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PROCARYOTIC "COELACANTHS":
TUBE-FORMING MICROORGANISMS FROM SUBMARINE HYDROTHERMAL ENVIRONMENTS

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It has now been established that the extensive communities of unusual and oversized animals associated with present-day hydrothermal systems do not derive their nutrients from photosynthetically-fixed carbon but rather from chemosynthetic bacteria [1, 2, 3]. The source of nutrients for these bacteria is the hydrothermally-derived reduced gases, such as H_2S , H_2 , NH_3 and CH_4 , and various reduced metals, such as Fe and Mn [1, 2]. While it is apparent that the major source of bacterial primary production is within the vents [1], there are also extensive epiphytic colonies of bacteria on the surfaces of rocks and animals [2, 3]. Samples from the Galapagos hydrothermal vent communities have been previously studied [2, 3], and in November, 1979 samples were obtained from the East Pacific Rise diving site at 21°N.

Some of the hydrothermal vents at 21°N emit water at temperatures greater than 300°C [4]. Sulfides precipitate out of the hot vent waters to form chimneys. Pieces of these chimneys and their associated fauna (white-tubed polychaetes, small limpets and small crustaceans) comprised the sample suite upon which this report is based. Microbiological analyses of these samples revealed two groups of dominant microorganisms which form hollow, often filamentous, tubes. The tubes are readily encrusted with silica and other hydrothermal precipitates, giving the organisms the appearance of living fossils. Even more remarkably, they are morphological analogues of fossil organisms found in rocks from the Precambrian.

Figures 1 and 2 show two of the dominant microorganisms which were found on the sulfide chimneys from EPR 21°N. The filamentous tube structures seen in Figure 1 have an inside diameter of approximately

Figure 1 (A-J). Scanning electron micrographs showing one of the dominant tube-forming microorganisms found on the sulfide chimney rocks obtained from hydrothermal vents along the East Pacific Rise at 21°N. (A) A sulfide crystal. Note the many filamentous microorganisms. Arrow points to vertical filaments. Bar is 25 μm . (B) An extensive colony of thin tube structures showing many hollow openings at the ends of the tubes. Top arrow points to one of the hollow ends; bottom arrow points to branching of the tubes. Bar is 10 μm . (C) High magnification of the tube structure denoted by the top arrow in Fig. 1B. Bar is 1 μm . (D) Side view of the tube showing the tapering end. Bar is 1 μm . (E) Hollow tube extending out of the sulfide crystal; there appear to be bands around the tube. Arrow points to an apparently immature organism growing out of the crystal. Bar is 1 μm . (F) and (G) Tubes which have accumulated small sulfide crystals and other precipitated salts; precipitates significantly increase the width of the tubes. Bar in both figures is 10 μm . (H) Some of the commonly observed swollen or bulblike structures which are connected by the hollow tubes. These were most frequently seen when the chimney rock samples were crushed. Frequently, the ends of some of the tubes showed closed swellings existing either as a single structure or in pairs (Fig. 1I; lower arrow in Fig. 1B). Bar in Fig. 1H is 5 μm ; bar in Fig. 1I is 1 μm . (J) Filamentous tube with a dark band (arrow). Bar is 2 μm . Bands were frequently observed (Fig. 1H, arrow). The samples were fixed in sterile artificial seawater containing 2% glutaraldehyde within minutes after the Alvin surfaced. Sterile techniques were used with all specimens. The fixed samples were dried by the critical point method, then mounted on aluminum stubs and coated under a vacuum with a layer of gold 10-20 nm in thickness. The samples were viewed using an International Scientific Instruments Mini-SEM, Model MSM-2, scanning electron microscope.

