9(a) Paleogeography of Microbial Mats in Terrigenous Clastics – Environmental Distribution of Associated Sedimentary Features and the Role of Geologic Time

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Introduction

In classical studies of the relationships between organisms and environments, the environment or palaeoenvironment is defined by a range of physical and chemical parameters (water depth, energy regime, temperature, salinity, etc.). Whether or not an organism can live in a given environment depends on its ability to tolerate or adapt to the given conditions, and whether suitable food sources are available. For elephants for example, the environment needs to be situated in tropical latitudes and must support sufficient plant growth, and as a consequence elephants only occur in tropical Africa and Asia. Other organisms, such as rats, are known for their ability to extract sustenance from a great range of environments and are found across the globe. Thus, in general terms one should expect that environmental parameters do have an impact on what types of organisms will thrive in a given locale.

Yet, biofilms and microbial mats have been reported from such a wide range of environments that one might think that environmental parameters exert little influence. Once a moist substrate and an energy source are provided, microbial mats will enter the scene quickly as long as grazers are kept at bay. Most of us can probably recall multiple examples of 'opportunistic' mats (Figure 9(a)-1) from visits to construction sites and other areas affected by human impact. Microbial mats are found in the deep oceans surrounding hot spring vents (Figure 9(a)-2A), and even deeper, coating fracture surfaces within ocean floor basalts (Cregg et al., 1992; Reysenbach and Cady, 2001). They occur near methane seeps at various depths, on the ocean floor, the continental slope, and even the continental shelf (Joye et al., 2004; Reitner et al., 2005). We also find them in areas where oxygen concentrations are below the threshold of metazoan grazers (Schulz et al., 1996; Bernhard et al., 2000), regardless of actual water depth (Figure 9(a)-2B). Because of comparatively easy access, the study of tidally influenced sedimentary environments has generated the largest number of published records on modern microbial mats (e.g., Gerdes et al., 2000a; see Chapter 2 for images). Yet, modern microbial mats do not stop at the ocean's edge. We find them in fluvial settings, such as in rivers and streams with a low sediment load (Figures 9(a)-2C, -2D), in lakes (Figure 9(a)-3A) and hot spring pools (Figure 9(a)-3B) (Ward et al., 1998; Last and Ginn, 2005), in deserts as cryptobiotic soil crusts (Figure 9(a)-3C) (Belnap and Gardner, 1993; Eldridge and Green, 1994), and in the frozen expanses of Antarctica beneath the permanent ice cover of lakes (Figure 9(a)-3D) (Hawes and Schwarz, 1999; Sabbe et al., 2004).

Once the above examples (Figures 9(a)-2 and -3) are examined in detail it becomes clear, however, that each given environment presents unique challenges, and that in each case different consortia of bacteria are involved in mat formation. Biofilms and microbial mats are ubiquitous in a multitude of environments not because they are some highly adaptable organism, but rather because mat formation appears to represent a very effective strategy for optimising microbial survival in a wide range of environments. It is a strategy that apparently is employed with great success by a large variety of microbial communities (Figures 9(a)-2 and -3). Common to many mats is that they enhance sediment cohesion and resistance to erosion, as well as stabilizing vertical chemical gradients within the sediment. Thus, their mechanical interactions with the sediment, such as for example the formation of fold-overs, rip-ups, roll-ups, ripple patches, domal buildups, etc. (see Chapter 3), may be

qualitatively similar for mats that were produced by distinctively different microbial consortia. In the rock record, therefore, we may find that sedimentary features left behind by photosynthetic cyanobacterial mats that thrived in the photic zone (Figure 9(a)-1B and Chapter 2), may be quite similar to those found in much more distal and deeper water settings that may actually testify to the former presence of chemosynthetic microbial mats (Figure 9(a)-2B and Chapter 7(e)). Yet, although features due to mechanical interactions can not help us to make that distinction, the associated diagenetic minerals, as well as geochemical fingerprints, may point us in the right direction (Logan et al., 1999a).

