tion of *Vibrio* species with crustaceans and other invertebrates suggests that further studies on the association of vibrios with their invertebrate hosts would provide a better understanding of the pathogenic mechanisms of these bacteria. Enterotoxin produced by *V. cholerae* and by some strains of *V. parahaemolyticus* (*23*) may impart a significant advantage to the vibrio in its association with invertebrates and zooplankton. Indeed, extracellular substances produced by vibrios may prove to be ectocrines, as defined by Lucas (*24*). The epidemiology and pathogenicity of *V. cholerae*, *V. parahaemolyticus*, *V. alginolyticus*, *V. anguillarum*, and other *Vibrio* species would be better understood if the pathogenic and nonpathogenic *Vibrio* species were considered in the perspective of microbial-host dynamics in aquatic ecosystems.

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Archean Microfossils Showing Cell Division from the Swaziland System of South Africa

Abstract. *A newly discovered population of organic walled microstructures from the Swaziland System, South Africa, is considered to be biological on the following grounds: (i) the structures are carbonaceous and occasionally have internal organic contents; (ii) the population has a narrow unimodal size frequency distribution (average diameter, 2.5 micrometers; range, 1 to 4 micrometers); (iii) the structures are not strictly spherical, but are commonly flattened and folded like younger microfossils; (iv) the sedimentary context is consistent with biogenic origins; and (v) various stages of binary division are clearly preserved.*

Discrete organic microstructures have been known from sediments of the Archean Swaziland System of South Africa for more than a decade (*1–6*), but the problem of their biogenicity has recently been questioned and is not satisfactorily resolved. Several investigators have voiced their skepticism of many of the reports of algalike fossils from these ancient rocks (*7, 8*), and with good reason. Most of the described spheroids are very large compared to extant prokaryotic cells and bona fide prokaryotic unicellular microfossils and, when subjected to elementary statistical tests, these Archean assemblages have often been found to have size frequency distributions quite unlike those of living and fossil unicell populations (*7, 9*). In addition, it should be noted that Swaziland assemblages have until now consisted almost solely of unelaborated individual spheroids (*10*), although Muir and Grant (*6*) have described what they interpret to represent paired cells in a poorly preserved assemblage from the Kromberg Formation. Primitive microbes are now and were assuredly in the past morphologically very simple; many extant prokaryotic taxa consist entirely of smooth coccoidal unicells. The only way one could hope to distinguish fossil populations of such primitive cells from abiotically formed spheroids would be to find assemblages some of whose members exhibit interpretable biological activity. In morphological terms, this criterion focuses on finding evidence of cell division. We here report the discovery of a well-preserved population of microstructures from the Swaziland System that contains not only isolated individuals and common paired cells, but also the intermediate stages of binary fission. We believe that the data described here constitute cogent evidence for the presence of discrete algalike biological remains in rocks exceeding 3 billion years in age (*11*).

The Swaziland System is an ancient Archean greenstone belt exposed in the Barberton mountain land of the eastern Transvaal, South Africa, and in adjacent Swaziland. Because of their great antiquity and remarkably low degree of metamorphic alteration, the carbonaceous sedimentary rocks of this sequence have been the focus of much scientific inquiry into the nature of early life on the earth. The general geology of the system has been elucidated in many publications (*12*) and need only be briefly outlined here. The Onverwacht and Fig Tree Groups of the Swaziland System include nearly 17,000 m of interbedded sedimentary rocks and volcanics. Conspicuous among the sediments are bedded cherts that are often rich in organic matter. The carbonaceous cherts in which we have found evidence of cell division come from an outcrop of the Swartkoppie Formation exposed in the valley of the Umsoli River 19 km southwest of the town of Barberton. Most geologists have considered the Swartkoppie to be the uppermost formation in the Onverwacht Group, but it is really transitional with the conformably overlying sediments of the Fig Tree Group. In fact, Reimer (*13*) now feels that this cherty horizon should definitely be regarded as Fig Tree in age. At our fossil locality, shallow-water to nearshore depositional conditions are indicated by the presence of oolites, cross-bedding, and flat-pebble conglomerates (*14*). Detrital mineral grains are generally absent, but millimeter-sized matlike organic clasts are common (*14*), showing clearly the redeposition of organic sediments. In outcrop, the chert has a waxy black luster remarkably similar to those of the fossiliferous siliceous beds of the Proterozoic Gunflint (*15*) and Bitter Springs (*16*) Formations and shows no signs of recrystallization. Petrographic examination corroborates this observation; silica crystal diameters are very small (5 to 15 μm in organic-rich areas and up to 25 μm in relatively kerogen-free regions). Radiometric dating of layered rocks of the Onverwacht Group indicates a depositional age of approximately 3400 million years for the system (*17*). It is likely that the date of 2980 $\pm$ 20 million years obtained for rocks of the Fig Tree Group (*18*) reflects a subsequent thermal event, a conjecture supported by analyses of granites intrusive into the system that yield radiometric dates of approximately 3000 million years (*19*).

