Heliotropism in Modern Stromatolites

STANLEY M. AWRAMIK AND JAMES P. VANYO

Modern microbial mats and stromatolites exhibiting a preferred orientation toward specular sunlight were found at two sites. In Hamelin Pool of Shark Bay, Western Australia, subtidal decimeter-sized columns and intertidal centimeter-sized tufts were found pointing north. In thermal spring effluents and pools of Yellowstone National Park, mats were found with columnar and conical centimeter-sized structures inclined to the south. These examples of heliotropism in modern stromatolites are each built by a different community of photosynthetic microbes under markedly different environmental conditions. These new observations support the proposal that stromatolites can orient themselves toward the sun.

STROMATOLITES, ORGANOSEDIMENTARY constructions produced by photosynthetic microorganisms that trap, bind, or precipitate sediment (*1*), require sunlight to form. Most researchers stress the interaction of sediment with the stromatolite-building microbes (*2*). A complete assessment of stromatolite morphogenesis should include the biological response to sunlight in a sediment–accumulating environment. In most stromatolites, photosynthetic microorganisms live at or near a sediment-fluid interface in an environment that favors sediment accumulation rather than sediment removal. Microorganisms position themselves at discrete levels for optimal exposure to sunlight. Phototropism and phototaxis are requisite responses (*3*) or the microorganisms will be buried. Filamentous stromatolite-building oscillatoriacean cyanobacteria have these attributes and are the most widespread and successful microbes involved in stromatolite construction (*4*). The interaction of these photoresponsive microbes with an environmental mosaic of sediment, light, temperature, chemistry, other organisms, and time results in stromatolites.

Inclined fossil stromatolite columns and domes have been described by a number of investigators (*5, 6*). Two explanations are commonly offered: (i) stromatolites grow toward specular sunlight and (ii) inclination is caused by other physical factors such as waves, currents, or position near a migrating shoreline, with sediment supply or wind direction forming the orientation factor.

Nordeng and Vologdin (*5*) found inclined Proterozoic stromatolite columns and proposed that inclination was due to heliotropism. They deduced that this information could be used to determine paleolatitudes. They did not, however, have independent evidence to support their proposal.

Others working on fossil (*7*) and recent stromatolites (*8*) found inclinations that were a response by the structure to waves and currents. Stromatolites commonly orient and incline in the upcurrent direction toward the sediment supply (*9*) and, under these conditions, local environmental conditions exercise greater influence on morphology than does sunlight. It was also concluded that the microorganisms that build stromatolites have no control over shape (*10*). In one occurrence, inclined fossil lacustrine stromatolites apparently were produced as a result of rising water level (*11*).

In a study of the Late Proterozoic columnar stromatolite *Anabaria juvensis* from the Bitter Springs Formation, we found evidence that the columns grew toward the sun (*12*). The evidence, a conspicuous columnar sine wave growth pattern, led us to propose that the stromatolites, built by photoresponsive microbes growing in clear, shallow, quiet water at low latitude, tracked the sun over the seasons. Well-preserved laminae when counted and extrapolated to one sine wave, yielded a best estimate of 435 laminae per sine wave. An assumption that laminae were daily features and that one sine wave was completed in a year, led to a paleontological estimate of approximately 435 days in the Late Proterozoic year—a figure that is in accordance with theoretical estimates of deceleration of spin rate (*13*) and paleontologically extrapolated estimates from Phanerozoic invertebrate fossils (*14*).

The model required that the microorganisms influencing stromatolite shape responded to specular sunlight and tracked the seasonal inclination of the sun. This assumption was a motivating factor in a systematic search for heliotropism in modern stromatolites.

Abundant microbial mats and decimeter- to meter-sized columns built by photosynthetic microorganisms occur in Hamelin Pool, Western Australia (Fig. 1A), a hypersaline marine embayment. Two types of stromatolitic growths exhibiting heliotropism were located at this site.

