 1990) versus late burial (Dix and Edwards, 1996). Even the biota of the Middle Cambrian Burgess Shale have been implicated in a scenario of metalliferous brine seepage at the base of the Cathedral and Eldon escarpments, British Columbia (e.g., Johnston and Collom, 2001; Powell et al., 2004). In practice, identification of ancient vent–seep deposits requires a careful, multi-proxy approach that firmly embeds and associates mineralogic, isotopic and biotic elements in a detailed geologic and paragenetic framework (Table 1; cf. Cook and Stakes, 1995; Cavagna et al., 1999; Peckmann et al., 1999a, 2002, 2003; Playford and Wallace, 2001; Campbell et al., 2002; Goedert et al., 2003a; Conti et al., 2004; Peckmann and Thiel, 2004).

Even with integrated, detailed studies, some ancient deposits have unusual, uncertain or no modern analogs, and therefore can present challenges with regard to placement in vent–seep settings sensu stricto. Fascinating examples include Paleoproterozoic "SEDEX" Zn–Pb deposits of northern Australia, typified by crinkly, microbial laminites and stromatolites in pyrite, and molecular biomarkers for sulfide-oxidizing bacteria (Logan et al., 2001; McGoldrick, 2004). In addition, metalliferous ores in Lower Cambrian black shales, China, have been proposed as seafloor–hydrothermal in origin, and contain fossils of bivalved arthropods (*Perspicaris*), sponges, and giant, sheathed sulfur bacteria (Steiner et al., 2001; Erdtmann and Steiner, 2002). Furthermore, Carboniferous

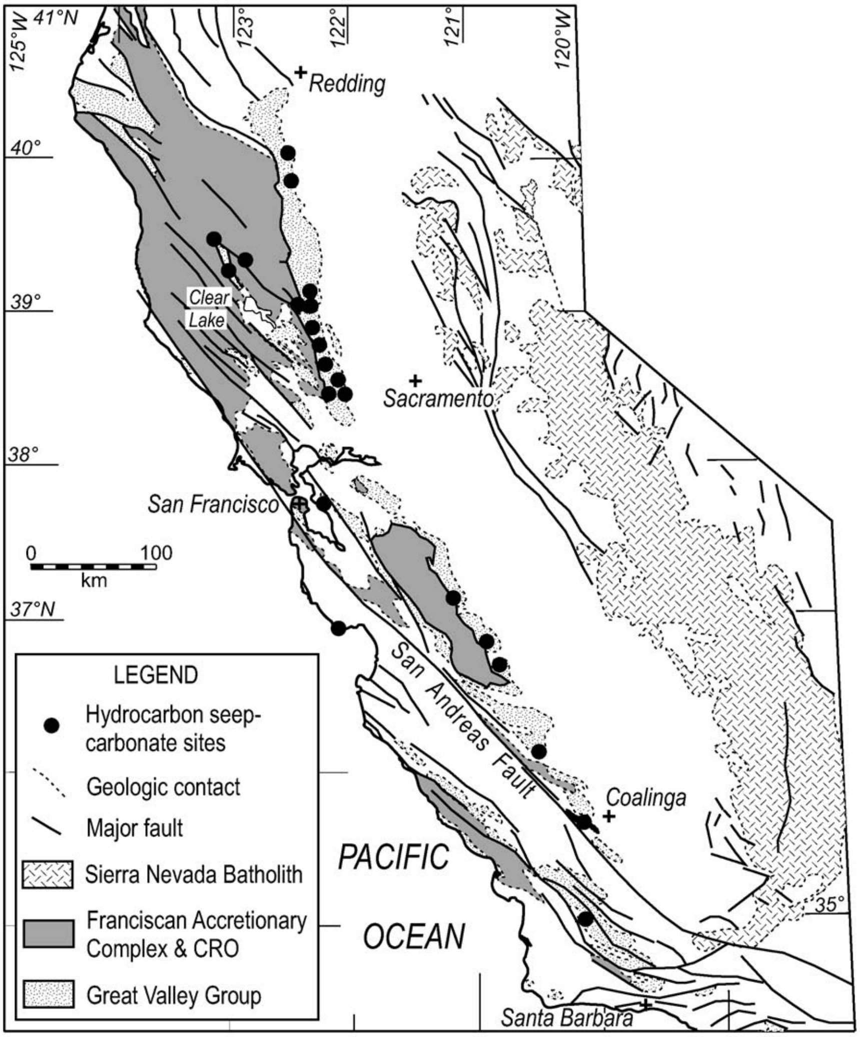


Fig. 5. 22 Mesozoic and Cenozoic seep-carbonate occurrences (black circles), California, showing their geologic setting and geographic extent, some of which comprise numerous individual deposits in the same area. Relevant geologic features of the north–south trending, Mesozoic–Palaeogene convergent margin include: belts of mélange, broken formation and ophiolites (Franciscan Accretionary Complex, Coast Range Ophiolite, CRO); siliciclastic forearc turbidites (Great Valley Group); and present-day root of the volcanic arc (Sierra Nevada Batholith). Geology simplified from the 1 : 2,500,000 Geologic Map of California (1966, U.S. Geological Survey and California Division of Mines and Geology). Most of these seep deposits have yet to be formally studied for their taxonomic and/or geochemical content (but see Squires and Gring, 1996; Campbell et al., 2002; Schwartz et al., 2003; Hepper, 2004; Kiel and Campbell, in press). Most were identified through old literature reports, paleontological museum collections, and knowledge from local geologists, using seep-specific taxa as a search criterion.

stratiform barites with worm tubes (?) in the Brooks Range, Alaska, recently have been inferred as methane seeps (Johnson et al., 2004), an alternative to the previously suggested model for their formation from the mixing of buoyant hydrothermal plumes with suboxic seawater (Moore et al., 1986). Similarly, Devonian stratiform barites lacking polymetallic sulfides, and associated with worm tubes and brachiopods in Nevada and Mexico, recently have been inferred as hydrocarbon seeps (Torres et al., 2003). These new interpretations for stratiform barites have been made following their recent discoveries in seep provinces along present-day continental margins, which are among the largest known barium sulfate

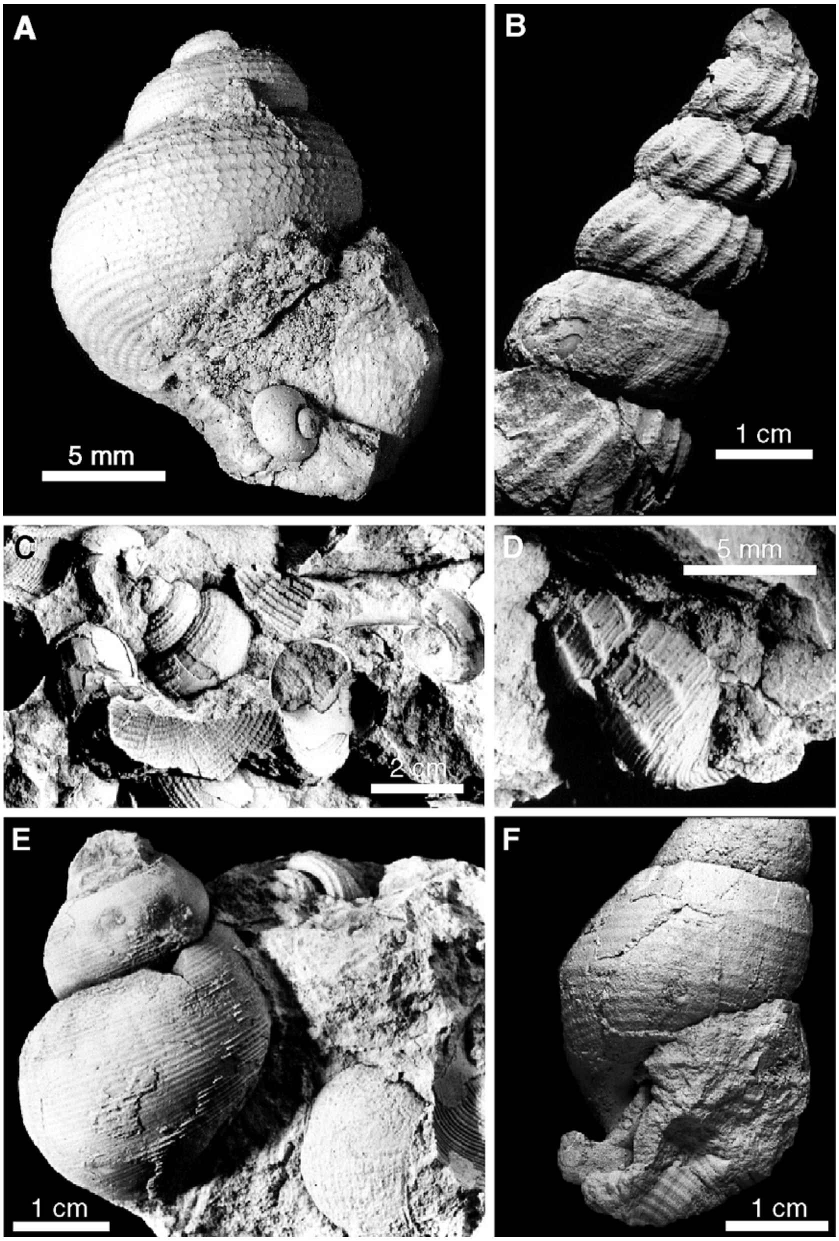


Fig. 6. Seep-related gastropod fossils from Upper Jurassic to Lower Cretaceous seep-carbonates, Great Valley Group, California (cf. Fig. 5). All are currently under detailed taxonomic study. (A) Thin-shelled possible provannid with distinctive scaley ornament from Rice Valley site. Apertural area of the shell is folded and hosts an attached microgastropod. (B) Large, high-spired abyssochrysid, from Berryessa site. (C) Provannid (?) coquina, from Priest Valley, Coalinga site. (D) Small abyssochrysid or cerithid, Paskenta site. (E) Large, globose provannid (?) with thin spiral threads and extremely thin shell (≤1 mm thick), Morgan Valley. (F) Lower body whorls of slender possible provannid (cf. *Atresius liratus* of Stanton, 1895), displaying deformed shell at apertural area. Rocky Creek site, Morgan Valley.