Chronology of microbial mats

At the very beginning of the history of life on Earth, primitive life forms may well have tested multiple approaches to optimise microbial survival. By the time of the Apex Chert microbiota (Schopf, 1993), however, at ~3.5 Ga, microbial fossils are already so similar to modern counterparts that they must represent considerable evolution from the earliest microorganisms. At this point in time as well, microbial mats and stromatolites already show the structural and textural features that they maintain for the remainder of Earth history (Hofmann et al., 1999). We must conclude then that at least as far back in time as 3.5 Ga, microbial mats comparable to modern counterparts were already a common presence in marine and marginal marine environments. Evidence for microbial mats in

terrestrial environments, such as rivers and lakes, goes back as far as 2.7 Ga (Buck, 1980; Buick, 1992), and geochemical considerations suggest that as early as 2.6 Ga microbial mats had become a factor in soil formation (Watanabe et al., 2000). It is therefore reasonable to assume that by Late Archaean times at the latest, microbial mats most likely flourished in all environmental settings that we find them in today. In essence, from that point forward we can expect to find them in any conceivable environment that meets their moisture, nutritional, and energy needs.

Microbial mats and (palaeo-)environmental settings

As indicated above, because of the ubiquity of microbial mats across a broad range of environments, the mere presence of mats in a given rock unit has limited value for the assessment of palaeoenvironment. In Precambrian sediments, however, this shortcoming is partially mitigated by the lack of bioturbation that allows much better preservation of all types of sedimentary features, including those that are related to mat-sediment interaction. In addition, specific features of microbial mat deposits, such as for example elongated domal buildups, 'soft' microbial sand chips, and rigid curved sand chips (Garlick, 1981, 1988; Schieber, 1998a; Pflüger and Gresse, 1996; Bouougri and Porada, 2002; Sarkar et al., 2006), can give information about environmental energy levels, episodes of desiccation and reworking, etc., and thus allow narrowing of the number of feasible environments.

The published literature gives the impression that microbial mat features are most common, in the rock record, from deposits formed within high energy shallow marine settings. This, however, is most likely a perception skewed by fortuitous availability of exposures (sandstones make better exposures than mudstone-dominated successions) and because their identification is easier due to an abundance of modern analogues (see Chapter 2). Scattered reports of, for example, subtidal, distal deep basin, fluvial, and lacustrine environments (e.g., Schieber, 1986; Eriksson et al., 2000; Yeo et al., 2002; Prave, 2002; Sur et al., 2006) indicate that future systematic study of all terrigenous

clastic rock types is likely to erase this bias.

Having indications of terrestrial and potentially pedogenic microbial mats as early as the Late Archaean (Watanabe et al., 2000) also speaks to another conundrum, the common occurrence of extremely pure quartz arenites in Proterozoic and lower Palaeozoic strata. While long thought of as a result of multicycling and aeolian abrasion, we do have evidence for first-cycle quartz arenites in the Proterozoic that formed in the absence of the efficient chemical weathering that we associate with vascular land vegetation (Dott, 2003). This suggests that microbial crusts like the one illustrated in Figure 9(a)-3 already occupied Precambrian land surfaces, promoted intense weathering and destruction of chemically labile components, and left behind a quartzose residue that was then reworked into quartz arenites (Dott, 2003).

Many of the classic occurrences of microbial mat features in terrigenous clastics are found within epeiric marine coastal settings, such as for example the Mid-Proterozoic Belt basin of North America and the Palaeo- to Neo-proterozoic Vindhyan basin of India. The sandy nearshore facies of these basins has much in common with the famous tidal flats of Mellum Island in the North Sea, where much of the research on sandy microbial mats has been undertaken (see Chapter 2). Because most large basins preserved on cratons tend to be marine and are affected by relative sea level movements of both global and local origin throughout their history, widespread coastal marine facies will tend to dominate their rock record. Apart from anything else, the arenitic rocks formed within

most coastline settings will resist weathering and erosion more easily, and be topographically more prominent in forming accessible outcrops than central-basinal argillaceous rocks. Disputed ophiolites apart, very little of the Precambrian seafloor has been preserved in the record, once again enhancing the apparent importance of coastal

arenitic settings. However, in the succeeding section of this chapter, Catuneanu discusses the fact that certain mat-related features may have been preferentially preserved in Precambrian subtidal shelf settings rather than the higher energy coastal palaeoenvironments. He attributes this feature to enhanced wind regimes (and thus concomitantly, enhanced wave energy) that affect the preservation potential of mat related structures within coastal facies.