A field of several tens of northerly inclined (21° average zenith angles) columnar stromatolites was found in the subtidal region about 15 m off the northwest corner of Carbla Point in about 2 m of water (Fig. 2A) (*15*). Inclination is normal to water current and sediment supply. Such northerly inclined columns are not ubiquitous; others in the same general area are vertical to westerly oversteepened (in the direction of sediment supply). Playford and Cockbain (*16*) looked for but did not find any northerly inclined columns (*17*). Unlike most known recent stromatolites, these subtidal forms have a surface community dominated by motile diatoms (*18*).

Tufts of a high intertidal mat were found inclined to the north at two sites (Fig. 1A). The first occurs in the northeastern corner of Gladstone Embayment, where isolated patches (less than 2 m^2 in size) of inclined

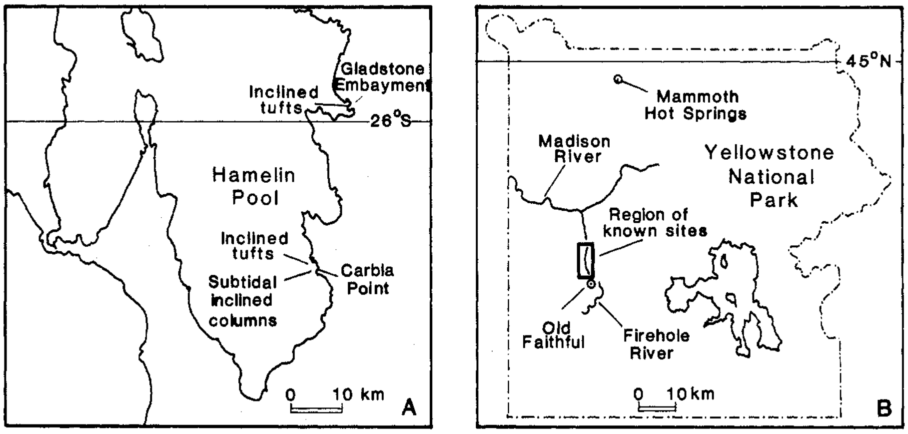

Fig. 1. Maps of (A) Hamelin Pool and (B) Yellowstone National Park showing approximate locations of heliotropic stromatolitic structures.

S. M. Awramik, Department of Geological Sciences, Preston Cloud Research Laboratory, University of California, Santa Barbara 93106.
J. P. Vanyo, Department of Mechanical and Environmental Engineering, University of California, Santa Barbara 93106.

