The background of the entire page is a dense field of fossilized trilobites, showing their characteristic segmented bodies and three-lobed heads. The fossils are preserved in a light-colored matrix, and the entire image is overlaid with a semi-transparent purple filter. A black rounded rectangle is superimposed on the upper portion of the image, containing the title and authors' names in white text.

Middle Proterozoic (1.5 Ga)
Horodyskia moniliformis Yochelson and
Fedonkin, the Oldest Known
Tissue-Grade Colonial Eucaryote

MIKHAIL A. FEDONKIN
and
ELLIS L. YOCHELSON

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Middle Proterozoic (1.5 Ga) *Horodyskia moniliformis*
Yochelson and Fedonkin, the Oldest Known
Tissue-Grade Colonial Eucaryote

Mikhail A. Fedonkin
and *Ellis L. Yochelson*



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ABSTRACT

Fedonkin, Mikhail A., and Ellis L. Yochelson. Middle Proterozoic (1.5 Ga) *Horodyskia moniliformis* Yochelson and Fedonkin, the Oldest Known Tissue-Grade Colonial Eucaryote. *Smithsonian Contributions to Paleobiology*, number 94, 29 pages, frontispiece, 19 figures, 2002.—“Problematic bedding-plane markings” discovered by the late R.J. Horodyski from the Appekunny Formation in Glacier National Park, Montana, and dated at approximately 1.5 giga-annum (Ga), were never formally named. We are convinced the specimens are biogenic and have placed them within Linnaean nomenclature as *Horodyskia moniliformis* Yochelson and Fedonkin. An apt description of the locally abundant fossils is “string of beads.” On each string, beads are of nearly uniform size and spacing; proportionally, bead size and spacing remain almost constant, regardless of string length or size of individual beads. They may not be related to any other known fossil, and their position within highest levels of the taxonomic hierarchy is enigmatic. We judge they were multicellular, tissue-grade, colonial eucaryotes. Similar strings have been reported from Western Australia, but nowhere else. The general geologic setting in Montana, details of sedimentation, and taphonomy suggest the organisms were benthonic, growing upward about 1 cm through episodically deposited eolian dust. During life, specimens were stiff and relatively strong, but show no evidence of a mineralized skeleton. They lived in poorly oxygenated water with the body progressively subjected to anaerobic conditions. Their energy source is obscure; their mode of growth and several features of interpreted environment lead us to speculate that *Horodyskia* likely lived primarily by ingesting chemosynthetic bacteria rather than by photosynthesis. This notion should be tested by searching red, fine-grained, subaqueous arenites of approximately the same age throughout the world for additional occurrences.