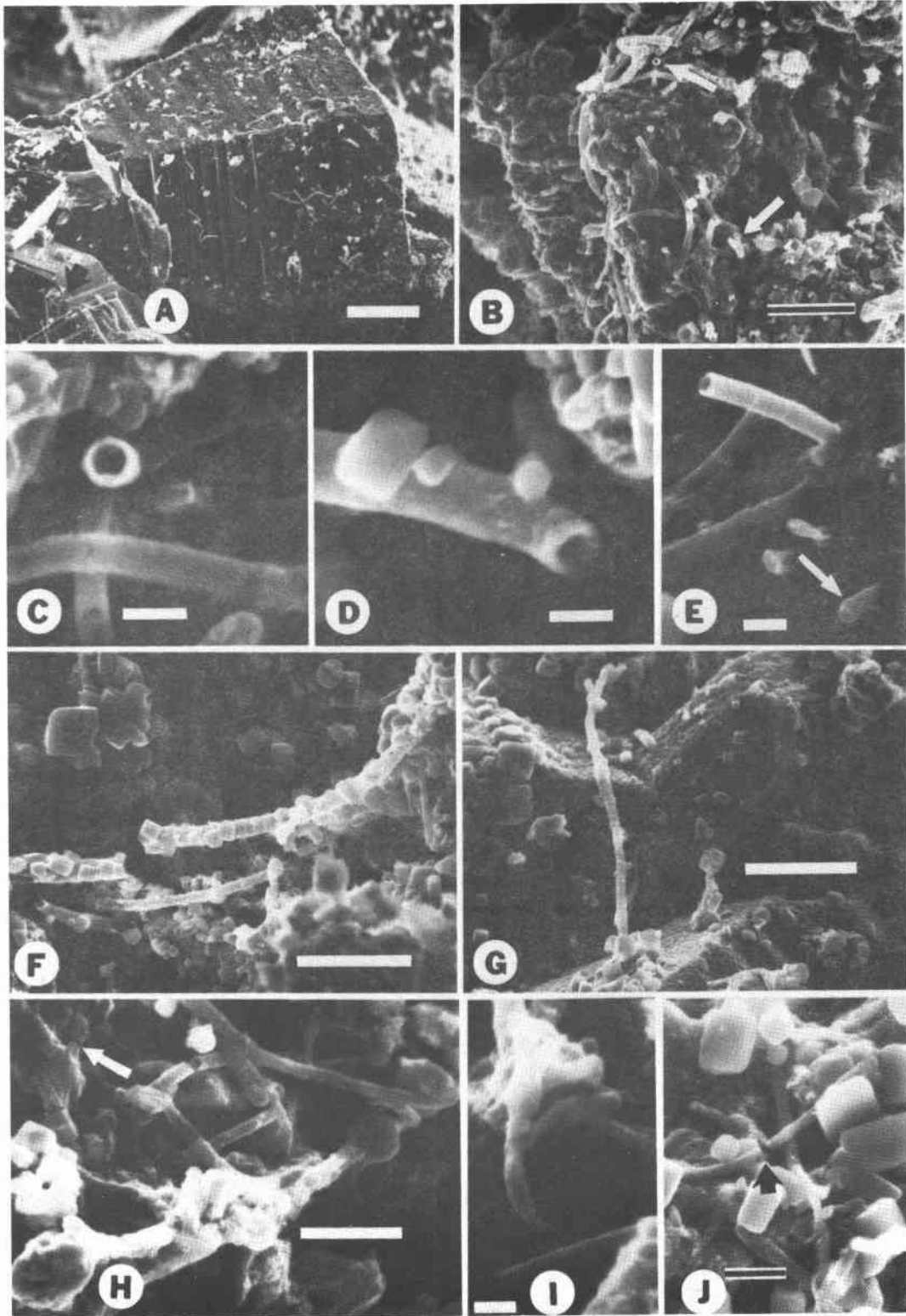


Figure 1.

0.5 μm and appear as hollow sheaths which are either attached to spherical, swollen, cell-like structures (Figure 1I) or have a closed and swollen end (Figure 1B, J). The latter structures are most frequently observed in crushed sulfide chimney samples. These tube-forming organisms resemble to some extent known metal-oxidizing, sheath-forming bacteria such as Leptothrix and Sphaerotilus spp. [5, 6]. However, the results of an EDS analysis of the tubes showed that they were composed mainly of silicon and that the levels of Fe, Mn, and Cu were minimal (Figure 3A). These were the most abundant tube-forming microorganisms observed.