ore deposits in the world (Greinert et al., 2002; J. Greinert, pers. comm., 2004). Finally, cap carbonates overlying Upper Neoproterozoic glacial deposits of the “Snowball Earth” period have been inferred as hydrocarbon seeps associated with large-scale, methane hydrate destabilization during the post-glacial warming (Jiang et al., 2003). Some of these purported vent–seep deposits, though unusual, have already become firmly embedded within the growing list and variety of vent–seep paleoenvironments sensu lato (e.g., Torres et al., 2003). With further scrutiny, however, other proposed vent–seep deposits may ultimately be omitted from the list.

2.5. Hydrothermal vents and hydrocarbon seeps—terms and definitions

Given the variety of settings proposed to be related to hot or cold fluid emissions in seafloor or near-seafloor (paleo)environments, precise definitions of the terms “hydrothermal vent” and “hydrocarbon seep” have been somewhat elusive to attain. They are applied variably by different researchers under varying conditions, and hence can confound evaluation of some transitional deposits, or those with physico–chemical characteristics that fall outside the commonly accepted purview of a typical hot vent or cold hydrocarbon seep setting. Classic hydrothermal systems are encountered at seafloor spreading centers, usually envisioned as the typical, “end-member,” black and white smokers spouting high-temperature, acidic, metal- and sulfur-rich fluids. They are found in extensional, volcanic ocean–ocean arc, ocean–continental arc and backarc rift basins (Hannington et al., 1995; Franklin and Hannington, 2002), and display both vigorous hydrothermal venting and diffuse warm seepage. Nonetheless, styles of hydrothermal emissions are even further varied, with the recent discovery of serpentinite-hosted, steep-sided carbonate chimneys (30–60 m tall) that precipitate from warm (40–90 °C), alkaline hydrothermal seepages in an off-axis vent field, “Lost City,” 15 km from the Mid-Atlantic Ridge (MAR) spreading center at 30°N (Kelley et al., 2001, 2005). Other settings of low-temperature (<60 °C), diffuse, hydrothermal fluid-flow can produce little mineralization (Hannington et al., 1995), or may promote accumulation of fine-grained, metalliferous sediments (Little et al., 2004a). Recently, submarine travertines also have been discovered at 85 °C vents in <10 m water depth offshore of western Mexico (Canet et al., 2003). The Mexican deposits display unusually low $\delta^{13}C$ values to -39‰ PDB, suggestive of methane oxidation typically recorded in hydrocarbon seep-carbonates.

In comparison, hydrocarbon seepage (slow emission rate) and venting (fast emission rate) are generally characteristic of low-temperature, fluid expulsion systems of sedimentary basins (Aharon, 1994; Parnell, 2002). Their typical geological products have been termed chemoherms — “buildups of chemical carbonates and calcareous skeletal debris of chemosymbiotic fauna whose carbon is primarily derived from microbial processes in domains of cold hydrocarbon venting, and which possess anomalously negative carbon isotope compositions relative to the seawater carbon pool” (Aharon, 1994, p. 71). However, such values are but one variety of hydrocarbon-seep isotopic signal (e.g., Roberts and Aharon, 1994, Fig. 9; Greinert et al., 2001, Fig. 3; Campbell et al., 2002, Fig. 16; see Section 3 for further discussion). Furthermore, many modern seep-carbonates have formed at or beneath the seafloor owing to anaerobic microbial processes, and do not display the primary, positive relief that might warrant this bioherm-like terminology. It is recommended here that the term chemoherm be restricted to those seep-carbonates that are or were formed as free-standing edifices in contact with the water column (e.g., Han et al., 2004; Teichert et al., in press). For both modern and ancient seep-carbonates under consideration as possible chemoherms, it is important to establish the relative timing of exposure to seafloor environments because: (1) shells can become incorporated in carbonate cements that formed during post-burial fluid-flow; and (2) erosion may exhume “chimneys” or other carbonate features that originally developed in the subsurface (cf. discussion in Díaz-del-Río et al., 2003; Paull et al., 2005; Burns et al., in press).

Aharon (1994) has commented that the terms “hot vents” and “cold seeps” sensu lato are used as a matter of convenience in the literature, rather than expressly defined by measured temperatures and rates of emissions. Modern hydrocarbon emissions, for instance, range from slow and diffuse, forming seep-carbonates, to fast and vigorous, developing chimneys and mud volcanoes (Ritger et al., 1987; Aharon, 1994). Aharon (1994) has proposed that all seafloor emissions be called “vents” (hydrothermal or hydrocarbon) where emission rates are unknown, i.e., for many deposits in the geologic record. It is suggested here that different water–rock interactions, and thus sources of fluids, continue to warrant basic divisions of terms. Those discharges of varying rates and temperatures, ultimately derived from interactions between hot igneous rock and circulating seawater, are termed hydrothermal vents throughout this paper. In contrast, the term hydrocarbon seep is used herein for fluid discharge of varying rates and temperatures generated from the accumulation and burial of organic matter, its transformation to hydrocarbons, and their migration and release from sedimentary basins. In places, vents and seeps could be forming within the same geotectonic region. Two modern examples include the Guaymas Basin, Gulf of California, where a thick sediment blanket overlies a transitional oceanic–continental rift system (Simoneit et al., 1990), and the cold-seeps and hydrothermal vents affiliated with Lihir Volcano, New Ireland forearc basin, Papua New Guinea (Schmidt et al., 2002). In an example from the geologic record (Svensen et al., 2003), magmatic sill emplacement and phreatic eruptions in the Paleocene Vøring Basin, Norwegian Sea, triggered development of hundreds of gaseous hydrothermal vent complexes, as well as long-lived (Eocene–Pliocene) seep-carbonate formation in overlying siliciclastic deposits.

For many ancient vent and seep deposits, the relative rates of fluid flow and formation temperatures can be estimated. For example, paleo-temperatures can be evaluated for some ancient deposits using oxygen isotopes of unaltered shells or early diagenetic cements, and fluid inclusion analysis of minerals (e.g., Hannington et al., 1995; Little et al., 1999a; Greinert et al., 2001). Moreover, features associated with vigorous flow have been identified in both modern and ancient deposits (e.g., some hydrocarbon migration-related mud volcanoes, breccias, chimneys, doughnuts; Fig. 4C, D), and hence could be associated semantically with the term “vent”, with indicative relative temperature modifiers, as appropriate (cf. Aharon, 1994). Ancient seep deposits that imply more diffuse flow (e.g., scattered accumulations of fine-grained carbonate lenses, slabs, seafloor pavements and nodules enclosed within siliciclastics; Fig. 4B) also have been recognized (e.g., Schwartz et al., 2003; Nesbitt and Campbell, 2004a,b). Some modern and ancient hydrocarbon seeps are, in fact, zoned such that fibrous cements (vigorous flow, venting) comprise central portions of the carbonate deposits; whereas, detrital micrites and micritic nodules (diffuse flow) are prevalent at their outer margins, where seepage was dominant (e.g., Ritger et al., 1987; Beauchamp and Savard, 1992; Campbell, 1995; Campbell et al., 2002; cf. Greinert et al., 2001). Therefore, a seep deposit could contain one or several vent conduit areas. Modern venting or seepage rates, and ages of deposits (cf. Aharon et al., 1997; Lalou et al., 1993; Torres et al., 2001, 2002; Teichert et al., 2003), may be useful for estimating longevity of emissions for deposits with similar geochemical signals, physical structures, or styles of buildups in the geologic record (e.g., Johnson et al., 2004). This continuum in types of venting and seepage thus begs the question of whether strict definitions for hydrothermal vents and hydrocarbon seeps are necessary or always useful. If each deposit is assessed using a targeted, multi-proxy approach, relative rates of flow and temperature estimates are likely to emerge from the analysis.