Phanerozoic microbial mats

While today we still find microbial mats in all the ecological niches and environments that they presumably occupied in the Precambrian (Figures 9(a)-2 and -3), the advent of metazoans in the Cambrian effectively ended 3 billion years of mat-dominated surface environments (Garrett, 1970). Yet, while metazoans might have laid waste to surficial mats, they did not eliminate their constituent microbes. The latter point is easily demonstrated by stratified and mat-forming

microbial assemblages in Winogradsky columns (microbiological enrichment columns; Sagan and Margulis, 1988) prepared from random soil and sediment samples (Figure 9(a)-4). In essence, the microbes that potentially form mats are ever-present in the environment, they just need a chance to thrive (Figure 9(a)-4). Thus, just like in areas disturbed by human activity (Figure 9(a)-1) where microbial mats are early colonisers, they probably did the same in Phanerozoic environments when the prior ecosystem had been disrupted by 'catastrophes', such as storms, volcanic eruptions, impacts, etc. If these disruptions were short-lived, the mats probably were soon after eaten and/or destroyed by returning metazoans, making for negligible preservation potential. If, on the other hand, disruptions resulted in environmental change that adversely affected metazoans, such as high salinity, lack of oxygen, etc., thick mats with a potential to be preserved in the rock record could form. Thus, although the evolution of metazoans in the Cambrian caused a major shift in mat preservation, mats could still develop given an opportunity.

The Proterozoic–Phanerozoic transition not only witnessed a major reduction of threedimensional mat proliferation, but also a shift to abundant development of thin biofilms around discrete particles (Seilacher and Pflüger, 1994). Fragmentation of sandy or muddy mat surfaces by metazoans, in tandem with current and wave reworking, probably was a major factor in the formation of features like 'algal biscuits', oncoids, and generally coated grains. These mobile 'granular mats', such as microbially formed oncoidal pyrite grains in the Ordovician Winnipeg Formation of Saskatchewan, Canada (Schieber and Riciputi, 2005), might have been of less interest to metazoans because they did not offer a contiguous food supply, and as loose grains were more difficult to graze on. Regard-less of these changes, however, we still find evidence of mat colonisation in Phanerozoic terrigenous clastics (see Chapter 7), and a growing awareness on how they might be identified will probably lead to recognition in many additional places, even when partially obscured by grazing and bioturbation.

Conclusions

As pointed out above, although in times past microbial mats may have been as widespread environmentally and geographically as today, not all locales may have offered the same preservation potential. While processes of mat erosion and deformation may well be similar between environments occupied by photosynthetic mats versus those covered by chemosynthetic mats, the mats might have offered different levels of 'resistance' under otherwise identical conditions of flow. Because photosynthetic cyanobacteria are very adept at mat generation (Chapter 2), lighting conditions are most likely an important factor for the growth of many structured mats in the rock record. Our current knowledge base about modern mats constructed by chemoautotrophs is much smaller than that for photosynthetic microbes. More work needs to be done on modern chemosynthetic mats if we, for example, want to evaluate whether coccoidal bacteria-rich mats from the Triassic deep sea (Mastandrea et al., 2006) could indeed form a sustainable mat.

If one sees microbial mat-related structures as part of the larger continuum of physically-formed sedimentary structures, such as suggested by Noffke et al. (2001a) in an adaptation of the well-known Pettijohn and Potter (1964) classification, then mat-induced features may not be any more facies-specific than their physically-formed counterparts.