While it is not known whether the silicon tubes are formed biotically or abiotically, the physical conditions in the environment around the chimneys definitely favor abiotic silicification. Hot vent waters enriched in silica are expelled into the cool ambient bottom water where the moderate hydrostatic pressures and alkaline pH of seawater favor precipitation of silica [7, 8, 9]. Amorphous silica was found to be a common constituent of the mounds and chimneys around vents along the East Pacific Rise [4]. The abiotic precipitation of silica sheaths around bacteria is known to occur in alkaline hot springs at Yellowstone National Park where modern silica stromatolites have been observed [10]. It is interesting to note that the silicification of procaryotic cells increases the apparent size of an organism and also results in the formation of distinct morphological characteristics more indicative of eucaryotic organisms. Thus, the interpretation of microfossils having a coating or sheath of silica or carbonate can be quite difficult [9]. The morphological forms shown in Figure 1 include classical akinite

structures, terminal branching, and ridge-like and septa-like bands around the tubes.

The elaborate tube-forming microorganisms shown in Figure 2 (A to I) have been observed on the surfaces of rocks and animals obtained from both the EPR at 21°N and the Galapagos Rift. These organisms form tubes which have a flexible top. The top extends over the inner vegetative cell. When the flexible tube is compressed, a head-like structure can be seen (Figure 2D). Usually only the accordion-like portion of the tube is observed. There is also an arrow-shaped hold-fast structure at the end of the tube. It is apparent that the structure of the organism is quite complex. The diameters of these tubes range from approximately 1 μm in the larger structures to less than 0.2 μm in the smaller forms. Analysis of these tubes showed that they did not contain significantly higher levels of silicon than the surrounding sulfide crystals; they also did not contain significant concentrations of iron and phosphorus. Because silicon and calcium are lacking and the levels of iron are low, it is presumed that the tubes are composed of an organic material, such as chitin or cellulose. The flexibility of the complex top portion of the tube implies that it must be composed of a non-rigid organic compound rather than a rigid inorganic polymer. Jannasch and Wirsen observed organisms similar to these on the surfaces of mussels obtained from the Galapagos Rift. On the basis of thin-section observations, they classified the organisms as procaryotes [2]. If this classification is correct, these highly-differentiated organisms are among the most complex procaryotes ever observed.

Fossil organisms identical in size and morphology to these chimney organisms have been described from many Precambrian formations. In

Figure 2 (A-J). Scanning electron micrographs showing a frequently-observed microorganism having a flexible tube. These organisms have been found attached to the surfaces of small limpets living on the sulfide chimneys of the East Pacific Rise at 21°N. (A) The surface of a limpet extensively colonized by these organisms. Bar is 5 μm . (B) Side view of the tube structures at different stages of development. Bar is 2 μm . (C) Top view of the tube-forming microorganisms; the flexible, "accordion-pleated" tubes are clearly visible and appear to be mostly collapsed. Bar is 2 μm . (D) The tubes here show extended tips of what are probably the microorganisms. Bar is 1 μm . (E) A view of the entire cell structure showing the flexible head on a tube which terminates in an apparent arrow-like holdfast structure. Bar is 2 μm . (F) A high magnification of the head structures showing the accordion-like pleats. Note the wide variation in the size of these structures. Bar is 2 μm . (G) A tube-forming organism found on the surface of a sulfide chimney rock which shows a structure on the tip of the tubes which appears to have the capability of opening and closing. Bar is 2 μm . The samples were prepared as described in the caption of Figure 1.