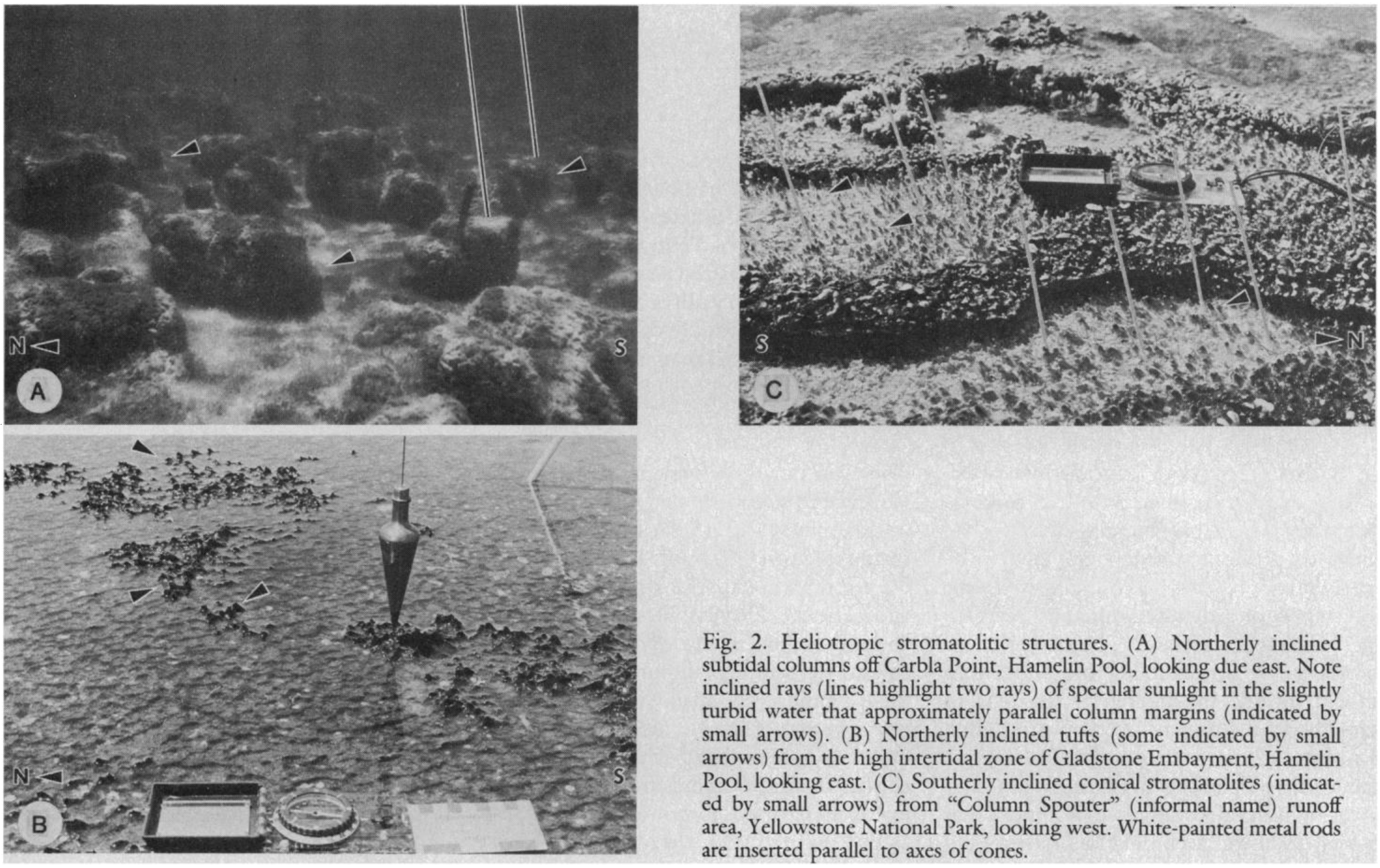

Fig. 2. Heliotropic stromatolitic structures. (A) Northerly inclined subtidal columns off Carbla Point, Hamelin Pool, looking due east. Note inclined rays (lines highlight two rays) of specular sunlight in the slightly turbid water that approximately parallel column margins (indicated by small arrows). (B) Northerly inclined tufts (some indicated by small arrows) from the high intertidal zone of Gladstone Embayment, Hamelin Pool, looking east. (C) Southerly inclined conical stromatolites (indicated by small arrows) from "Column Spouter" (informal name) runoff area, Yellowstone National Park, looking west. White-painted metal rods are inserted parallel to axes of cones.

tufts were found (Fig. 2B). Tufts here are less than 1 cm high, less than 0.75 cm in diameter at the base, with rounded tips, and inclined to the north at zenith angles of 27° (seven tufts measured). Tidal water movement is normal to tilt. Prevailing winds are from the southeast to south (*19*). Winds during the period of study were light easterly in the morning and strong west southwest in the afternoon. The second site is located about 30 m south of an unnamed point 2 km north of Carbla Point (Fig. 1A). This high intertidal area is shoreward of well-developed decimeter-sized stromatolitic ridges produced by the cyanobacterium *Gardnerula corymbosa*. Tufts are the same general size and shape as the Gladstone tufts, are patchily distributed, and zenith angles average 33° to the north (seven tufts were measured). Inclination here is also normal to water flow and at high angle to wind directions. A major difference between this occurrence and that at Gladstone is the steep shoreline. Tufts are subjected to wave turbulence during high tide. Both occurrences of inclined tufts are built by a community dominated by the cyanobacterium *Lyngbya aestuarii*.

