Chapter 4
Microbes in Modern and Ancient Hydrocarbon Seeps

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4.1 Introduction

Microbial ecosystems, chiefly consortia of methane-oxidizing archaea and sulfate-reducing bacteria, drive the metabolic factory at methane seeps. The higher trophic levels of these nutrient oases include brachiopods, mollusks, and vestimentiferans that feed off of the energy supplied by the microbes. The geological record of seeps as anomalous deposits of carbonate is also a byproduct of redox changes around localized microbial ecosystems. Paradoxically, the fossil record of the microbes themselves is very sparse and difficult to ascertain even though modern systems host up to hundreds of microbial aggregates per mg wet weight (Marlow et al. 2014; Knittel et al. 2018).

The difficulty in recognizing a fossil record of microbes at ancient methane seeps is related to several factors connected to fossilization. As body fossils, bacteria and archaea are rarely preserved in any environment due primarily to degradation by other organisms. Should a cell escape predation, the lack of a robust cell wall relative to diagenetic processes means that most organic material is altered to unrecognizable carbon deposits. If a cell happens to be permineralized or molded by carbonate or other minerals prior to structural destruction, its small size (~1–5 μm typical) makes it challenging to recognize. Further complicating recognition is the near lack of distinct morphological features associated with simple cocci and filaments. Of the known extant groups, all form simple spheres, rods, or spherical aggregates (Boetius et al. 2000; Orphan et al. 2002; Reitner et al. 2005). Trace fossils, such as stromatolites or thrombolites (Shapiro 2007), provide a better target, but the record of well-established microbialites at methane seeps is still poorly developed.

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A. Kaim et al. (eds.), *Ancient Hydrocarbon Seeps*, Topics in Geobiology 53,
https://doi.org/10.1007/978-3-031-05623-9_4

In this chapter, the current state of knowledge of modern seep microbial ecosystems is briefly reviewed, then there is a discussion of taphonomy, followed by a review of the known fossil record. The final section provides suggestions for a search strategy in future studies.

4.2 Current Knowledge on Extant Systems

The composition and metabolic pathways at modern seeps are well characterized at higher taxonomic levels and are driven by the primary fuel sources of methane and sulfate (Orphan et al. 2004). Consortia of anaerobic methane-oxidizing archaea (ANME-1, ANME-2, and ANME-3) and sulfate-reducing bacteria (SRB) belonging to the *Desulfocsarcina*/*Desulfococcus* group dominate (Hinrichs et al. 1999; Boetius et al. 2000; Lanoil et al. 2001; Orphan et al. 2001; Michaelis et al. 2002; Knittel and Boetius 2009; Niemann et al. 2006) (Fig. 4.1a). Specifically, pore water sulfate is reduced as a consequence of organic matter oxidation. Additional organic matter is consumed by methanogens (Martens and Berner 1974) producing methane in shallow sediments and defining a sulfate-methane transition zone (SMTZ). Methane in