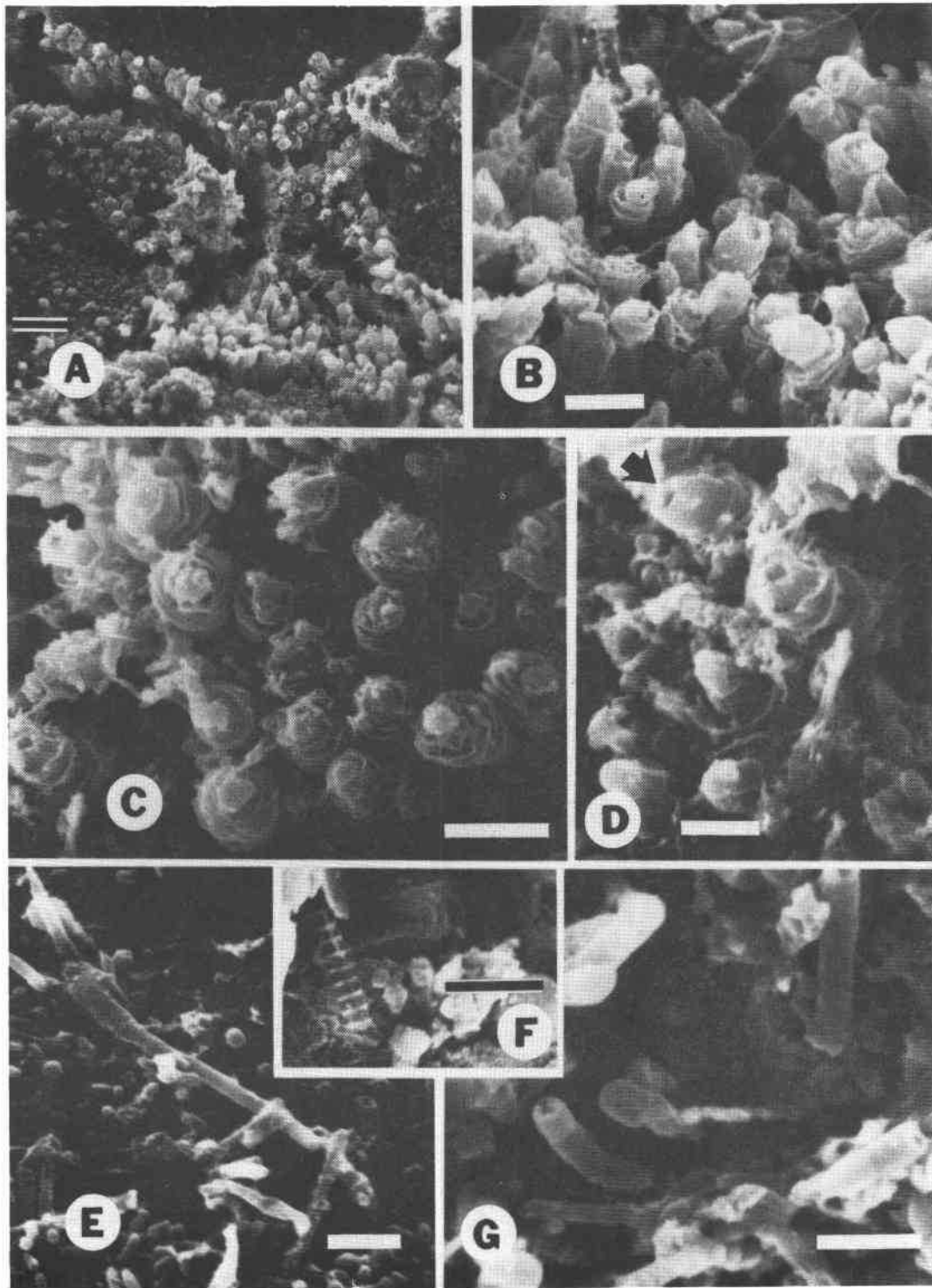


Figure 2.

particular, we will briefly discuss fossil occurrences in the Onverwacht Series, the Gunflint Chert, the Pahrump Group in northeastern San Bernardino County, and the Chuar Group from the Eastern Grand Canyon of the Colorado River.