Preserved in the Swartkoppie chert are abundant microstructures that in younger rocks would without hesitation be called algal microfossils. These microspheroids have smooth organic walls and occasionally have internal organic contents (Fig. 1d). The size frequency distribution of a sample population (N = 200) is plotted in Fig. 2 (*20*). In their small size (average diameter, 2.5 μm; range, 1 to 4 μm), low divisional dispersion index of 4 (*7*), and standard deviation of 0.5 μm or 20 percent of the mean diameter, these microstructures are quite similar to many extant prokaryotic algal species (*7*). In contrast, they are rather unlike many of the previously described Archean spheroids. For example, an average member of this population has a volume only 0.2 percent as large as that of a typical *Archaeosphaeroides* individual of the type originally reported by Schopf and Barghoorn (*1*). Other Swaziland structures that do resemble our Swartkoppie spheroids in size are the assemblages containing paired cells found in the underlying Kromberg Formation by Muir and coworkers (*5, 6*). Like the microstructures discussed by Muir *et al.*, our microspheroids are not randomly distributed throughout the chert, but are found along organic-rich bedding planes, a sedimentary context that is consistent with the hypothesis of biogenicity.

Whereas the large *Archaeosphaeroides*-type individuals (*1-3*) are spherical or nearly so, our newly discovered microstructures are variously elongated, flattened, wrinkled, or folded (Fig. 1) in a manner strikingly similar to the morphology of microfossils in Proterozoic rocks. In younger formations, such morphologies are indicative of postmortem microbial degradation processes and early-stage sediment compaction, and it is tempting to interpret our material in a similar fashion.

While the observations discussed above make a biological hypothesis attractive, it is the preservation of various stages of binary division that makes this interpretation persuasive. As can be seen in Fig. 1, b to e, a sequence of morphologies indicative of binary fission can be constructed from members of the Swartkoppie population. One can observe numerous solitary unicells (Fig. 1b), elongated individuals beginning to constrict in the equatorial plane (Fig. 1c), hourglass-shaped individuals in which division is nearly complete (Fig. 1d), and newly formed daughter cell dyads whose adjacent walls remain appressed (Fig. 1e). Fully 25 percent of the cells observed in the population were preserved either in the process of division or as dyads (Fig. 1, f and k). Divisional patterns such as we have observed are common among extant cyanophytes (Fig. 1, g to j) and have also been convincingly documented in the Proterozoic fossil record (*16, 21*).

Reviewing the salient characteristics of the new Swaziland System population, we find that (i) the organic constitution of the microstructures is similar to