Noffke and co-workers (e.g., Noffke et al., 2001a, 2006a, 2006b) instead suggest that microbially-induced sedimentary structures (MISS) are very facies-specific. They also relate them to regression-transgression turning points, and thus imbue them with very specific sequence stratigraphic meaning as well. As can be seen in Section 9(b) of this chapter, this is to be disputed. Those who work in modern mat-bound clastic sedimentary settings, such as the famous Mellum Island in the North Sea, or the tidal flats and sabkhas of the Tunisian coast, will obviously find it easy to establish direct relationships between mat-related structures and well-defined depositional environments (e.g., Gerdes et al., 1985b, 1985c; Noffke et al., 2001b). The same applies, however, to most investigations

of modern sedimentary settings and their component physically-formed sedimentary structures. Elucidation of palaeoenvironments from the rock record is almost always a much greater challenge with a less certain result.

The relatively limited reports on the occurrence of ancient mat-related structures and the observed distribution of their modern counterparts can be integrated to predict the palaeoenvironmental distribution of the various mat-related features. Because the palaeoenvironmental relationships of mat features is seldom very specific, they are presented here within a broad framework: coastal, shallow sea/lake, deep sea/lake, fluvial and aeolian settings. The first includes beach, intertidal–supratidal, delta plain, coastal swamp, etc. above mean sea level, while the second includes the generally agitated shallow water environments like the shoreface and the shelf beneath mean sea level.

The third covers the quiet deep-water environments, which may only occasionally be agitated. Table 9(a)-1 shows features in sandstone, and Table 9(a)-2 their equivalents in shale, in their respective palaeoenvironmental context (bar thickness stands for relative abundance, as reported or projected).

In summary we can say that probably since the Late Archaean, microbial mats and the microbial communities that form them have occupied every conceivable ecological niche on the planet, much as they do today (Figures 9(a)-1, -2 and -3). Many published examples of microbial mats in terrigenous clastics are from marginal marine sandy deposits, both in the Precambrian and the Phanerozoic. This bias, however, will probably gradually disappear as we learn how to more reliably identify microbial mat deposits in other facies and lithologies. A major shift in mat preservation occurred with the evolution of metazoan grazers in the Cambrian. Mats still grew whenever given a chance, but typically were 'eaten' or destroyed almost as fast as they formed. Thus, extensive sediment colonisation with a potential for preservation in the rock record was severely curtailed. Nonetheless, we do find evidence of mat colonisation in Phanerozoic terrigenous clastics (see Chapter 7), and a growing awareness on how they might be identified will probably lead to recognition in many other places, even when partially obscured by grazing and bioturbation. Integration of textural studies that focus on sediment rheology as influenced by microbial binding, with mineralogical/geochemical studies should help our ability to identify which microbial 'lifestyle'

(e.g., photosynthesis versus chemosynthesis) dominated a given mat community.

	Table 9-1: Features in Sandstones (see Chapter 3)							
		+	Shallow	Deep	oenvironm Fluvial	ent Aeolian	Remarks	
eatures	Multi- directed, Palimpsest Ripples		Sea/lake	Sea/lake			Very shallow water to fair weather wave base. Most likely preserved in coastal to shallow sea/lake settings.	
	Surface Ornamentation, Wrinkle Structures, ''Elephant Skin" etc.						Judging from modern analogs these should be most common in coastal to shallow sea/lake settings. Potentially also associated with shallow water bodies on floodplains and coastal plains.	
	Domal, Convex-Up Features						Current energy required for accretion, thus more likely in shallow water settings. In high energy coastal settings poorer development due to erosion? May occur locally in fluvial channels with strongly episodic sediment transport.	
	Petecs & Ridges						Modern analogs suggest need for at least one of the following: strong shear forces, desiccation, or gas expansion. Thus, coastal and other very shallow water environments most likely.	
Mat-related features	Cements & Floating Grains						It helps if surface sediment maintains similar pore space chemistry for extended time periods (small sedimentation rates). Coastal to shallow/deep sea/lake should be most common environments.	
	Sand Cracks, Manchuriophycus etc.						Requires desiccation, thus mainly expected in coastal and fluvial environments. Also possible in intermittently moist interdune depressions.	
	Ripple Patches						Within fair weather wave base, need for powerful erosive events. Coastal setting most likely. Minor occurrences shallow offshore?	
	Flip-Overs, Roll-Ups, Sand Chips						Strong currents/wave action needed. Most likely to form in coastal environments. Petering out into deeper water. Potentially also in moist terrestrial settings.	
	Curved Samd Chips						Desiccation and strong currents required. Most likely in terrestrial and coastal environments	
	Gas Domes & Kinneyia						Shallow water favors formation of larger gas buildups. Likely environments are coastal and possibly shallow ponds on floodplains.	