The Onverwacht Series (> 3.2 billion years old) has been recently reinterpreted as being the remnant of an ancient oceanic spreading center [11]. Microfossils found in the Onverwacht and in the stratigraphically overlying Fig Tree Series were believed to be the oldest known fossils until the Isua discoveries [12, 13]. Engel, et al. [12] reported the discovery of filamentous and spheroidal forms of microorganisms. In some cases the spheroidal forms are closely associated with kerogen-bearing filamentous forms. They described these fossils as being "alga-like". The fossils are frequently found in chert horizons indicating that dissolved silica was abundant in the environment of deposition and that the conditions for the sort of abiotic silicification described above existed at that time. We have previously noted [14] the remarkable similarity between the kerogen-bearing filamentous microfossils in the Onverwacht and the strands of organic matter found on the surfaces of crystals, rocks and animals which we have observed on samples from the Galapagos Rise and the East Pacific Rise.

The Gunflint Chert (~ 2 billion years old) is part of the Animikie Series in the Thunder Bay District of Ontario, Canada. It seems highly probable that the environment in which the Gunflint formed included hydrothermal activity. Diabase intrusions outcrop along the southern edge of the Animikie between Gunflint Lake and Thunder Bay [15]. South of Horn, Ontario, the Animikie sediments rest on "ellipsoidal greenstones"

Figure 3 (A, B). Scanning electron microscopic and energy dispersive x-ray spectroscopic (EDS) analyses of the tube structures shown in Figures 1 and 2. (A) The top curve is a line scan of silicon over one of the tube structures from Figure 1. The uninterrupted line represents the area of x-ray analysis. The bottom scan is a total elemental analysis of the tube showing that it contains predominantly Si with small amounts of Fe and Zn. The same levels of Fe and Zn were found in the surrounding sulfide crystals. Bar is 2 μm . (B) A total elemental scan of the tube structures seen in Figure 2, A-E. The top scan line shows the elemental composition of the micro-organism, and the bottom scan shows the composition of the surrounding sulfide-coated limpet shell. The microbial tubes show higher levels of phosphorus (middle arrow) and iron (right arrow) than the surrounding surface material. The level of Si (left arrow) in the tubes is not significant. The samples were prepared for analyses in the manner described in the caption for Figure 1. They were observed and analyzed using a JEOL JSM-35 scanning electron microscope with EDS capability.