3. Significance of variability at all scales in vent–seep (paleo)environments

3.1. Variability and stability in vent–seep settings

Despite broad similarities in faunas and deposit types that enable recognition of vent–seep settings, modern and ancient deposits are highly variable in size, estimated duration of their development, mineral components, biotic content, and geotectonic context. Spatial and temporal heterogeneity is well-documented in modern hydrothermal vent and hydrocarbon seep settings. It typically reflects the dynamic interactions between organism habitat preferences and fluctuating geochemical and physical parameters of fluid expulsion, both locally and regionally (e.g., MacDonald et al., 1989, 1990; Tunnicliffe and Juniper, 1990; Van Dover, 2000; Sahling et al., 2002; Treude et al., 2003; Sassen et al., 2004; Levin, in press). Vent–seep plumbing is continually self-sealing (cf. Cook and Stakes, 1995; Hovland, 2002). Nascent hot vents initially spurt out reduced fluids and clouds of bacterial floc from the subsurface, followed by rapid colonization of new vent areas, such as the

1991 9°N eruption, East Pacific Rise (EPR; Haymon et al., 1993). Within 4–5 years, mussels, serpulid worms and anemones surrounded well-established tubeworm thickets at still-active vents, and community die-off has been witnessed at sites of waning flow (Shank et al., 1998). Thus, changes in fluid distributions and intensities have dramatic effects on community structure and succession over the short term (Van Dover, 2000; Raulfs et al., 2004). At modern seeps, for instance, the typically patchy availability of local sulfide and methane in pore waters has produced: (1) circular haloes of mats surrounded by rings of vesicomyid clams (Rathburn et al., 2003); (2) different sulfide preferences in different *Calyptogena* species (Barry et al., 1997); (3) physiological variability in the seep mussel *Bathymodiolus childressi* (Bergquist et al., 2004); and (4) *Beggiatoa–Calyptogena–Acharax* zonations at Hydrate Ridge (cf. Fig. 7; Sahling et al., 2002; Treude et al., 2003).

Long-term stability in many vent communities is also well known. Along some ridge segments, a shared species pool can distribute similar taxa among individual vent fields that wax and wane in activity (Van Dover and Hessler, 1990). Across ocean basins, phylogenetic relatedness is fairly common at higher taxonomic levels, yet different geographic regions also sustain distinctive vent communities (cf. Van Dover, 1990). In comparison, hydrocarbon seeps generally support fluid flow over long durations, and provide a relatively steady supply of sulfide and methane because of long-term accumulation, compaction and over-pressuring of organic-rich pore waters at continental margins (Sibuet and Olu, 1998). In general, continental margins are ideally positioned to accumulate and bury organic matter, transform it to hydrocarbons, as well as provide several mechanisms for fluid transport and expulsion to the seafloor (Fig. 7).

3.2. Organism–fluid relations at ancient seeps

Zonation of fossils and cement types has been documented for several seep deposits (e.g., Beauchamp and Savard, 1992; Campbell, 1995; Kauffman et al., 1996; Campbell et al., 2002; Peckmann et al., 2002; Nesbitt and Campbell, 2004a), indicating organism responses to variable, local fluid distributions and compositions. For instance, Campbell et al. (2002) showed that megafaunal activity in Mesozoic seeps from California was restricted to early seafloor seepage, with mollusks preserved in earliest detrital micrites, formed by relatively diffuse methane emission in low-oxygen conditions. Worm tubes also became established in seafloor settings, which were buried and entombed in cements that reflect relatively more ventilated conditions. Microbial activity was recorded by micritic laminites covering H_2S-corroded surfaces in the early seafloor stage. However, microbes persisted in cavities and pore spaces long after the megafauna disappeared, as fluid plumbing became more restricted during later self-sealing (Campbell et al., 2002).

This pattern of changing fluid composition, as recorded in different cements, and which co-varies with organism distributions (e.g., megafauna restricted to early seafloor events in the life of a seep), has been found in several geographically far-flung, Jurassic–Cretaceous age seeps in California and the Canadian Arctic. Geotectonic settings of these seep-carbonates differ, from forearc basin turbidites and serpentinite diapirs (Campbell et al., 1993) to fault-grabens and salt diapirs (Beauchamp and Savard, 1992), yet the broad fossil-cement paragenesis is very similar. This finding suggests comparable fluid histories in the birth, growth, death and burial of ancient hydrocarbon seeps, at least for these Mesozoic examples (Campbell et al., 2002).

3.3. Seep biogeochemistry — past and present

Stable isotopes of carbon and oxygen in seep-carbonates are biogeochemical archives of past fluid activity and composition. Measured values of seep-carbonates cover a broad range, both within individual sites and across the geologic history of these deposits. At the outcrop scale, particular flow-conduit structures can show fine-scale isotopic change throughout their growth and development. For instance, several adjacent conduit features from an Upper Jurassic seep deposit in California (Fig. 8A,B) reveal precipitates of multiple horizons of isopachous, fibrous cement. From rim to core in one conduit, a ~5‰ PDB shift in δ^{13}C and δ^{18}O values was recorded over a few millimeters (Fig. 8C), indicative of evolving fluids during self-sealing. More broadly, the classic, isotopically depleted, carbonate–carbon signals recorded in some seep deposits, as in this example, were derived from

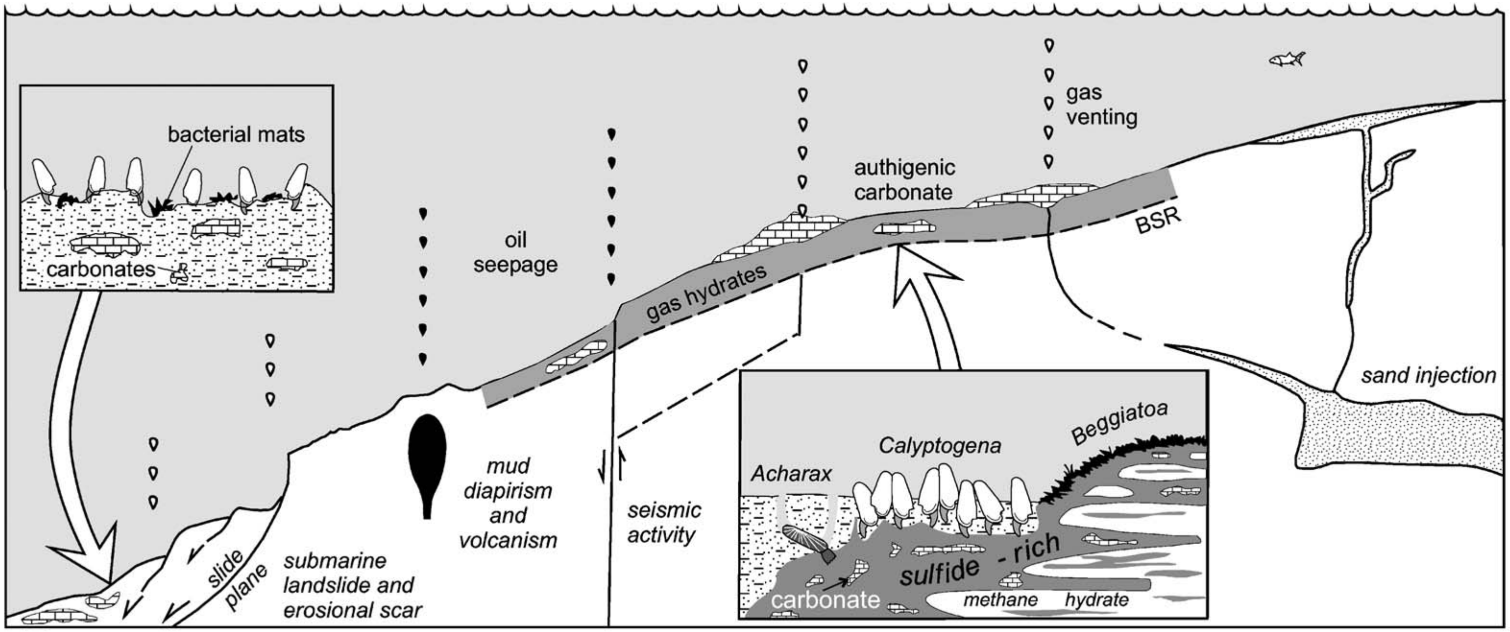


Fig. 7. Schematic diagram linking fluid migration pathways of seep plumbing, gas hydrate distribution, fluid expulsion features, authigenic carbonate precipitates, and typical seep communities in continental margin areas charged with hydrocarbons. Fluid over-pressuring (increase from hydrostatic to near lithostatic) occurs with sediment loading and/or convergence-related deformation to yield high-permeability, especially within dilated fault zones and via buoyant mud volcanoes and diapirs (cf. Carson and Screaton, 1998). Hydrocarbons are transported via sand injection, through trapping/release of free gas beneath methane clathrates (visualized by the distribution of the bottom simulating reflector, BSR), fault conduits, mud diapirism and volcanism, and leakage from sites of submarine slides/tectonic erosion. Diagram modified from Bohrmann et al. (2002), Parnell (2002), and Sahling et al. (2002).