In six thermal springs at Yellowstone National Park, conical to pillar-shaped microbial growths were found inclined to the south (*20*) (Fig. 2C). Southerly zenith angles 7.3° to 26.5° were observed in fields containing hundreds of columns. Inclination is not related to wind or water current direction. The Yellowstone growths are produced by a combination of the cyanobacterium *Phormidium tenue* var. *granuliferum* and the anoxygenic photosynthetic bacterium *Chloroflexus aurantiacus* often in the presence of *Synechococcus lividus* and *S. minervae* (*21*).

Heliotropically oriented stromatolites are not ubiquitous at all sites. Apparently similarly behaving microbes sometimes produce heliotropically oriented columns when the environmental conditions allow for the maximum expression of heliotropic responses. Less than optimal conditions apparently result in nonheliotropic construction.

Tips of tufts and small columns are the most active sites of tropic activity, increasing the probability of heliotropic response. Heliotropism in decimeter-sized columnar stromatolites, on the other hand, is probably decoupled from tropisms and taxes operating at the microorganism level. In large structures there is no concentrated, active locus of growth activity; microbial growth must be distributed over a large surface area for columnar morphogenesis. The ability of this broad growth surface to express an orientation directly toward specular sunlight may be suppressed easily by other environmental factors. Sediment accretion and microbial interaction with sediment are important aspects of large column growth, while the genesis of tufts and minicolumns is predominantly microbiological. We conclude that in the few localities known where large modern columnar stromatolites occur, heliotropism may be an uncommon phenomenon. However, with the large number of Proterozoic columnar stromatolites known and the numerous fossil lacustrine columnar stromatolites being found, we expect more examples of heliotropism.

Extrapolation of these columnar heliotropic stromatolites to fossil examples supports the paleolatitude proposal of Nordeng and of Vologdin (who use columnar average inclination) and the days per year proposal of Vanyo and Awramik (who use seasonal variation of inclination). Taken together, and especially when combined with paleomagnetic analyses, the procedures yield an impressive array of data on the early Earth and Earth-sun-moon histories (*12, 20*).

Our discovery of recent stromatolitic columns inclined toward the sun in both hemispheres, occurring in widely different environments and built by very different photosynthetic microorganisms, indicates that heliotropism in stromatolites may be widespread. Sunlight must be considered as a major driving force in stromatolite morphogenesis.

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15. Declination of the inclined subtidal stromatolites was not measured in situ but from photographs. Observations and photography (March 1985) were made while facing due east. The rays of specular sunlight in the slightly turbid water provide documentation (Fig. 2A).
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17. It is curious that both in Hamelin Pool and in Yellowstone, previous investigators looked for, but did not find, evidence of heliotropically inclined recent stromatolites [see (*16*) and Walter *et al.*, in (*21*)]. We cannot explain this discrepancy. Detection of north-south tilt is enhanced when the observer looks due east or west at about ground level especially in conjunction with precise vertical and north-south reference instruments. Southerly inclined, desiccated, *Lyngbya*-dominated tufts were found (July 1985) in Bonaire, Netherland Antilles, employing this method.
18. Dominant diatoms are *Mastogloia* spp., *Nitzschia* sp., *Amphora* spp., *Diploneis* sp., *Anomoeoneis* sp., *Navicula* sp., and *Fragilaria* sp. [identifications by R. W. Holmes].
19. P. E. Playford, in (*9*).
20. J. P. Vanyo, R. A. Hutchinson, S. M. Awramik, *Eos*, in press. Observations were made in September 1984 and March 1985. March zenith angles tended to be greater, reflecting the winter inclination of the sun.
21. D. Ward (personal communication) confirms the presence of these microorganisms as initially reported by M. R. Walter, J. Bauld, T. D. Brock, in *Stromatolites*, M. R. Walter, Ed. (Elsevier, Amsterdam, 1976), pp. 273–310.
22. We thank D. Pierce, R. W. Holmes, R. A. Hutchinson, D. Ward, and P. E. Playford for their expertise and assistance. Appreciation to the Department of Conservation and Land Management (on the recommendation of the Department of Mines), Western Australia, and the U.S. National Park Service for permission to conduct research in Hamelin Pool and Yellowstone National Park. Thanks also to WQED Pittsburgh "Planet Earth" project for the opportunity to visit Hamelin Pool. Supported by grant EAR83-03754 from the National Science Foundation. Contribution 147 of the Preston Cloud Research Laboratory.