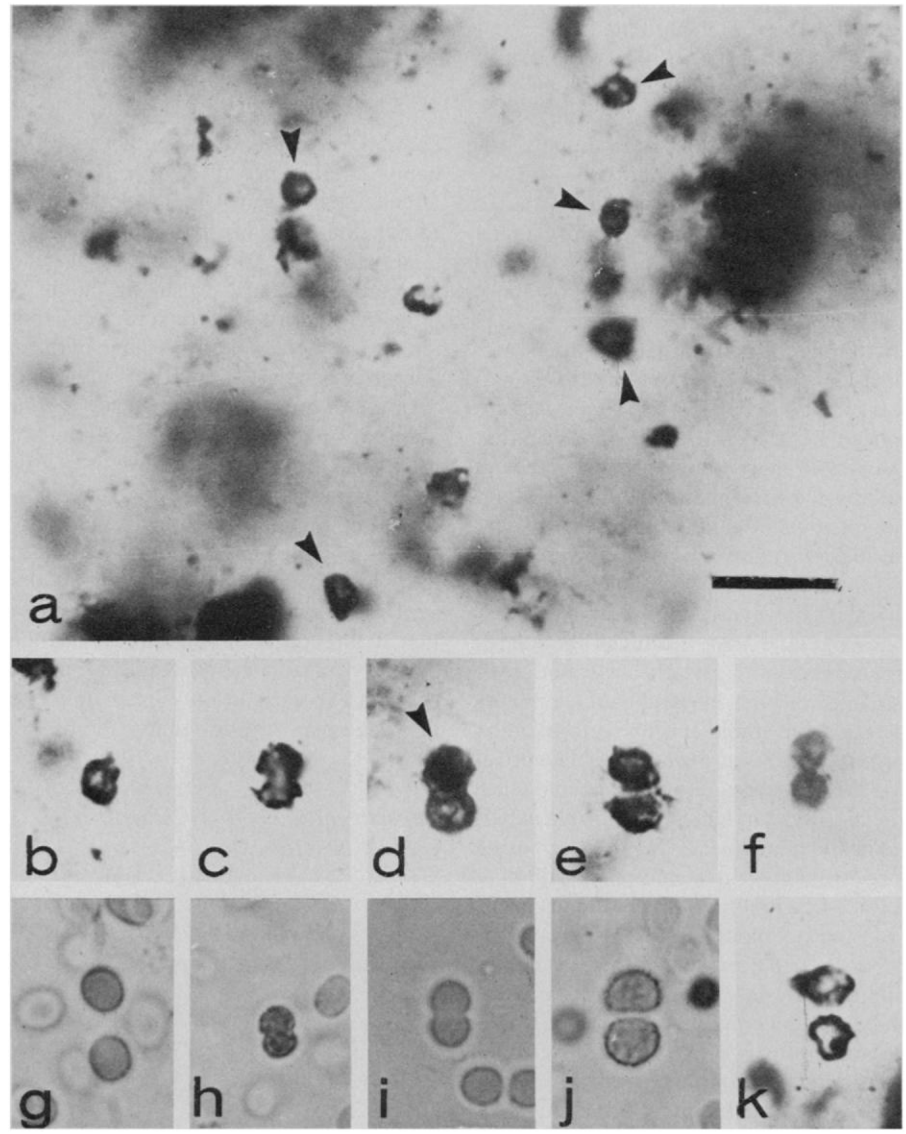

Fig. 1. (a) Distribution of microfossils in carbonaceous laminae of the Swartkoppie Formation, South Africa; arrows designate discernible individuals. (b to e) Stages in cell division preserved in the Swartkoppie population; the arrow in (c) points to dark organic contents within the upper half of the dividing cell. (f and k) Dyads in the Swartkoppie population. (g to j) *Aphanocapsa* sp., illustrating binary cell division in modern prokaryotes. All photographs, $\times$ 1600; scale bar, 10 μm.

that of geologically younger fossil organisms; (ii) the morphology of the microstructures resembles that of partially degraded microfossils in younger rocks; (iii) the size frequency distribution of the microstructures is similar to that of both fossil and extant microbial populations; (iv) the microstructures are found in a sedimentary context similar to those from which Proterozoic microfossils are well recognized and accepted; and most importantly, (v) the microstructures have been preserved in the process of binary division. These five lines of evidence collectively constitute cogent testimony for a biological population.

Alternative possibilities must be entertained. If these structures were diagenetic or metamorphic in origin, then similar bodies should be observable in younger carbonaceous cherts. Purely physical phenomena should be independent of age. However, in examining black chert from more than 50 localities ranging in age from Archean to Devonian, we have found only one type of structure which closely resembles the Swartkoppie microstructures—fossil microbes. The occasional presence of internal organic contents and the otherwise empty interiors of the microstructures preclude the possibility of organic condensation about spheroidal mineral grains (*22*).

Although it is true that the only structures in younger rocks that closely resemble the Swartkoppie spheroids are indeed microfossils, it is also true that the simple morphology of these Archean microstructures makes their 100 percent unequivocal identification as biological entities virtually impossible. The argument persists that some abiological processes, however improbable or unknown, could have produced the microspheroids. Similarly, the distribution of organic carbon in Archean sediments (*23*) and the stable carbon isotope ratios of this ancient kerogen (*24*) are identical to the patterns observed in younger rocks—rocks in which their origin is biologically controlled. One can hypothesize prebiological means of distributing reduced carbon in sediments; one can also construct models whereby carbon isotopes are fractionated in the absence of photosynthesis. However, in each case, the observed continuum between Archean and younger rocks would have to be considered fortuitous. That sediments from the Swartkoppie Formation have an organic carbon distribution similar to that of younger rocks, contain kerogen whose isotopic composition parallels that of younger rocks, and contain carbonaceous bodies that in younger rocks would be interpreted as microfossils

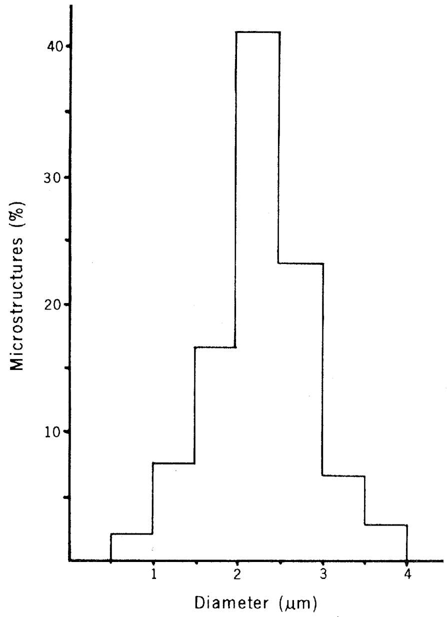

Fig. 2. Size frequency distribution of microfossil population from black cherts of the Swartkoppie Formation, Swaziland System, South Africa.

could be explained by hypothesizing the happy coincidence of several fortuitous circumstances, but it is far more logical to conclude that in the Archean Swaziland sea, just as in Proterozoic and Phanerozoic basins, organisms, some of them photosynthetic, thrived, and that under favorable conditions some of these microbes became fossilized.

In conclusion, then, the most reasonable explanation for this population of microstructures is that it consists of fossil microorganisms arrested and preserved in the midst of biological activity. Although it does not constitute a proof of the biogenicity of any previously described Swaziland spheroids, we believe that it does provide cognitive evidence that recognizable morphological remains of primitive prokaryotes exist in rocks that have persisted for almost 3½ billion years.

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