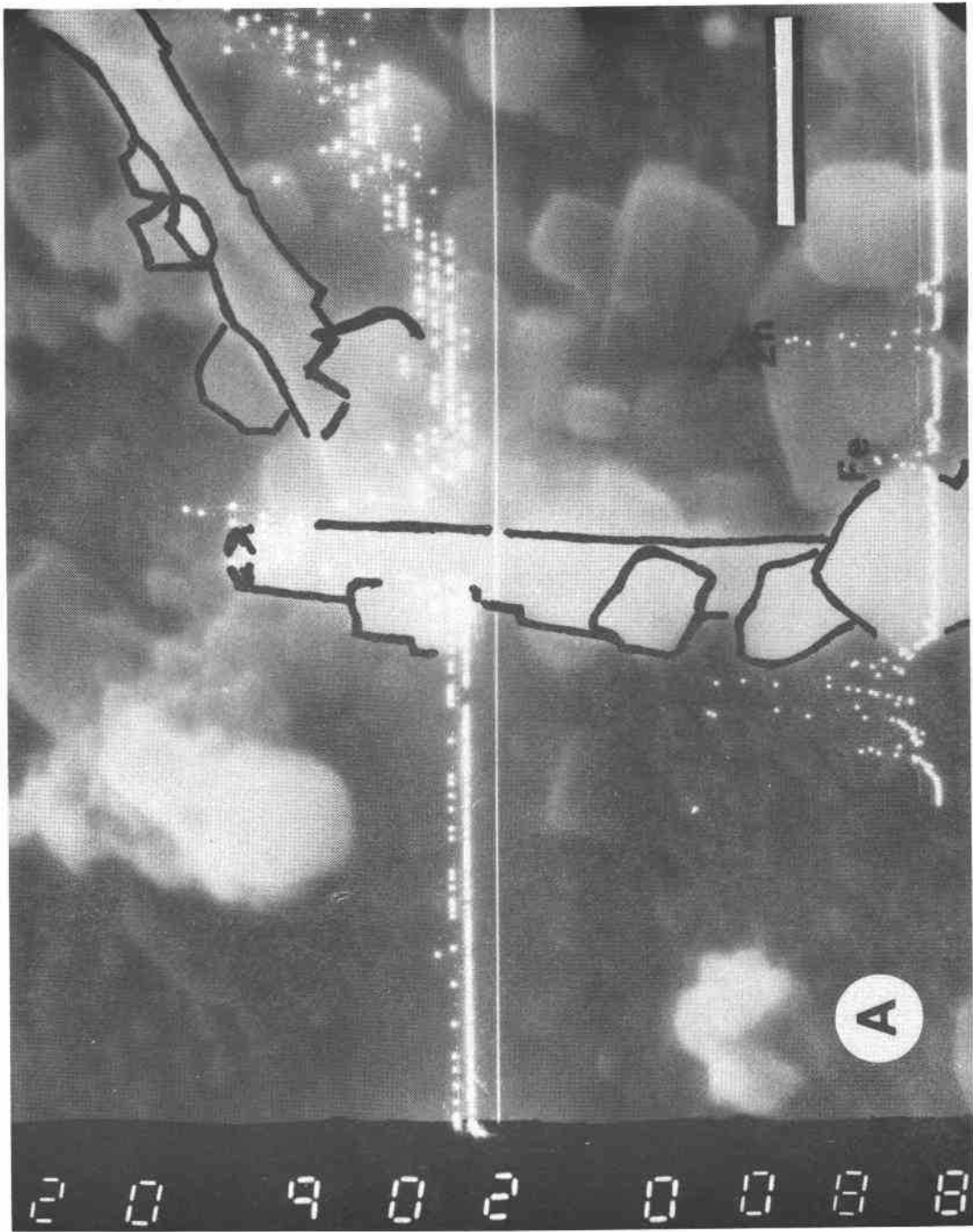


Figure 3A.