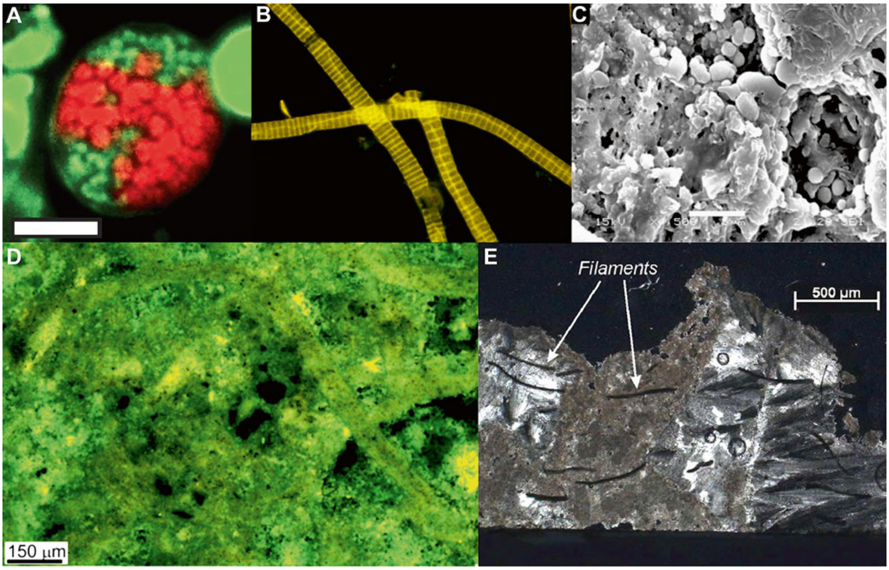

Fig. 4.1 Microbes in extant and fossil seeps. (**a**) Fluorescence imagery of an aggregate of an inner core of archaeal cells of ANME-1 surrounded by an outer shell of sulfate-reducing bacteria. (**b**) View of large sulfur-oxidizing bacteria typical of an active seep courtesy of Dr. Karen Lloyd. (**c**) SEM image of purported fossilized cells preserved within extracellular polymeric substance at a Cretaceous seep (Shapiro 2004). (**d**) Fluorescence image of fossilized filaments attributed to large bacteria from the Miocene of Italy (Dela Pierre et al. 2012). (**e**) Photomicrograph of sulfur oxidizers preserved in the carbonates at Hydrate Ridge (Teichert et al. 2005)

the SMTZ may also be supplied by older sources, either biological or thermogenic, migrating along faults and fractures or released by destabilizing frozen clathrates. In modern oceans, the sulfate reduction zone is generally 1–10 m thick, while the methane source zone may extend for 100 s of meters (Pohlman et al. 2013). In addition to the sulfate-driven-anaerobic oxidation of methane (SD-AOM) community, relatively large filamentous sulfide-oxidizing microbes such as *Beggiatoa*, *Thioploca*, *Thiothrix*, and *Arcobacter* are typically found at the sediment surface feeding off the sulfide byproduct (Jannasch et al. 1989) (Fig. 4.1b).

With regard to linking extant localized ecosystems to the fossil record, there are several potentials. First, because the process of SR-AOM raises alkalinity and draws down CO_2, there is the potential to preserve microbes in authigenic carbonates (Melim et al. 2016). Secondly, there are geochemical signatures, either as biomarkers or isotopic shifts, that might be preserved in the early cements showing sulfate reduction, methane oxidation, or a combination of the two processes. Finally, there is the rock record itself of anomalous deposits, primarily carbonates, that may show a linkage to a microbial origin.

4.3 Paths to Fossilization (Taphonomy)

As noted above, the fossil record of microbes at seeps is scanty, which is non-intuitive, as the microbial ecosystem fosters rapid precipitation of calcium carbonate (as well as barite, locally) and should favor entombment and preservation. However, the cells themselves are a rich source of organic carbon and thus are rapidly degraded in the natural setting.

Cells may fossilize through permineralization and more rarely secondary silicification. As in other, non-seep carbonate settings, most of the microbes are not obligate calcifiers, but their cell walls serve as a source for the nucleation of crystals. Rapid permineralization is required to preserve the cells in three dimensions. Once entombed, cells may be preserved as carbonaceous structures and recognized as such via Raman spectroscopy or similar analysis. In addition to carbonate, barite ($BaSO_4$) and sulfides are other potential primary precipitates that could persist in the rock record. Following entombment and burial, it is possible that subsurface fluids could foster replacement of the carbonate with silica, though evidence for this in the literature is not clear. Though not the focus of this chapter, it should be noted that a more likely path to fossilization is the preservation of more diagenesis-resistant biosignatures such as lipids and other chain hydrocarbons (see Miyajima and Jenkins this volume).

4.4 Microbial Fossil Record at Seeps

Microbial body fossils have only been recorded from a few seep locations in the rock record. This is not surprising as the most well-known microbe repository—stromatolites and similar structures—are only known to host fossil microbes in less than 1% of all reported cases. Very few papers purport to find microfossils in seeps—even in modern settings (e.g., Cavagna et al. 1999; Chen et al. 2005; Bojanowski 2007; Martire et al. 2010) (Fig. 4.1c–f).