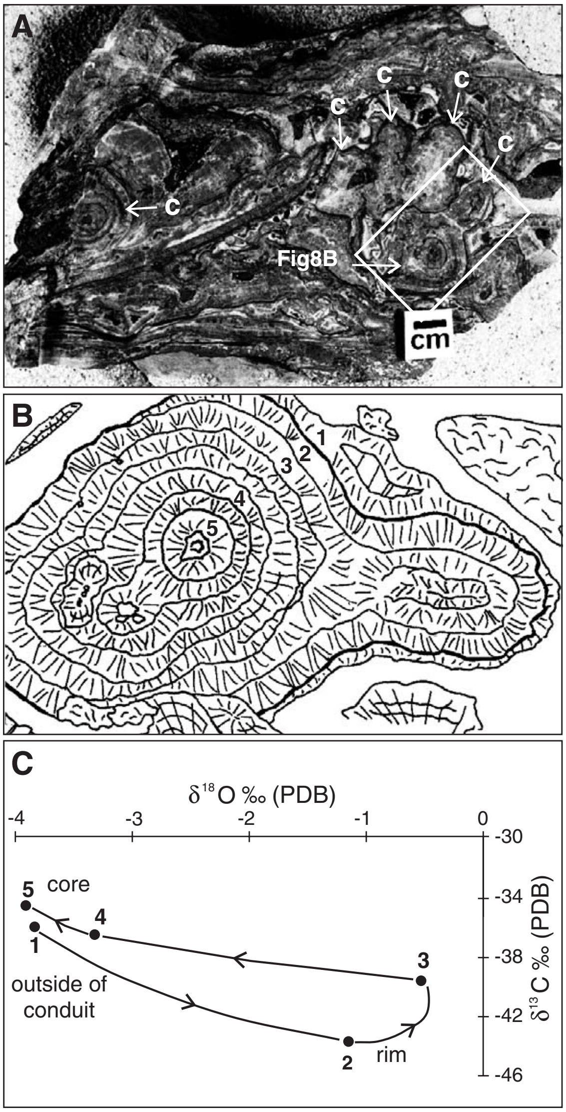
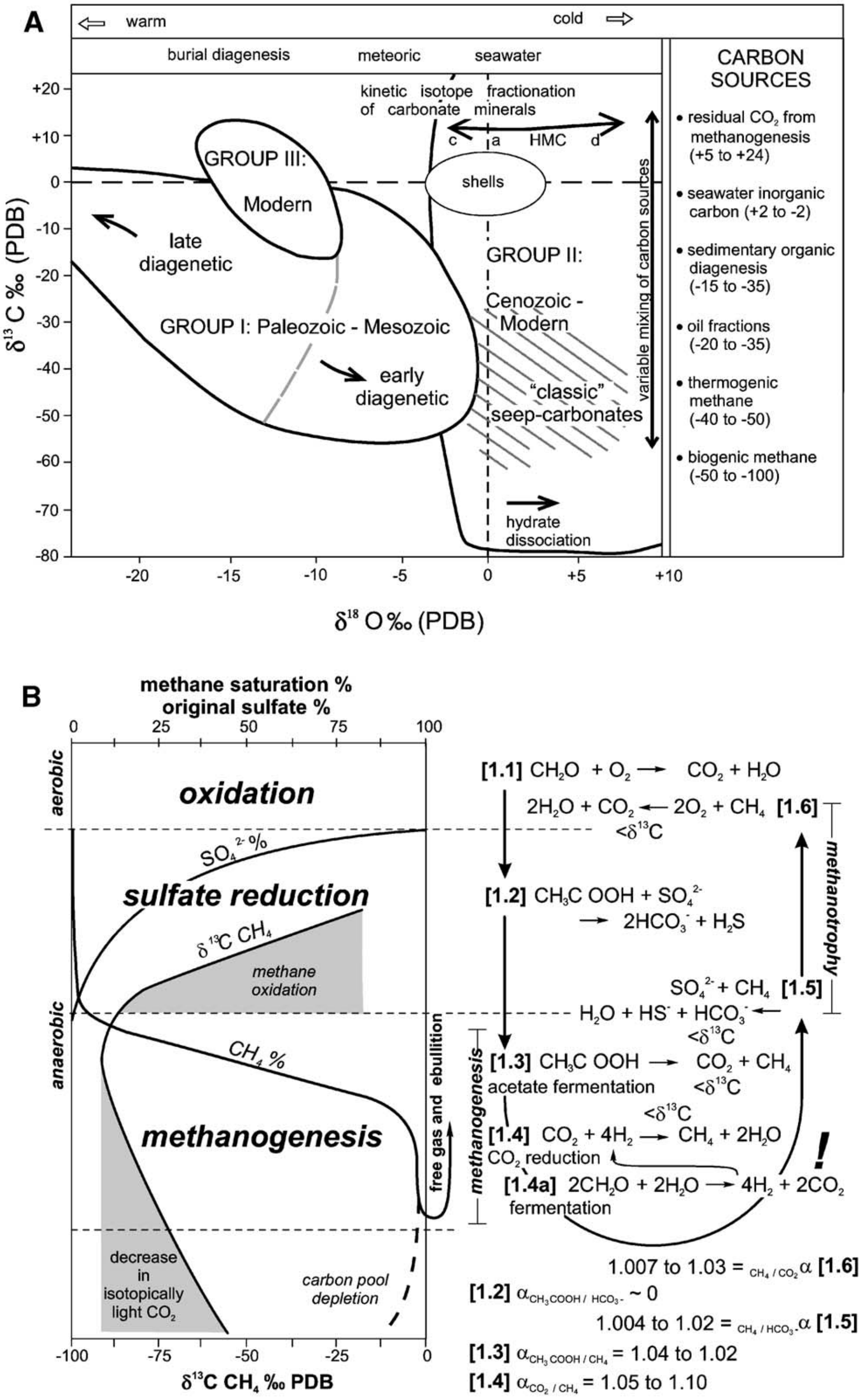


Fig. 8. Fine scale variability in carbon and oxygen stable isotopic signatures across a small fluid conduit feature of layered fibrous calcite cement. Late Jurassic (Tithonian) Paskenta seep-carbonate, Great Valley Group, California, U.S.A. (A) Cut slab of fibrous cement block exhibiting numerous small conduits (c). (B) Drawing of one conduit feature, showing concentric cementation and micro-sample locations for stable isotope analyses. (C) Cross-plot of isotope data, from rim to core of cement-filled conduit.

microbially mediated, anaerobic oxidation of methane (AOM) in the sulfate reduction zone (see below; reviewed in Han et al., 2004). However, they occupy only one portion of a wide spectrum of isotopic signatures possible for Phanerozoic seep-carbonates worldwide (Fig. 9A). Variation in both carbonate–carbon and –oxygen values is dictated by several processes, including kinetic isotope fractionation, hydrate dissociation, variable mixing of carbon sources, tapping of deep burial fluids (via faults or erosion), clay mineral dehydration, and diagenesis (Fig. 9A; cf. Sample and Reid, 1998; Han et al., 2004).

As mentioned above, the most common tool used to elucidate a methane origin for the carbonate–carbon of a particular deposit is its stable isotopic composition. Methane can form during burial of organic-rich marine sediments by several processes (Fig. 9B; Greinert, 1999). For example, thermal maturation of organic matter produces thermogenic methane, with δ^{13}C values varying between -30‰ to -50‰ PDB (Whiticar, 1999). Biogenic methane forms via microbial degradation of organic matter (cf. Irwin et al., 1977). In this pathway, organic material is partly consumed and oxidized in the aerobic zone at the sediment–water interface. In anaerobic sedimentary pore waters, following the reduction of nitrate and iron, sulfate-reducing bacteria further decompose the degraded organic matter, and release HCO_3^- (Eq. (1.2) in Fig. 9B) without a significant fractionation in the carbon isotopes (Whiticar, 1999). In other words, the HCO_3^- has the same isotopic signal as the source organic material, which usually varies between δ^{13}C -20‰ and -25‰ PDB in the marine environment (Whiticar, 1999). The increased alkalinity promotes carbonate formation in the sulfate reduction zone (Irwin et al., 1977), in places producing concretions that are imprinted with this negative isotopic signal of organic matter degradation, in contrast to the normal δ^{13}C signature of ocean water (~ -3‰ PDB). Where sulfate has been consumed entirely, methanogenesis occurs via CO_2-reduction (Eq. (1.4) in Fig. 9B) or other pathways. The CO_2 pool becomes progressively enriched in ^{13}C with ongoing methanogenesis, because Archaea mediating the process preferentially use CO_2 containing the light carbon isotope. Hence, the biogenic methane produced in this reaction can display δ^{13}C values lower than -100‰ PDB (Whiticar, 1999).