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Human Melanoma Proteoglycan: Expression in Hybrids Controlled by Intrinsic and Extrinsic Signals

WOLFGANG J. RETTIG, FRANCISCO X. REAL, BARBARA A. SPENGLER, JUNE L. BIEDLER, LLOYD J. OLD

Human malignant melanoma cells express specific chondroitin sulfate proteoglycans (mel-CSPG) on the surface, both in vivo and in vitro. Melanocytes in normal skin show no detectable mel-CSPG but can be induced to express the antigen when cultured in the presence of cholera toxin and the tumor promoter 12-*O*-tetradecanoylphorbol-13-acetate. Most other cell types do not express mel-CSPG either in vivo or in vitro. A study was designed to examine regulatory signals controlling mel-CSPG expression. The gene encoding mel-CSPG was mapped to human chromosome 15, and this chromosome was introduced into rodent cells derived from distinct differentiation lineages. Three types of mel-CSPG–expressing hybrids were found: (i) hybrids derived from human melanomas; (ii) hybrids derived from human cells that do not express mel-CSPG; and (iii) hybrids derived from human cells expressing mel-CSPG that are antigen-negative but that are induced to express mel-CSPG when cultured on extracellular matrix instead of plastic surfaces. Thus, mel-CSPG expression can be controlled both through intrinsic signals, provided by the differentiation program of the rodent fusion partner, and through extrinsic signals, provided by specific cell-matrix interactions.

MONOCLONAL ANTIBODIES HAVE been used to identify a large number of surface antigens on human melanoma cells (*1*). One of these antigens, a high molecular weight glycoconjugate, shows a highly restricted distribution on cultured cells and in tissues (*2–6*). Biochemical analysis has shown that the antigen is a chondroitin sulfate proteoglycan (mel-CSPG), consisting of a 250-kD core glycoprotein and a number of characteristic glycosaminoglycan side chains (*7*). The molecular basis for the expression of this proteoglycan in melanomas is not known. Since normal skin melanocytes do not express detectable levels of mel-CSPG in vivo, antigen expression in melanomas may be part of their transformed phenotype. However, nevi, which are benign disorders of melanocytic cells, and skin melanocytes cultured in vitro in the presence of cholera toxin and the tumor promoter 12-*O*-tetradecanoylphorbol-13-acetate also express mel-CSPG (*3–5*). Hence, antigen expression is not restricted to malignant tumors. The extracellular and cell membrane localization of proteoglycans in other cell types suggests that these molecules have a role in cell-matrix interactions and tissue organization. Because mel-CSPG may have a similar role in cells expressing this antigen (*7*), we investigated the relation between mel-CSPG expression and cell lineage and cell-matrix interaction through analysis of rodent-human somatic cell hybrids.

Rodent-human hybrid clones were generated by fusing different types of human cells (melanoma, neuroblastoma, lymphocytes, and kidney epithelial cells) with rodent cells (L-cell and A9 mouse fibroblasts, N4TG-1 and NS20TG11E mouse neuroblastomas, RAG mouse renal cancer cells, and YH21 Chinese hamster ovary fibroblasts). The human chromosomes retained in the hybrid clones were determined by karyotype analysis and typing for human isozyme and cell surface markers (*8, 9*). Expression of mel-CSPG in hybrid cells was tested with monoclonal antibodies in mixed hemadsorption (MHA) assays and radioimmunoprecipitation tests. Six monoclonal antibodies recog-

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Memorial Sloan-Kettering Cancer Center, New York, NY 10021.