In an early paper, Shapiro (2004) presented morphological evidence for microbes in the Cretaceous Tepee Buttes seep carbonates of Colorado. He noted that micropeloids (also known as "structure grumeleuse" in the literature; Bathurst 1976) potentially represent degraded microbial mats or extracellular polymeric substances (Fig. 4.2). The interpretation is based on the dominance of dark organic matter, indistinct margins compared to larger fecal pellets, and the variable sizes. Thus, micropeloid is a descriptive feature and is unrelated to fecal pellets. Other authors have used similar arguments to justify a biological origin for micropeloids (Chafetz 1986; Buczynski and Chafetz 1993; Peckmann et al. 2002). Though rare, morphological evidence for several different potential microfossil types is presented with caution and also acknowledging the context within the microfabrics. Coccoids, 0.5–1 μm in diameter, are found within micropeloids, specifically at the margins where cements initiate off of micropeloids. Though sheaths are also discussed, there is more caution in assessing a biological origin.

In a critical study of the offshore Eel River seep carbonates (Pleistocene), Bailey et al. (2010) employed multiple techniques toward morphologically distinctive clusters in the carbonates. The clusters resembled ANME colonies but lacked organic carbon. They concluded that the clusters are not biological but rather a diagenetic feature after framboidal pyrite. Similar features were also noted in Shapiro (2004). Framboidal pyrite is common in seep carbonates as well as in fossil whale falls (e.g., Shapiro and Spangler 2009) and other reducing environments and is not a

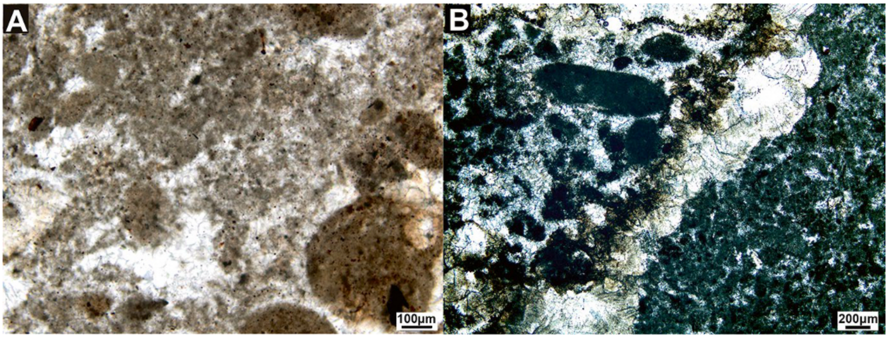

Fig. 4.2 Micropeloids. Two different images showing contrast of sub-micrometer micropeloids with diffuse boundaries associated with fecal pellets. (**a**) Cretaceous Tepee Buttes, Colorado, USA. (**b**) Jurassic Bedford Canyon, California, USA. Both views, plane-polarized light

robust biogenic feature. Interestingly, other authors have used the presence of framboidal pyrite as evidence of biological activity in seeps (Cavalazzi et al. 2012), burrows (Gong et al. 2008), and other environments. The argument is that while framboids may be created by abiotic processes, such as volcanism (e.g., England and Ostwald 1993), the temperatures are much higher than recorded in carbonate environments. In other words, at near standard surface temperature and pressure conditions, biological processes favor framboid formation (e.g., Ohfuji and Rickard 2005). Clearly, this is an exciting area, but more research needs to be carried out.

While the focus thus far has been on looking for fossil evidence of ANME colonies, there have also been reports of large fossilized filaments, suggestive of sulfide-oxidizing bacteria, similar to modern *Beggiatoa*. Teichert and others (2005) described such filaments from the sub-fossil Hydrate Ridge chemoherms. The thread-like, unbranched filaments are 7–25 μm in diameter and 120–715 μm long within the carbonate. The authors drew the similarity to the *Beggiatoa* filaments found at the surface. Similar structures were also noted by Barbieri and Cavalazzi (2005) in the Miocene of Italy who linked the preservation to the early extracellular production of aragonite, as described by Peckmann and others (2004). Putative filaments were also figured from the Miocene (Messinian) carbonates of northwest Italy by Dela Pierre and others (2012) and linked to coupled sulfate reduction-anaerobic oxidation of methane.