In areas of voluminous methane production such as hydrocarbon seepage provinces, methane can migrate upward to form gas hydrates near the seafloor, and/or is released directly into the water column as seeps and flares (cf. Merewether et al., 1985; Ginsburg et al., 1993; Hornafius et al., 1999; Egorov et al., 2003). In


A
warm
cold
burial diagenesis
meteoric
seawater
kinetic isotope fractionation of carbonate minerals
c
a
HMC
d
GROUP III: Modern
shells
late diagenetic
GROUP II: Cenozoic - Modern
GROUP I: Paleozoic - Mesozoic
early diagenetic
"classic" seep-carbonates
variable mixing of carbon sources
hydrate dissociation
δ^{13} C ‰ (PDB)
+20
+10
0
-10
-20
-30
-40
-50
-60
-70
-80
-20
-15
-10
-5
0
+5
+10
δ^{18} O ‰ (PDB)
CARBON SOURCES
• residual CO_2 from methanogenesis (+5 to +24)
• seawater inorganic carbon (+2 to -2)
• sedimentary organic diagenesis (-15 to -35)
• oil fractions (-20 to -35)
• thermogenic methane (-40 to -50)
• biogenic methane (-50 to -100)
B
methane saturation %
original sulfate %
0
25
50
75
100
aerobic
anaerobic
oxidation
SO_4^{2-} %
sulfate reduction
$\delta^{13}C$ CH_4
methane oxidation
CH_4 %
methanogenesis
free gas and ebullition
decrease in isotopically light CO_2
carbon pool depletion
-100
-75
-50
-25
0
$\delta^{13}C$ CH_4 ‰ PDB
[1.1] $CH_2O + O_2 \rightarrow CO_2 + H_2O$
$2H_2O + CO_2 \leftarrow 2O_2 + CH_4$ [1.6]
$<\delta^{13}C$
[1.2] $CH_3COOH + SO_4^{2-} \rightarrow 2HCO_3^- + H_2S$
methanotrophy
$SO_4^{2-} + CH_4$ [1.5]
$H_2O + HS^- + HCO_3^- \leftarrow$
$<\delta^{13}C$
methanogenesis
[1.3] $CH_3COOH \rightarrow CO_2 + CH_4$
acetate fermentation
$<\delta^{13}C$
$<\delta^{13}C$
[1.4] $CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$
CO_2 reduction
!
[1.4a] $2CH_2O + 2H_2O \rightarrow 4H_2 + 2CO_2$
fermentation
1.007 to 1.03 = ${}_{CH_4/CO_2}\alpha$ [1.6]
[1.2] $\alpha_{CH_3COOH/HCO_3^-} \sim 0$
1.004 to 1.02 = ${}_{CH_4/HCO_3^-}\alpha$ [1.5]
[1.3] $\alpha_{CH_3COOH/CH_4} = 1.04$ to 1.02
[1.4] $\alpha_{CO_2/CH_4} = 1.05$ to 1.10

the sediments, some of this upwardly mobile methane becomes anaerobically oxidized in the sulfate reduction zone through microbially mediated AOM to produce HCO_3^- (Eq. (1.5) in Fig. 9B). This accompanying increase in alkalinity drives carbonate precipitation in seepage areas at or near the seafloor (cf. Paull et al., 1992; Ritger et al., 1987), yielding measured seep-carbonate signatures as low as $\sim -75‰$ PDB (Campbell et al., 2000). Nevertheless, the admixture of carbon from normal organic matter degradation (Eq. (1.2) in Fig. 9B) and ocean water can modify the ^{13}C signal of the original biogenic methane, shifting the $\delta^{13}C$ values in the forming carbonates toward those more typical of thermogenic methane. Hence, a range of isotopic signatures is possible for the carbonate–carbon formed in marine sediments associated with methane seepage (Fig. 9A). The resulting deposits are designated as "methane-derived carbonates", or seep-carbonates.

The zone of AOM may occur at depth in the sediment column or, if in a region of advective seepage of methane, it might be located only a few cm's below the sediment–water interface (cf. Mazzullo, 2000). AOM may also occur at the seafloor or in the water column, in settings bathed by oxygen-depleted seawater (e.g., Black Sea microbial carbonates; Thiel et al., 2001; Michaelis et al., 2002). In sediments beneath the zone of AOM, continuing CO_2-reduction in an almost closed system drives methanogenesis such that the residual CO_2-pool becomes increasingly enriched in ^{13}C. Carbonates may precipitate from the isotopically-enriched CO_2, with $\delta^{13}C$ values up to $+34‰$ PDB (Budai et al., 2002). These ^{13}C-enriched carbonates are not specifically considered to be markers for methane seepage because they form in a variety of environments in the zone of (archaeal) methanogenesis (e.g., Budai et al., 2002; Hesse et al., 2004; Jahren et al., 2004). However, in some places where active methane migration has occurred, these isotopically distinctive carbonates may develop at shallower depths, owing to sulfate-depletion caused by methane oxidation (cf. Gaillard et al., 1992; Mazzullo, 2000; Greinert et al., 2001; Burns et al., in press). They also may form as late-stage, pore filling cements during burial diagenesis of seep-carbonates (e.g., Peckmann et al., 2002). This isotopically unusual type of deposit can even be found in seafloor environments, where erosion and submarine canyon formation have exposed otherwise deeply buried sediments (cf. Sample and Reid, 1998; Stakes et al., 1999; Paull et al., 2005).

During carbonate development in the sediment column of seepage areas, the potential for mixing of carbon sources can produce overprinting or masking of the original conditions. Moreover, in Mesozoic and Paleozoic seep deposits, burial diagenesis has commonly influenced isotopic signals, especially for oxygen (Fig. 9A; Campbell et al., 2002). Hence, interpretation of a methane association for any marine calcareous deposit cannot rely solely on the stable isotopic signatures of the carbonate. An integrated analytical approach is the best method to elucidate hydrocarbon seepage and its effects on organisms and sediments, especially for ancient deposits (e.g., Campbell et al., 2002; Peckmann et al., 2002, 2003; Conti et al., 2004).

Stable isotopic signals from other materials besides authigenic carbonates also provide clues to the intricacy of biogeochemical cycling at seeps. These include records from the sulfur isotopes of pyrite, carbon and oxygen isotopes of benthic foraminiferal tests, and the composition and ^{13}C content of microbial sedimentary lipids. For example, low,

Fig. 9. The products (A) and processes (B) of carbon flow and isotopic fractionation in seep-carbonates. (A) Carbon and oxygen stable isotope distributions of Phanerozoic seep-carbonates, their sources, and main biological and chemical factors that influence variability in their signatures. Modified from Campbell et al. (2002). Carbon source(s) of Group III modern category may have originated from meteoric input, deep-seated fluids tapped by faults or tectonic erosion, clay mineral dehydration and/or diagenesis (cf. Sample et al., 1993; Terzi et al., 1994; Sample and Reid, 1998; Stakes et al., 1999). HMC, high magnesian calcite; c, calcite; a, aragonite; d, dolomite. (B) Schematic diagram of the oxic, sulfate reduction and methanogenic zones, and the related methane–carbon isotopic signatures (left; after Whiticar (1999)). Right side shows important geochemical reactions for organic matter degradation (1.1, 1.2), methane formation (methanogenesis; 1.3 and 1.4 + 1.4a), and methane consumption (methanotrophy; 1.5 and 1.6), as well as the types of carbon species formed, and where enhancement of carbonate precipitation occurs due to release of HCO_3^- (1.2 and 1.5). The respective fractionation factors α indicate, for example, a very strong enrichment of ^{12}C in biogenic methane produced via CO_2-reduction, which at seeps might be transported into the sulfate reduction zone where AOM converts it back to HCO_3^-. Fractionation equations and C-pathways are from Iversen and Jørgensen (1985), Alperin et al. (1988), Masuzawa et al. (1992), Botz et al. (1996) and Whiticar (1999). Diagram modified from Greinert (1999) and used with the author's permission.

but highly variable $\delta^{34}S$ signals in framboidal pyrites of modern and ancient seep-carbonates illustrate the importance of bacterial sulfate reduction as the source of sulfides (Kohn et al., 1998; Peckmann and Thiel, 2004). Furthermore, $\delta^{13}C$ and $\delta^{18}O$ values of benthic foraminifera have been used to demonstrate historical methane fluxes within modern and ancient seep sediments (e.g., Martin et al., 2004; Martin and Nesbitt, 2004; reviewed in Levin, in press). The variable and negative carbon isotopic signatures of foraminiferal tests may be better hallmarks of methane flux through sedimentary pore waters than larger seep mega-invertebrates such as clams, which secrete their shells over a broader range of conditions (Rio et al., 1992; Levin, in press; but see also Ba/Ca ratios in vesicomyid shells in Torres et al., 2001). Negative carbon isotope excursions from methane-influenced, benthic foraminifera and diagenetic carbonates have been used to implicate abrupt, widespread gas hydrate release at various times in Earth's history (Dickens et al., 1995; Kennett et al., 2000; Pierre and Rouchy, 2004). However, foraminiferal tests must be free from diagenetic alteration in order to provide meaningful paleoenvironmental signals (Cannariato and Stott, 2004; Martin et al., 2004).

The isotopic composition of lipid biomarkers measured in sediments from modern Eel River seeps yield consistent values despite spatial variations recorded in pore water geochemistry and $\delta^{13}CH_4$ (Orphan et al., 2004). Hence, biomarkers are refractory in nature, recording past methane-oxidizing microorganism assemblages that are sometimes discordant with present-day geochemical profiles (Orphan et al., 2004). In fact, time-averaging of infaunal foraminifers at seeps, methane isotopic overprints upon sediments, and unusual sedimentary distributions of methanotrophic microbial lipids, all introduce greater complexity in attempts to reconstruct the geochemistry of sedimentary pore waters through time (cf. Inagaki et al., 2001; Barbieri and Panieri, 2004; Cannariato and Stott, 2004; Martin et al., 2004).