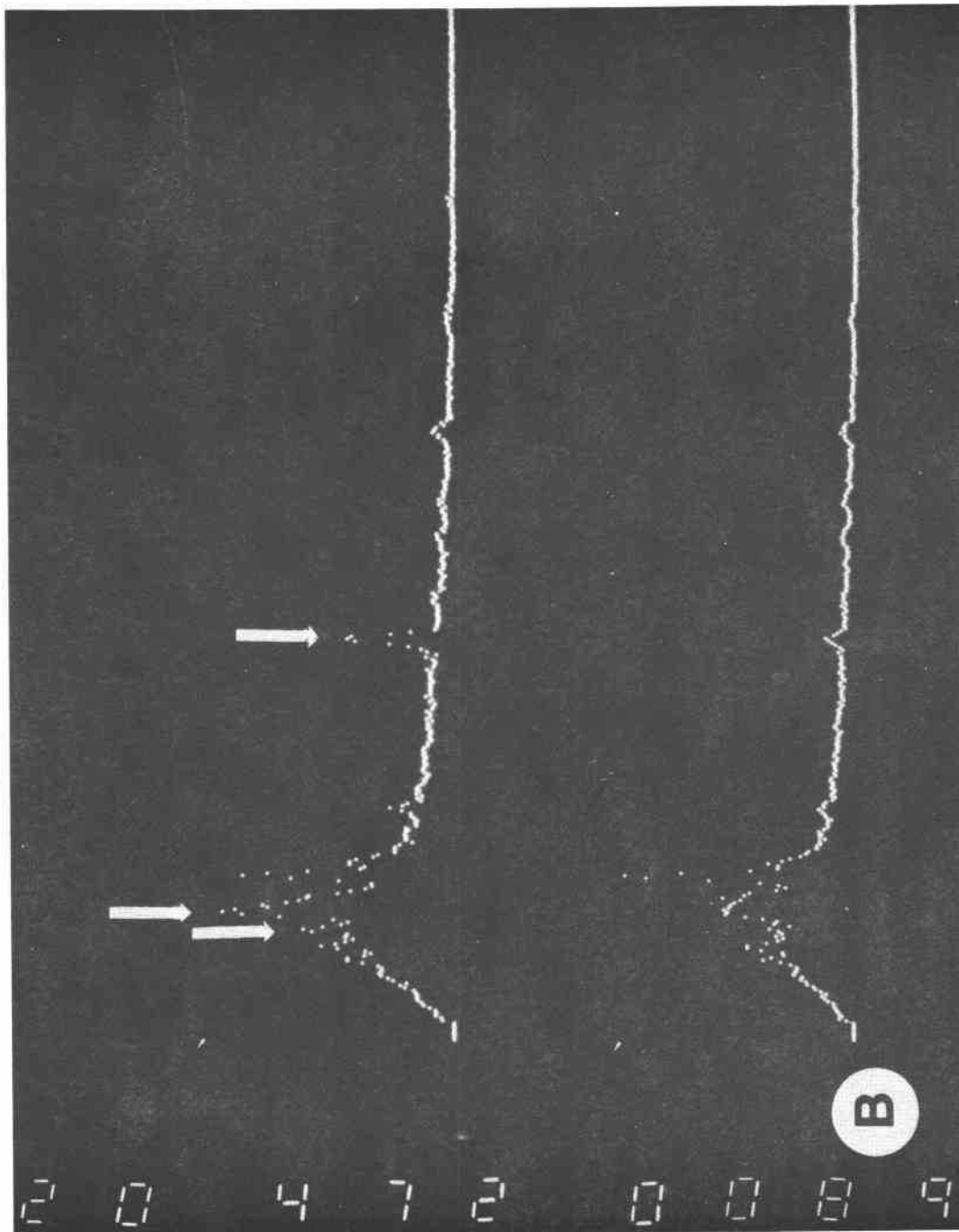


Figure 3B.

[15] which we believe to be metamorphosed pillow basalts. Hydrothermal cooling and alteration of the diabase intrusions and pillow basalts would have provided the dissolved silica for the formation of the cherts and the clay minerals which ultimately formed the associated shales. Barghoorn and Tyler discussed the occurrence of layered black chert domes which had developed over greenstone boulders, another indication of the hydrothermal alteration of pillow basalts and the deposition of dissolved silica. The black shales overlying the "algal cherts" are pyritic and pyrite layers occur within the black chert domes. Oolitic chert embedded in a fine-grained chert matrix also occurs within the domes [15].

The microfossils from the Gunflint include tangled filaments very like organic matter which we previously described from present-day hydrothermal vents (Gunflintia minuta Barghoorn) [14, 15], tubelike forms with bulblike swellings (Archaeorestis schreiberensis), and a problematical organism described as being "a sphere within a sphere" and containing tubercle-like structures in the area between the spheres (Eosphaera tyleri Barghoorn) [15]. The inner spheres seen in specimens of E. tyleri Barghoorn are often ruptured and appear to show a kind of protuberance. Electron microscope photographs of the Gunflint fossils by Shimizu, et al. [16], show even more remarkable resemblances to present-day organisms. Shimizu, et al. observed spherical and filamentous forms as well as a tubulous organism which appeared to have a structure formed from gelatinous substances [16].

The Pahrump Group (Crystal Spring Formation, Beck Spring Dolomite, and Kingston Peak Formation, ~ 1.3 billion years old) also appears to have at least some hydrothermal activity associated with its paleo-

environment. We base our conclusion once again on the existence of diabase sills in the Crystal Springs Formation along with black cherts and stromatolitic structures [17, 18]. The fossils in the Pahrump Group also include both spheroidal and filamentous forms. Some of the filamentous forms appear to form sheaths. Once again, there are pronounced resemblances to present-day bacteria found at EPR 21°N.