It should also be noted that an earlier paper on barite beds within the Devonian Slaven Chert of Nevada noted large fossil filaments (Graber and Chafetz 1990). Since that publication, the barite beds have been re-interpreted—at least in part—to be connected with methane seeps. This is based on the presence of limestone with ^{13}C-depleted isotope signatures and the presence of the dimerelloid brachiopod *Dzieduszyckia*. Subsequent studies have not identified the filaments for an updated context.

Larger, macroscale microbialites are more difficult to assess at seep localities. Structures that could be defined as stromatolites by displaying a laminated structure accreting off of a hard surface are rare, though described from modern seeps (e.g., Greinert et al. 2002; Himmler et al. 2018). They have also been described from the oldest known seeps, the Silurian El Borj limestone lenses of Morocco (Barbieri et al. 2004); Jurassic seeps of Antarctica (Kelly et al. 1995); Cretaceous Tepee Buttes of Colorado, USA (Shapiro 2004); and other locales (Fig. 4.3). A greater potential lies in deciphering the complex micrite and cement fabrics that are nearly ubiquitous at all seep sites throughout the geological column (e.g., Peckmann et al. 1999; Barbieri and Cavalazzi 2005). This alternation of euhedral-subhedral cements (aragonite or calcite), often with micrite, forming bands from millimeters to centimeters in thickness that "dome" across the deposits has typically been linked to redox changes in the venting fluid. Petrography and biomarker analysis were used in a study of Devonian Kess-Kess seep limestones from Morocco to suggest a clear microbial origin for laminated texture (Guido et al. 2013). Recently, Hryniewicz and others (2020) published descriptions of stromatolitic crusts dominated by crystalline calcite as opposed to micrite.

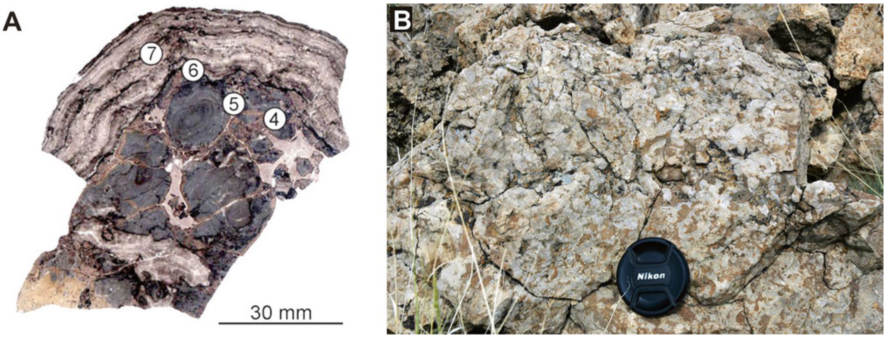

Fig. 4.3 Microbialitic textures. (**a**) Stromatolitic crust developing off of intraclasts, Miocene Tanohama Limestone, Japan (From Hryniewicz et al. 2020). (**b**) Field photo of thrombolItic textures, Cretaceous Tepee Buttes, Colorado, USA

4.5 Search Strategy for Future Studies

As demonstrated by this review, the microbial consortia, so ubiquitous in active seeps and responsible for the raising of alkalinity and production of carbonate, have largely eluded detection in the rock record. Future efforts are recommended to focus on the following strategies: target specific petrofabrics and fabric boundaries, incorporate new technologies as they develop, and connect potential morphological features to clearer geochemical proxies.