3.4. Ages of seep deposits

Ages of some modern and sub-Recent, methane seep-related carbonates and barites have been estimated using ^{14}C, $^{230}Th/^{234}U$, or $^{210}Pb/^{226}Ra$ dating (e.g., Aharon et al., 1997; Nähr et al., 2000; Greinert et al., 2002; Torres et al., 2002; Gulin et al., 2003; Teichert et al., 2003). For instance, Pb/Ra barite ages from Californian seeps suggest rapid growth rates of 0.2–1 cm/yr, implying that large barite deposits could build within 50 kyr at redox boundaries where ascending fluids with barium and methane would have encountered sulfate-rich marine waters (Nähr et al., 2000; Torres et al., 2002; Johnson et al., 2004). For authigenic carbonates, such as in the Gulf of Mexico (GOM), uranium–thorium measurements show that extinct seeps found at upper bathyal depths were active during the Late Pleistocene (195–13 ka; Aharon et al., 1997). Aharon et al. (1997) argued that the current phase of vigorous seepage at mid-bathyal and abyssal depths has occurred from 12.3 ka to the present, suggesting that sedimentary loading and salt diapirism opened fault conduits to the seafloor at the end of the last deglaciation. In another example from Hydrate Ridge, Cascadia, U/Th dating of authigenic, methane-derived carbonates indicates two distinct phases of precipitation. Gas hydrate-associated carbonates yielded an age range from ~1.4–4.7 ka (Teichert et al., 2003). The carbonates have positive $\delta^{18}O$ isotopic signatures owing to hydrate dissociation (cf. Fig. 9A). They also exhibit distinctive, vuggy lithologies typical of origination from gas hydrates, including mud-clast breccias cemented with high-magnesian calcite or aragonite, and yellow, layered to bubble-rich, pure aragonite precipitates (cf. Greinert et al., 2001; Bohrmann et al., 2002). These particular carbonate lithologies — termed "clathrites" — with their distinctive isotopic signatures, are now being utilized to fingerprint gas hydrate involvement in their formation (e.g., Han et al., 2004; Teichert et al., 2005). At Hydrate Ridge, long-lived, seafloor carbonate development occurred by vigorous methane seepage through faults, with an extended age range of 7.3–267.6 ka (Teichert et al., 2003). The seep-carbonates appear to have precipitated during glacial times at low sea level, thereby sensitively recording fluid flux changes in sedimentary pore waters (Teichert et al., 2003).

3.5. Deposit sizes and potential longevity indicators

Size of deposits and duration of venting and seepage have been used to assess the origin and significance of fluid cycling in Earth's crust through geologic time. For instance, the large size of some modern seafloor hydrothermal vent deposits forming at slow spreading ridges — e.g., TAG mound, MAR, indicating high-temperature activity of 40–50 kyr duration — appears to be the product of both a steady heat-source and long-lived, focused, structural conduits for fluid upflow (Lalou et al., 1993; Hannington et al., 1995). By contrast, faster spreading ridges (e.g., EPR) are more likely to produce smaller deposits from shorter-lived hydrothermal deposition because of the tectonically disrupted nature of their depositional settings (Hannington et al., 1995, Fig. 28, p. 146). Therefore, size appears to approximate duration of hydrothermal activity for at least some modern hydrothermal vent settings. Regardless, even large, modern hydrothermal vent deposits reach only 4 million tonnes in volume (TAG, MAR), which is small compared to many analogous, ophiolite-hosted VMS deposits in the geologic record (Hannington et al., 1995, Fig. 29, p. 147). Indeed, some ancient seafloor hydrothermal systems were significantly larger than those active at today's oceanic spreading centers, especially for brine related SEDEX deposits (Hannington et al., 1995). Of the largest ancient hot vent deposits, which are found in sedimented rifts, there is no modern analog for their development from plume fallout into stagnant basins over millions of years (Hannington et al., 1995, Fig. 30, p. 148). Thus, more diverse styles of venting and different types of volcano–tectonic host settings are represented in the geologic record compared to modern oceanic spreading centers.

In modern seeps, high carbonate content in sediments has been correlated with intense methane fluxes and concentrated, microbial AOM (Ritger et al., 1987; Orphan et al., 2004, and references therein). Some large ancient deposits also display a diverse fossil content (e.g., Eocene Bear River deposit, Washington, Goedert and Squires, 1990; Miocene Rocky Knob deposit, New Zealand, Campbell et al., 1999), which might be a tempting factor to correlate with seepage duration. Nonetheless, some small ancient deposits are taxonomically rich (e.g., Eocene Humptulips locality, Washington; Goedert and Squires, 1990), whereas some large deposits yield low diversity (e.g., West Fork Satsop River deposit, Washington; Campbell, 1995). Thus, sizes of ancient seep deposits are highly variable and diversity does not necessarily correspond with longevity. Instead, deposit size and fossil content may indicate other factors at play, such as diversity shifts with seafloor depth of seepage, differential predation pressures, influence of sea-level change on seepage, or precipitation mainly in the subsurface rather than at the seafloor (cf. Sibuet and Olu, 1998; Aiello et al., 2001; Campbell and Nesbitt, 2004; Majima et al., in press).

If deposits can be dated (Section 3.4), then dispersal mechanisms and longevity of vent–seep communities can be evaluated, particularly over geologically significant time intervals. Several studies have intimated that sites of cold hydrocarbon seepage are longer-lived, more chemically benign, and therefore ecologically more stable compared to hydrothermal vent environments (e.g., Sibuet and Olu, 1998; Turnipseed et al., 2003, 2004). Because taxa are shared between the two habitats at relatively high taxonomic levels, some have postulated that the modern hydrothermal vent fauna is derived from hydrocarbon seep groups (see Sections 4, 5). Callender and Powell (2000) studied the long-term history of chemosymbiotic clam faunas in the northwestern GOM using down-core trends in abundance, biomass and trophic dynamics. They found that some seep sites remained as continuously viable and geochemically optimal habitats over a few hundred years, but typically were not persistent over geologically relevant time periods (Callender and Powell, 2000). Levin et al. (2000, 2003) also have assessed patchiness and perseverance in modern seep habitats offshore of Eel River, northern California. They found that spatial patterns in sulfide availability influence the microdistribution of the smaller-sized infauna (Levin et al., 2003). However, the seeps also appear to function as ephemeral, small-scale disturbances, which do not persist long enough for chemosynthesis-based specialization to become established in the smaller size classes of infauna (Levin et al., 2000). Thus far, seep deposits in the stratigraphic record show a variable range of fossil diversity (Table 1) and size, from carbonate "needles in a haystack" within voluminous siliciclastics (e.g., Fig. 4B; cf. Nesbitt and Campbell, 2004a), to giant, long-lived systems showing linked plumbing and extensive features of seafloor expulsion (e.g., Schwartz et al., 2003).

4. Origin and evolution of the vent–seep fauna

The origin and evolution of an endemic vent–seep fauna is a complex and somewhat controversial topic. Two main hypotheses are currently being evaluated in the biological and paleontological literature, summarized here from Little et al. (1998), Little and Vrijenhoek (2003), and Yamaguchi et al. (2004). The first is the "glimpse of antiquity" hypothesis, i.e., that the modern vent and seep environment is an extinction-resistant refuge, harboring Mesozoic and Paleozoic relic taxa (e.g., barnacles of southwest Pacific vents and seeps). A second hypothesis is that rapid bursts of adaptive radiation, frequent extinction events, and repopulation from shallower (?) settings better characterize the vent–seep environment. The first hypothesis predicts similar taxonomic structure between modern and ancient vents, as well as direct ancestor–descendant relationships among at least some taxa. The second predicts fewer shared characteristics between modern and ancient groups.

Molecular studies of living vent–seep biota suggest fairly recent diversifications during the past 100 million years (reviewed in Van Dover et al., 2002). Some of these modern estimates correspond reasonably well with existing fossil data, i.e., the possible Mesozoic origin of vesicomyid bivalves (Kanie and Nishida, 2000; higher sequence divergences reported in Goffredi et al., 2003, than previously), or the likely Mesozoic origin of neomphaline gastropods (McArthur and Koop, 1999; Kiel and Campbell, in press). Others are more discordant, such as the apparent Silurian or Devonian origins of vestimentiferan tubeworms at vents and seeps based on fossils (Little et al., 1997, 1998; Peckmann et al., in press), versus molecular divergence estimates of no older than Mid-Mesozoic (~125 Ma; reviewed in Little and Vrijenhoek, 2003). In addition, the fossil record of mytilid bivalves extends back to the Late Jurassic (~150 Ma, Campbell et al., 1993; see also Section 5), yet limited 18S rRNA divergence among modern vent–seep bathymodiolin mussels implies a more recent origin (~22 Ma) from wood and whale bone habitats (Distel et al., 2002; Little and Vrijenhoek, 2003). It is equivocal whether older fossil vent–seep mytilids or worm tubes are closely related to modern groups. These taxa generally are characterized by morphological conservatism, a challenge for taxonomic identification (Little and Vrijenhoek, 2003). Also, the possibility exists that the modern vent–seep fauna may represent parallel or convergent radiations from common stem ancestors, with the implication that most modern vent–seep taxa are not living fossils from the Paleozoic (McArthur and Tunnicliffe, 1998; Little and Vrijenhoek, 2003; but see Yamaguchi et al., 2004 for continuing debate).