Mat Decay Minerallization	Permanently water-logged pores enhance preservation potential. Thus, preservation more likely in shallow-deep sea/lake settings. In terrestrial environments only if sediment is continuously water-logged for long periods of time.
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	Table 9-2: Features in Shales (see Chapter 3)								
	Palaeoenvironment								
Mat-related Features		Coastal	Shallow Sea/lake	Deep Sea/lake	Fluvial	Aeolian	Remarks		
	Wavy- Crinkly						Probably best preserved below storm wave base. Preservation unlikely in environments with ready oxygen access (oxidation of organic matter), such as terrestrial and supratidal. Exception for areas with permanent water cover (lakes, swamps, lagoons). Potential for preservation also in wet interdune depressions with clay-rich sediment.		
	Bed- Smoothing						Because the surface of coarser layers (granule to pebble size particles) is to be smoothed, more likely observed in coastal and shallow sea/lake settings.		
	Domal Build-up						Current energy probably required for accretion, thus more likely in shallow water settings. In high energy coastal settings poorer development due to erosion?.		
	Striped Shale						Requires episodic sedimentation to cover mats, thus not too distal is better. Coastal unlikely because of reworking. Shelf below storm wave base most likely. In deeper water only when influx of storm and flood reworked sediment possible.		
	False X-laminae						Best developed where there are abundant small sediment pulses during mat growth. Should be best developed in shallow sea/lake environments below storm wave base.		
	Lamina-specific Grain selection						Requires across-mat sediment transport by currents, thus effect seen more likely in higher energy settings.		
	Random Mica Flakes						Requires across-mat sediment transport by strong currents, thus effect seen more likely in higher energy settings. Also need for early cement formation. Thus not as likely in terrestrial environments.		
	Rafted Grain Cluster						Could occur everywhere, but best recognized in the most fine grained facies.		

-	Irregular Impressions			 Requires surfaces of still somewhat moist, stiff mud. Microbial flakes derived from dried out mats on mud surfaces. Impossible in permanently water covered areas. Most likely to occur in coastal supratidal settings, alluvial floodplains, and interdune depressions.
	Roll-Ups, & Flip-Overs,		 	 Related to erosion/transport, thus should be more typical for higher energy settings. Offshore transport has to be considered. Roll-ups of thin organic "skins" may also be found in current affected deeper water environments. Not as likely in environments affected by desiccation (rigidity factor), but desiccated-curled mat fragments may look very similar.
	Mat Decay Mineralization			 Permanently water-logged pores enhance preservation potential. Thus, preservation more likely in shallow-deep sea/lake settings.