Possible sheath-forming filamentous forms and spheroidal forms which may have an inner sphere were also found by Schopf, *et al.* [19] in the Chuar Group in the Grand Canyon (800 ± 200 million years old). The paleoenvironment of the Chuar Group is more problematical, but the presence of hydrothermally-produced minerals, such as pyrite, goethite and siderite, as well as the presence of sufficient dissolved silica for the formation of concentrically laminated siliceous pisoliths (which appear to be similar to the siliceous oncoids in the Pahrump Group described by Pierce and Cloud [18] and the oolitic chert in Gunflint black chert domes noted by Barghoorn and Tyler [15]) suggest that such activity may well have occurred.

From the foregoing discussion, it is apparent that filamentous microorganisms capable of forming sheaths evolved early in the Precambrian in hydrothermal environments. Initially these sheaths could have been metal oxides accumulated during microbial oxidation processes. Because of the large amount of dissolved material transported by seawater in hydrothermal systems, precipitates of silica, sulfides, and carbonates would rapidly accumulate along the sheaths of microorganisms. It is quite possible that organisms which form tubes as a survival-enhancing adaptation could have evolved from early sheath-forming

microorganisms. This could have been an early evolutionary adaptation of epiphytic bacteria in hydrothermal environments as the rapid precipitation of dissolved material from the cooling hydrothermal vent waters would inhibit the survival of most attached organisms unless they had a mechanism for reaching beyond the surface of precipitating material. The microorganisms would build tubes which could be rapidly extended outside the surface of accumulating precipitates and sediments and which would allow them to continue utilizing hydrothermally-derived dissolved gases and reduced metals.

It is interesting to note that one of the most successful animals found in hydrothermal vent communities are the vestimentiferan tube-worms. Although the heights of these animals range up to 3 m, there are definite resemblances between them and the tubulous bacteria whose length is a few microns. To what degree their similarities are due to analogy or to homology cannot at this time be assessed. It may simply be an instance of a very successful adaptive mechanism being adopted on two widely different scales of existence; however, it is tempting to speculate a similar evolutionary origin for both organisms.

Early Precambrian pyritic and siliceous rocks have been shown to contain a variety of fossil microorganisms that resemble both cyanobacteria and fungi in size and morphology [20]. It has always been difficult to explain the existence of these comparatively advanced organisms in early environments which were believed to be deficient in oxygen and organic material. If, however, these organisms were in fact chemosynthetic bacteria living within or near submarine hydrothermal vents, the source of their nutrients is no longer a problem. We believe

that chemosynthetic epiphytic bacteria evolved in hydrothermal environments before the formation of organic-rich stromatolites and that the filamentous tube-forming microorganisms found attached to surfaces in present-day oceanic hydrothermal environments represent living replicas of some of the fossil organisms found in hydrothermally-derived Precambrian strata. The organisms collected from the East Pacific Rise and the Galapagos Rift are definitely not photosynthetic and probably not heterotrophic. They are utilizing inorganic gases and metals, and they are probably procaryotic. We believe that a detailed study of the epiphytic bacteria associated with oceanic hydrothermal vents and chimneys will lead to an understanding of the physiological groups of microorganisms which existed in early Precambrian hydrothermal environments.

In a previous paper, we discussed the origin of life, showing how submarine hydrothermal systems provide an environment in which all of the necessary conditions for abiotic synthesis exist [14]. The flourishing animal communities found around present-day hydrothermal vents suggest to us that submarine hydrothermal activity in the Precambrian also provided the necessary environmental haven for evolutionary experimentation. We believe that further study of hydrothermal vent communities will enable us to answer one of the most vexing of all paleontological questions: from whence came the Cambrian explosion of fossil fauna?

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