Finally, the strong spatial association of certain rhynchonellide and terebratulide brachiopods from many older Mesozoic and Paleozoic vent–seep deposits appears to be a robust evolutionary pattern. Brachiopods were among the dominant vent–seep taxa from the Silurian through the Early Cretaceous (Fig. 10), but were largely replaced, beginning in the Late Jurassic, by various bivalve and gastropod families with modern affinities (Campbell and Bottjer, 1995a,b). Despite the gap in occurrences of vent–seep deposits worldwide from Early Carboniferous to Early Jurassic (Campbell and Bottjer, 1995a; Peckmann et al., 2001; Gómez-Pérez, 2003), vent–seep endemic "lineages" of rhynchonellides may have existed, such as the Carboniferous to Early Cretaceous *Dzieduszyckia–Ibergirhynchia–Peregrinella* "succession" (Campbell and Bottjer, 1995b; Gischler et al., 2003). This hypothesis has been challenged by Baliński and Biernat (2003), who suggest that structural comparisons of the crura among groups affords different familial placement. They also purport that shell and matrix carbonate from Devonian Polish and Moroccan localities bearing *Dzieduszyckia* do not show the classic seep signatures of ^{13}C-depletion in carbonate–carbon. However, carbon and oxygen isotopes of unaltered megafaunal shell material from modern and ancient seeps are expected to fall within a range close to normal marine conditions (cf. Fig. 9A). Furthermore, Peckmann et al. (unpublished data) have studied the *Dzieduszyckia* carbonates from the Khenifra site, Morocco, where they measured ^{13}C-depletion in carbonate–carbon indicative of derivation from hydrocarbon seepage.

The rare reports of modern vent–seep 'affiliated' brachiopods (listed in Little et al., 1998) appear to be related more to habitat preferences than signifying a direct physiologic relationship to venting. In other words, brachiopods appear to be attracted to a few vent–seep settings today because they serve as hardgrounds for attachment (cf. Díaz-del-Río et al., 2003) and/or provide access to high concentrations of bacterioplankton to be filtered from the water column.

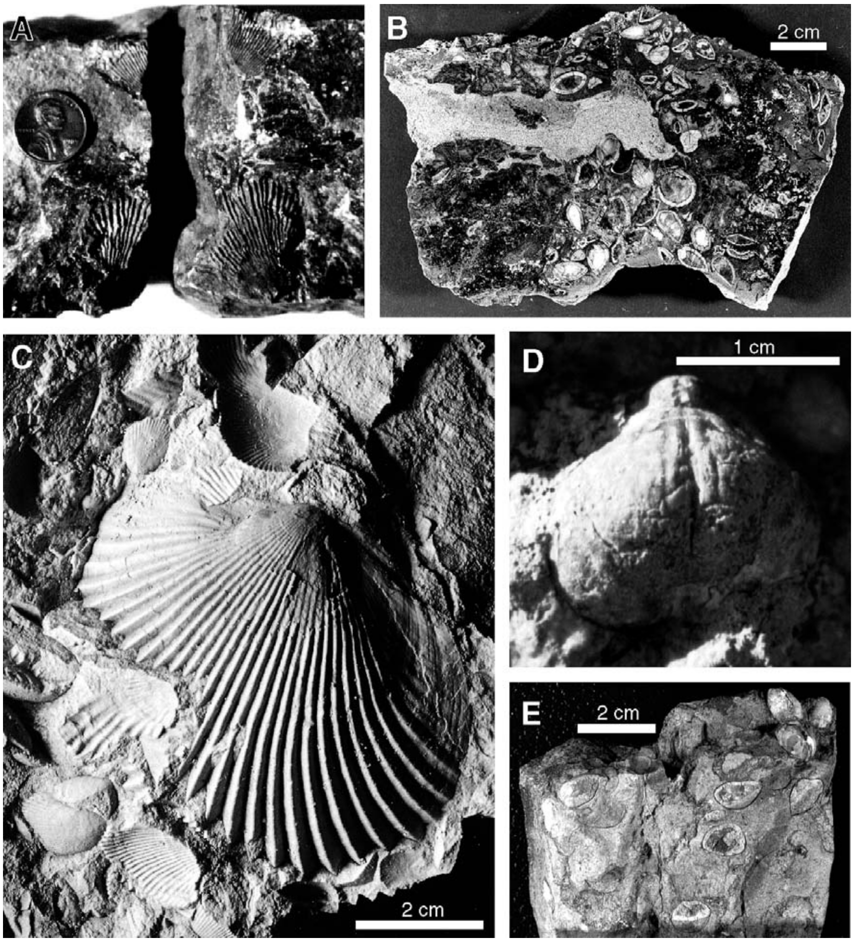


Fig. 10. Brachiopod fossils in some Paleozoic and Mesozoic hydrothermal vent and hydrocarbon seep deposits. (A) *Dzieduszyckia* sp. molds in massive barite, Devonian cold seep deposit, Lakes mine, Tuscaroa Range, Nevada, U.S.A. Photograph courtesy of T.E. Dubé. (B) *Ibergirhynchia contraria* in cross-section. Carboniferous seep-carbonate, Harz Mountains, Germany. Photograph courtesy of J. Peckmann. (C) *Peregrinella whitneyi*, Lower Cretaceous seep-carbonate, Wilbur Springs, California, U.S.A. (D, E) *Cooperrhynchia schucherti*, Upper Jurassic seep-carbonate, Paskenta, California, U.S.A.

As yet, there is no certain evidence that modern or ancient brachiopods are or were chemosymbiotic. In the past, they may have been ecological generalists in low-oxygen settings, as many brachiopods are today (Campbell and Bottjer, 1995b).

5. Vent–seep paleobiogeography

5.1. (Paleo)biogeography of selected taxa

Although taxonomic studies of ancient vent–seep fossils are by no means complete, various patterns already are emerging with respect to their paleobiogeographic associations. For example, vesicomyids are ubiquitous in modern hydrocarbon seeps and hydrothermal vents, and are known for their trans-oceanic migration capabilities using seeps, vents and whale falls as stepping stones for their dispersal (Peek et al., 1997; Sibuet and Olu, 1998; Van Dover et al., 2002; Kojima et al., 2004, and references therein). Similarly, fossil vesicomyids are also widespread in Cenozoic hydrocarbon seep deposits worldwide (Table 1). They are especially common in the seep fossil record of Japan (Majima et al., in press), where the oldest vesicomyid of Cretaceous age also has been reported

(Kanie and Nishida, 2000). However, the apparent prevalence of cryptic species among vesicomyids (e.g., Vrijenhoek et al., 1994) will be difficult if not impossible to resolve in the fossil record. At modern seeps, vesicomyids appear to be restricted to deep-water environments (Sahling et al., 2002, 2003; Kojima et al., 2004, and references therein; Paull et al., 2005; Majima et al., in press). Predation pressures in shallower waters (Sahling et al., 2003) and/or sea-level differences in the past (Majima et al., in press) have been suggested as explanations for the lack of these clams in shallow seep settings. Furthermore, the absence of vesicomyids was noted from a shallow-shelf, "diffuse" Pliocene seep deposit in western Washington (Nesbitt and Campbell, 2004a), where solemyids dominate the fossil assemblage (e.g., Fig. 4B). Compared to vesicomyids, solemyid bivalves are low-sulfide specialists (cf. Sahling et al., 2002), and therefore may have been better adapted to patchy, diffuse seepage in this high-sedimentation, shallow marine paleoenvironment.

One striking geographic aspect of modern seep faunas is the apparent absence of methanotrophic/thiotrophic bathymodiolin mussels from eastern Pacific sites of the remnant northern Farallon Plate region (i.e., offshore California, Oregon, Washington), despite their abundance in Atlantic and western Pacific hydrocarbon seep areas today. Sibuet and Olu (1998, p. 553) found this ". . .remarkable considering that several different areas along the American and South American margins have been explored. The genus *Bathymodiolus* is absent from all 11 hydrocarbon seep areas investigated in the eastern Pacific, even though species of this genus are elsewhere represented by large populations." More recently, mytilids have been reported from hydrocarbon seeps offshore Costa Rica (Bohrmann et al., 2002; Han et al., 2004). These seeps are associated with Cocos Plate subduction, representing the southern remnant of the once larger and contiguous Farallon Plate. In addition, the stratigraphic record of Mesozoic and Cenozoic seep-carbonates along the northeastern Pacific margin is replete with mytilid fossils. Eocene and Oligocene seep deposits in western Washington, U.S.A., commonly contain small mytilids (Goedert and Squires, 1990; Squires and Goedert, 1991; Goedert and Campbell, 1995; Goedert et al., 2000, 2003a), which recently have been placed by Kiel (in press) within *Bathymodiolus*, i.e., *B. willapaensis* (Squires and Goedert). Furthermore, *Modiolus modiolus* has been reported from Pliocene seep-carbonates of the Quinault Formation, western Washington (Campbell, 1992). Upper Jurassic and Lower Cretaceous seep-carbonates of California also enclose mytilid fossils, e.g., *Modiola major* (Gabb) (cf. Campbell et al., 1993, Fig. 2). The description of Gabb (1869, p. 192) noted "a fine species, well-characterized by its size, being the largest species of the genus with which I am acquainted. Some specimens are over six inches in length." With further taxonomic study, especially of juvenile forms (S. Kiel, pers. comm. 2004), it may be possible to establish the familial level placement of these northeastern Pacific, seep-associated mytilids.