Figures

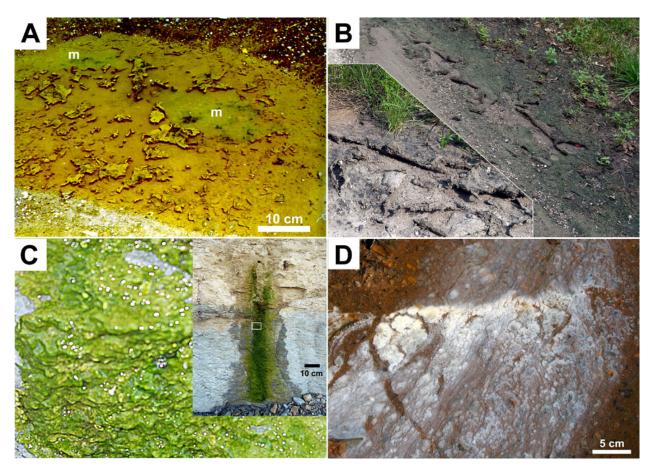


Figure 9(a)-1: 'Opportunistic' mats in modern settings. (A) A modern puddle with benthic cyanobacterial mat on mud substrate (marked 'm'). Portions of the mat have floated up because of attached oxygen bubbles. Photo by J. Schieber. (B) Modern cyanobacterial mat in a roadside ditch on a sandy substrate. Fast currents during rainstorms have caused the mat to be partially eroded and/or 'flipped over' at the edges. Inset shows dried-out, cracked and curled mat from same locality. Vegetation for scale. Photo by J. Schieber. (C) 'Vertical' microbial mat on the wall of a construction pit (inset). Water flow from a spring provides continuous moisture. Photo by J. Schieber. (D) Whitish mat of acidophile bacteria that thrive in low pH runoff from a weathering exposure of pyrite-bearing black shale. Pyrite oxidation is the cause for low pH values. Photo by J. Schieber.

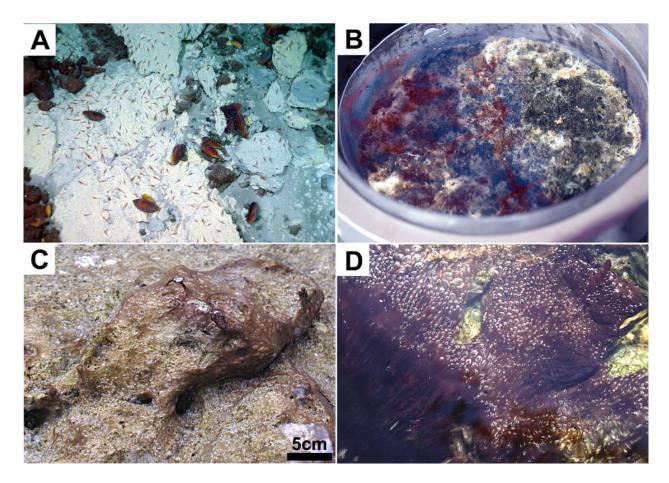


Figure 9(a)-2: (A) Thick, fragile mat of whitish sulphide oxidizing bacteria near a white smoker vent. The mat biomass constitutes the base of the food chain in this area and is utilized by small vent shrimp and larger mussels. Photo from NOAA Explorer web site,

http://www.oceanexplorer.noaa.gov/explorations/04fire/logs/april12/. (B) Top of sediment core from Santa Barbara Basin, offshore California. The whitish clumps and filaments are formed by the sulphide oxidizing bacterium *Beggiatoa*. This is a *Beggiatoa* mat in its early stages and will eventually cover the sediment surface with a solid layer of entangled filaments. Diameter of core barrel is 10 cm. Photo by J. Schieber. (C) Mat consisting of cyanobacteria and diatoms coating the bottom of a shallow creek near Sulfur, Oklahoma. The Creek normally has a very low sediment load because it is spring-fed. Photo by J. Schieber. (D) Same Creek as before, mat with abundant trapped oxygen bubbles (2-5 mm in size). Flow is from the upper right to the lower left. Photo by J. Schieber.