4.5.1 Targeting Particular Petrofabrics

Seep carbonates throughout the geological record share similar petrofabrics, specifically botryoidal cements, yellow calcite, micrite, and micropeloids. While none of these are unique to seeps, the mosaic of complex fabrics as well as dissolution boundaries typifies seep carbonates. Active microbial communities are often found at the interface of micrite and botryoidal cements (Fig. 4.4). Examining this boundary should be a primary target option. As noted in this review as well as previous papers, "micropeloids" on the order of 10s to 100s of micrometers in diameter and with diffuse margins may be directly related to microbial consortia or extracellular polymeric substances. This fabric in particular may yield preserved cells with proper preparation and study of extremely well-preserved deposits.

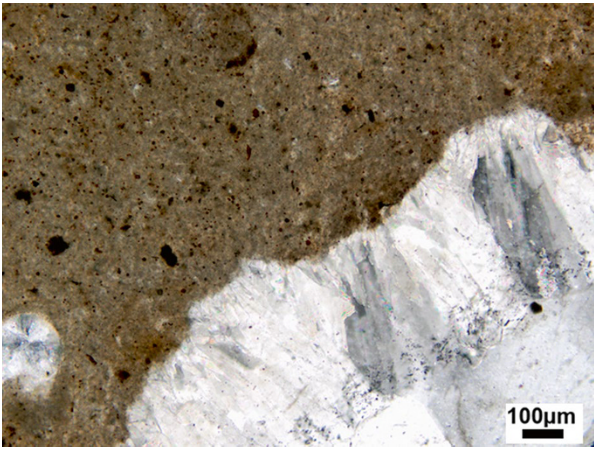

Fig. 4.4 Potential microfabric targets for future research. Interface of primary cements and underlying sediments

4.5.2 Utilization of More Focused Technologies

Twenty years ago, the major tools employed in the search of microbial fossils were high-resolution transmitted light and scanning electron microscopes. The ability to focus analyses such as cathodoluminescence, X-ray diffraction, and secondary ion mass spectrometry at the sub-micrometer scale will help target potential microfossils. These techniques, as well as others such as X-ray absorption and Raman spectroscopy, have already been applied to studies of ancient stromatolites (e.g., Brotton et al. 2007).

4.5.3 Connection with Clearer Geochemical Proxies

For many years now, paleontologists have relied on robust biomarkers such as isoprenoids and hopanoids to record preservation of the SD-AOM ecosystem (Peckmann and Thiel 2004; Birgel and Peckmann 2008). With increasing resolution requiring less material, specific petrofabrics can be targeted for biomarkers and then evaluated for microfossils. Additionally, there has been a recent drive to apply other techniques such as rare earth elements (Zwicker et al. 2018; Bayon et al. 2020; Smrzka et al. 2020), sulfur and other isotopes (Feng et al. 2016), and clumped isotopes (Thiagarajan et al. 2020) to pinpointing both evidence of microbial activity and specific metabolisms or vital effects (See Cochran et al. this volume).

4.6 Conclusions

The microbial fossil record at methane seeps is exceedingly poor compared with the density of cells at active seeps. This parallels the known record from other microbialites such as stromatolites and wrinkled sedimentary structures. Furthermore, reliance on morphological evidence is often dubious as the archaea and bacteria known from seeps have simple morphology and there are well-established pseudofossils developed from mineralogical precursors. While a few microbial trace fossils (e.g., stromatolitic or thrombolytic crusts) have been documented, other presumed, abiotic petrographic features such as crystalline bands, sulfides, and micropeloids need to be further explored. Finally, there needs to be stronger correlative evidence from biomarkers and other geochemical proxies to substantiate claims of recognizing fossilized microbial activity. These corroborating proxies are going to be most critical as evidence for past seeps are being pushed further back into the geological past beyond the macrofossil record.

Acknowledgments The author appreciates discussions over the years with Kathy Campbell, Jörn Peckmann, Andrzej Kaim, Robert Jenkins, Michal Jakubowicz, Victoria Orphan, and Shana Goffredi. Yusuke Miyajima and Jennifer Zwicker provided careful and valuable reviews that greatly improved this contribution.

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