Given the extensive fossil record of mytilids in ancient seeps of western North America, it is baffling to continue to chronicle the lack of modern chemosymbiotic mussels from seeps of the transpressive Californian margin, and those of subduction zones associated with the Juan de Fuca and Gorda Plates. Unsuitable habitats or larval migration barriers to this corner of the northeast Pacific (cf. Sibuet and Olu, 1998) appear to be untenable explanations for the missing mytilids, since they were abundant in western North American fossil seeps from the Late Jurassic through the Pliocene (~150–3.5 Ma). In the future, it is likely that at least the Central and South American record of modern and ancient seep-associated mytilids will increase with further discoveries along this less well-explored continental margin (cf. Bohrmann et al., 2002; Han et al., 2004).

Once a more complete, worldwide, vent–seep fossil taxonomic database is available (cf. Kiel, in press), then more detailed comparisons will be possible between similar modern and ancient groups. This will more accurately establish the timing and dispersal paths of various lineages. For example, Collins (1998) characterized three fossil species of bathymodiolin mussels in Miocene seep-carbonates of New Zealand. One of the fossil species is quite similar morphologically to the modern Japanese vent–seep mussel, *Bathymodiolus aduloides* (Collins, 1998). Another elongate form (Fig. 3; Collins, 1998) deserves comparison with the newly described bathymodiolin, *Gigantidas gladius*, from the Rumble submarine volcanoes of the southern Kermadec Ridge to the north of New Zealand (von Cosel and Marshall, 2003). In fact, several regions worldwide exhibit long histories of both offshore–modern and onshore–ancient seep occurrences (Japan, New Zealand, western U.S.A., Italy, Caribbean, South America; Fig. 1). Thus, there is much opportunity to compare taxonomic relatedness and history of fluid expulsion between geographically adjacent, past and present seep systems, especially for Cenozoic–Recent examples. Indeed, the fossil record of mussels throughout Phanerozoic vent and seep deposits may be critical in evaluating the hypothesis that modern deep-sea hydrothermal vent mytilids are derived from seep ancestors (Craddock et al., 1995).

5.2. Biodiversity considerations

Notwithstanding the limited fossil database at present, ancient hydrothermal vents (especially VMS deposits) are generally less diverse than ancient hydrocarbon seeps (Table 1). Some modern researchers have reported a similar pattern for some modern sites (cf. Sibuet and Olu, 1998; Turnipseed et al., 2003, 2004). Recently, however, Baco and Smith (2003) tabulated 469 macrofaunal species in hydrothermal vents worldwide, compared to 229 in seeps globally, utilizing data from both hard and soft substrates. It is well-known that taphonomic biases are especially prevalent in the hydrothermal vent fossil record, with taxa preserved only as external or internal molds in pyrite (Little et al., 1998, 1999a). Furthermore, small or soft-bodied taxa from ancient vents and seeps are still relatively underrepresented, but their numbers are rising with increasing scrutiny and taxonomic assessment, including that of trace fossils (Goedert and Benham, 1999; Little et al., 2002; Kiel, in press; Campbell and Nesbitt, 2004; Campbell et al., unpublished data). Hence, comparison of diversity among modern and ancient vent and seep sites is not a straightforward exercise at present.

On the other hand, study of ancient vent–seep deposits has some distinct advantages over their modern counterparts. For instance, evaluation of a modern soft-bodied infauna at vents and seeps is complicated by the requirement of box cores and sediment grab samples to appraise this buried biodiversity (cf. Sibuet and Olu, 1998; Levin, 2004). At ancient seeps, the abundance of trace fossils at some sites should provide clues to the nature and 3D distribution of the soft-bodied biota (e.g., Fig. 4B; Campbell and Nesbitt, 2004, and unpublished data). In addition, the preservation of a shelly infauna at ancient seeps is generally excellent (e.g., lucinid, thyasirid, solemyid, vesicomyid bivalves; Table 1). Moreover, organism–carbonate gradients have been recognized (e.g., Beauchamp and Savard, 1992; Campbell et al., 2002; Campbell and Nesbitt, 2004; Nesbitt and Campbell, 2004b). Finally, depth comparisons between modern vent–seep settings and their ancient counterparts also may widen understanding of the diversity and distribution of the associated organisms (cf. Majima et al., in press). For example, the solemyid bivalve, *Acharax*, is reported from modern seeps deeper than 2000 m (Sibuet and Olu, 1998). In contrast, this fossil is known to be abundant at a paleo-seep that was situated at shelf depths in the Pliocene (Campbell, 1992), and is also common in non-seep, reduced sedimentary paleoenvironments across varied paleo-depths. Thus, incorporating data from the fossil record provides a more complete picture of ecology and biogeography of vent–seep biota through time.

6. Research frontiers and future roadmap

Modern vent–seep research has exploded in its intensity in recent years, driven largely by several regionally extensive, well-coordinated and -funded research consortia of scientists from around the world (e.g., InterRidge program, ChEss project in Census of Marine Life Program, MBARI, and IFM-GEOMAR, to name a few). Through these and earlier efforts, it has become evident that hydrothermal vents and hydrocarbon seeps are ubiquitous in the world's oceans (e.g., Fig. 1; Van Dover, 1998). Studies of ancient vent and seep deposits also have increased (Table 1), but at a slower pace, and at the level of the individual researcher, or small groups of researchers typically working in discrete geographic areas. Hence at this juncture, several concurrent research paths are suggested to more fully elucidate the biogeochemistry, evolutionary history and biodiversity of vent–seep (paleo)environments worldwide.

6.1. Enhanced communication between biological and paleontological research teams

The time is ripe for research skills and perspectives from traditionally separate disciplines to be merged along several fronts, such as the study by Little and Vrijenhoek (2003) comparing vent fossils and molecular databases to identify research gaps and opportunities. The ChEss project in particular (ChEss Steering Committee, 2003) has held a workshop where biologists and paleontologists have identified key target areas for research that would enhance understanding of both modern and ancient systems. Some of these research foci for paleontologists include refining paleobathymetry; improving the known stratigraphic record of whale falls and their affiliated fossils (e.g., Squires et al., 1991; Goedert et al., 1995; Amano and Little, 2005; Nesbitt, 2005); identifying particular biogeographic patterns which may have traceable historical origins; initiating a vent–seep fossil database website linked to ChEss; and better integrating taxonomic, molecular biomarker, stable isotopic and mineralogic data sets for modern and ancient deposits (Little et al., 2003; Kiel and Gill, 2003). Moreover, molecular phylogenies should be completed for key living vent–seep taxa with familial representation in the fossil record (e.g., for provannid gastropods and stalked barnacles; Little and Vrijenhoek, 2003).

6.2. Taxonomic inventory of modern and ancient vent–seep sites

Typically the discoveries and identification of modern and ancient vent–seep (paleo)environments precede by several years the taxonomic work that must follow in order to inventory biodiversity and examine its (paleo)biogeographic patterns. Funding bodies are not well-known for rewarding taxonomic efforts of this kind, but such proposals must be argued for vigorously, especially in light of the global campaign to document biodiversity (e.g., Chirac, 2005), including that of the fossil record (Campbell, 2000). Both morphological and molecular studies should be conducted on modern vent–seep faunas. Long-lived lineages (e.g., lucinaceans, solemyids) should also be studied deep into the fossil record, as these groups have origins outside of seeps and vents, and provide evidence for the antiquity of the chemosymbiotic life strategy in bivalves (cf. Distel, 1998; Taylor and Glover, 2000).

6.3. Variability — causes and effects

The inherent variability of modern and ancient vent–seep settings has been more fully realized in the past five years. Future studies need to apply an integrated and comprehensive approach to characterizing known and newly discovered vent–seep (paleo)environments. Organism–fluid interactions could also be better elucidated at the scale of the organism (cf. Beauchamp and Savard, 1992; Campbell et al., 2002). Promising future research avenues include integrating suites of stable isotope measurements on carbonates, sulfides and sulfates, and fluid inclusion analyses, to better characterize the range in fluid types, pathways and geotectonic settings in which fluids cycle through Earth's crust. The timing of fluid flow during sedimentation, and the location of authigenic mineral formation (e.g., deep subsurface, or shallow near-seafloor) need to be better illuminated for modern and ancient deposits (cf. Campbell and Nesbitt, 2004). For ancient deposits, the magnitude and complexity of diagenesis needs to be unraveled to determine fluid types, geotectonic setting, and burial history. Also, the significance of recurring paragenetic sequences needs to be established with respect to this history, especially because similar mineral sequences have been identified in seep-carbonates of different ages and of widely separated paleobiogeography.

6.4. Paleobiogeography — patterns and their causes

The driving mechanisms for biotic transfer of vent–seep taxa across oceanic barriers and among habitats are variable and require further characterization. Well-preserved fossils remain the ground-truth for molecular divergence data derived from the living vent–seep fauna, allowing hypothesis testing with regard to possible biogeographic origins of modern groups (e.g., vestimentiferan distributions through time, discussed in Little, 2002). Furthermore, the generation, storage and migration of crustal fluids, and the distribution of tectonic plates through time exert fundamental controls on global vent–seep distributions, both temporal and spatial. Only coordinated geological and biological research efforts, in both ancient and modern systems, will allow visualization of the four-dimensional pattern of vent–seep (paleo)biogeography and evolution through time.

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