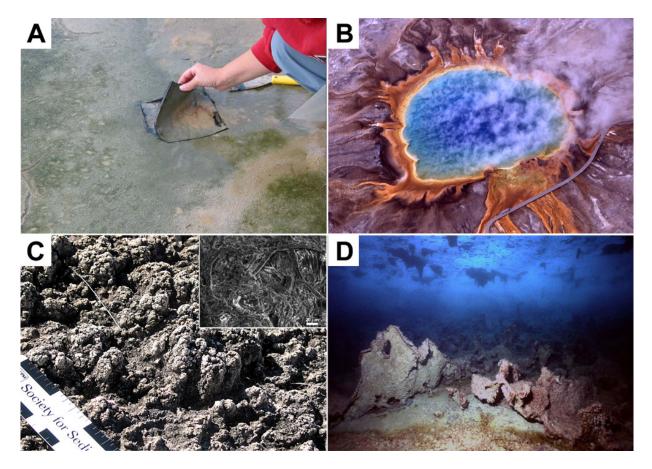


Figure 9(a)-3: (A) Example of living microbial mat near a saline spring, Lake Winnipegosis region, Manitoba, Canada. These mats can reach several centimetres in thickness and are often laminated (image courtesy of Last and Ginn, 2005). (B) Aerial view of the Grand Prismatic hot spring in the Midway Geyser Basin, Yellowstone National Park, USA. Steam is rising from the hot and sterile central portion (deep blue water). The orange colored periphery constitutes the much shallower overflow areas where the water cools rapidly as it moves away from the spring. The orange colour is due to microbial mats, and the concentric zonation marks microbial consortia with different temperature preferences. The spring is approximately 115 meters in diameter, and over 40 metres deep. Image courtesy of US National Park Service. (C) Rugged surface expression of cryptobiotic crust on desert soil from White Sands National Monument, New Mexico. Scale has long black bars of 1 inch length, and short black bars of 1 cm length. Inset shows scanning electron micrograph of crust surface with entangled microbial filaments and minerals grains. Both photos by J. Schieber. (D) microbial mats at the bottom of permanently ice covered Lake Bonney in Antarctica (depth ~ 5-6 m). These mats are photosynthetic in spite of low light intensities and can float up because of attached oxygen bubbles. Photo courtesy of Dale T. Andersen (© All Rights Reserved).

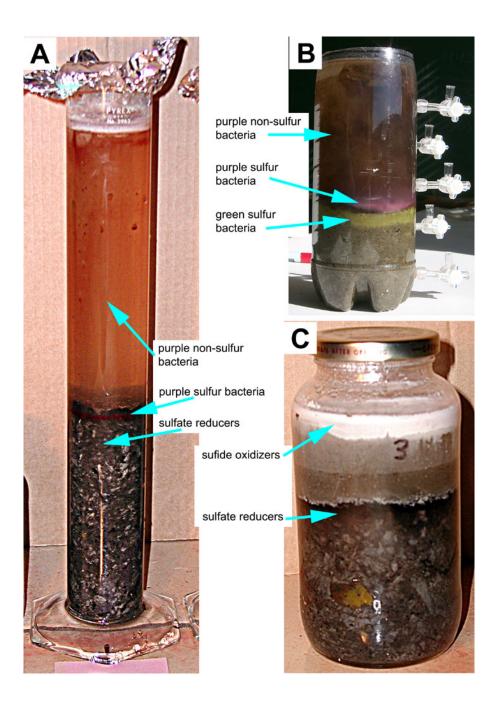


Figure 9(a)-4: Microbial stratification of Winogradsky columns prepared from lake mud. (A) Shows darkening by sulphate reducing bacteria in the bottom portion, a horizon with purple sulphur bacteria (anaerobic photosynthetic) just below the sediment/water interface, and purple non-sulphur bacteria (photoheterotroph, low H₂S tolerance) in most of the rest of the water column. Photo by J. Schieber. (B) Column has well developed zones of green and purple sulphur bacteria (just like in microbial mats from sandy tidal flats), overlain by water with purple non-sulphur bacteria. Image courtesy of Dr. Joe Vallino, Semester in Environmental Science, Marine Biological Laboratory, Woods Hole, MA 02543. (C) A column with restricted oxygen access. Shows well-developed darkened lower layer with sulphate reducing bacteria, and an upper layer (microbial mat) that consists of sulphide oxidizing bacteria. Photo by J. Schieber.

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