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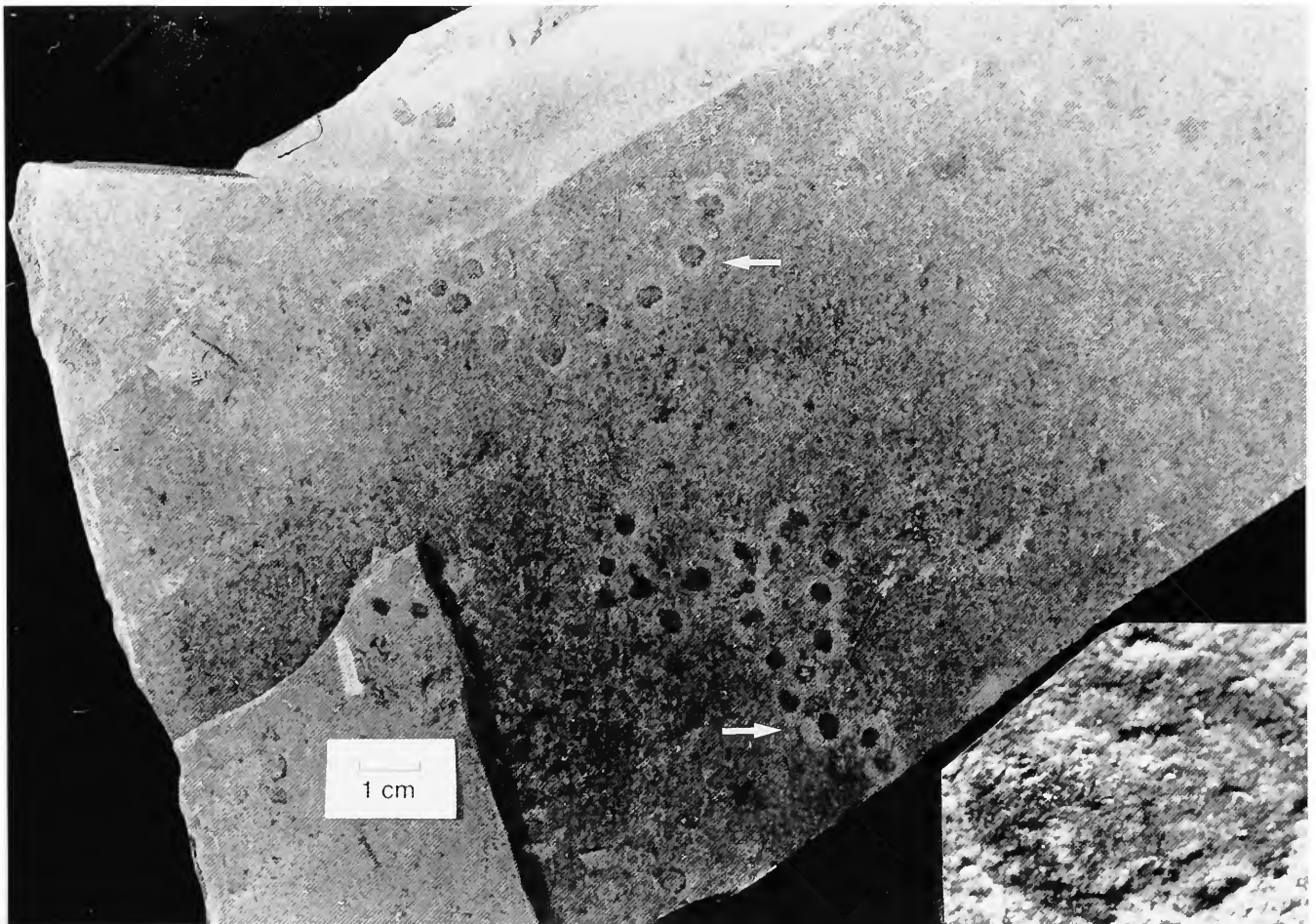
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FRONTISPIECE.—A dark gray slab from the Appekunny Formation, showing several strings of black-colored beads of varying lengths and configurations on the sole surface. A lighter-colored halo accentuates the beads. The curved strand trending left to right in the upper part of the photograph is designated as holotype. Several beads to the lower left where two strands cross show the inner ridges, but they are too small to be seen in this illustration. Above the scale, two beads are on a fragment of another sole surface and may be the upper parts of the string to their right. A similar view of this slab was figured in Yochelson and Fedonkin (2000). The corner insert is one of the beads from the holotype, indicated by an arrow, the upper surface of which is intact and standing slightly in positive relief; $\times 10$; see also Figure 17c. USNM 508100; Rising Wolf Mountain.

Middle Proterozoic (1.5 Ga) *Horodyskia moniliformis* Yochelson and Fedonkin, the Oldest Known Tissue- Grade Colonial Eucaryote

*Mikhail A. Fedonkin
and Ellis L. Yochelson*

Introduction

The rise of biological complexity is a fundamental problem that has been attacked by a wide variety of scientific disciplines. Models derived from various approaches are not always consistent. Even within one general approach, for example molecular biology, different models have been developed. At the core of some debates is the time of origin of the eucaryotic cell and the subsequent appearance of multicellular organisms.

The aim of this paper is to describe a new form, significantly older than presumed multicellular organisms heretofore reported in the literature. To support our interpretation that this taxon is of tissue-grade complexity, we have considered sedimentary environment, taphonomic effects, and paleoecology, among other points. The paleontology of the Proterozoic is still poorly known, and demonstrating that a multicellular form does occur in ancient rocks may help resolve the paradox between molecular clock models that predict an early rise of complex life forms and the relatively late appearance of such megafossils.

The late Robert J. Horodyski devoted his career to the study of Proterozoic life and was particularly zealous in field work. In 1992, we spent 10 days with him in Glacier National Park, Montana, mostly at Apikuni Mountain (Figure 1). The Appekunny Formation, Belt Supergroup, was named before the spelling of the mountain's name was changed to Apikuni. At this locality, Horodyski (1982:884) found "problematic bedding plane markings"; these are now described in detail and are discussed below. Other markings, possibly indicative of former megascopic forms of life, are associated with this form (Fedonkin et al., 1994). Following Dr. Horodyski's unexpected death on 9 September 1994, part of his collection was donated to the National Museum of Natural History (NMNH), Smithsonian Institution, and, combined with the Yochelson-Fedonkin material, forms the basis for this study.

ACKNOWLEDGMENTS

This project could not have been completed without the assistance of many persons. Ronald Parsley, Department of Geology, Tulane University, had the difficult task of organizing and distributing collections after the death of R.J. Horodyski. Authorities at Glacier National Park permitted our collecting of specimens. In 1992, Donald Winston, Department of Geology, University of Montana, introduced us to stratigraphy of the Belt Supergroup and has continued to share his wide experience with us. In particular, he pointed out the low hummock cross-bedding in the Appekunny Formation and the unique nature of this subaqueous red bed. Visits to Washington, D.C., by M.A. Fedonkin in 1992 and 1996 were made possible by the Office of Fellowships and Grants, Smithsonian Institution, and in 1999 by support from the Walcott fund. Fieldwork during

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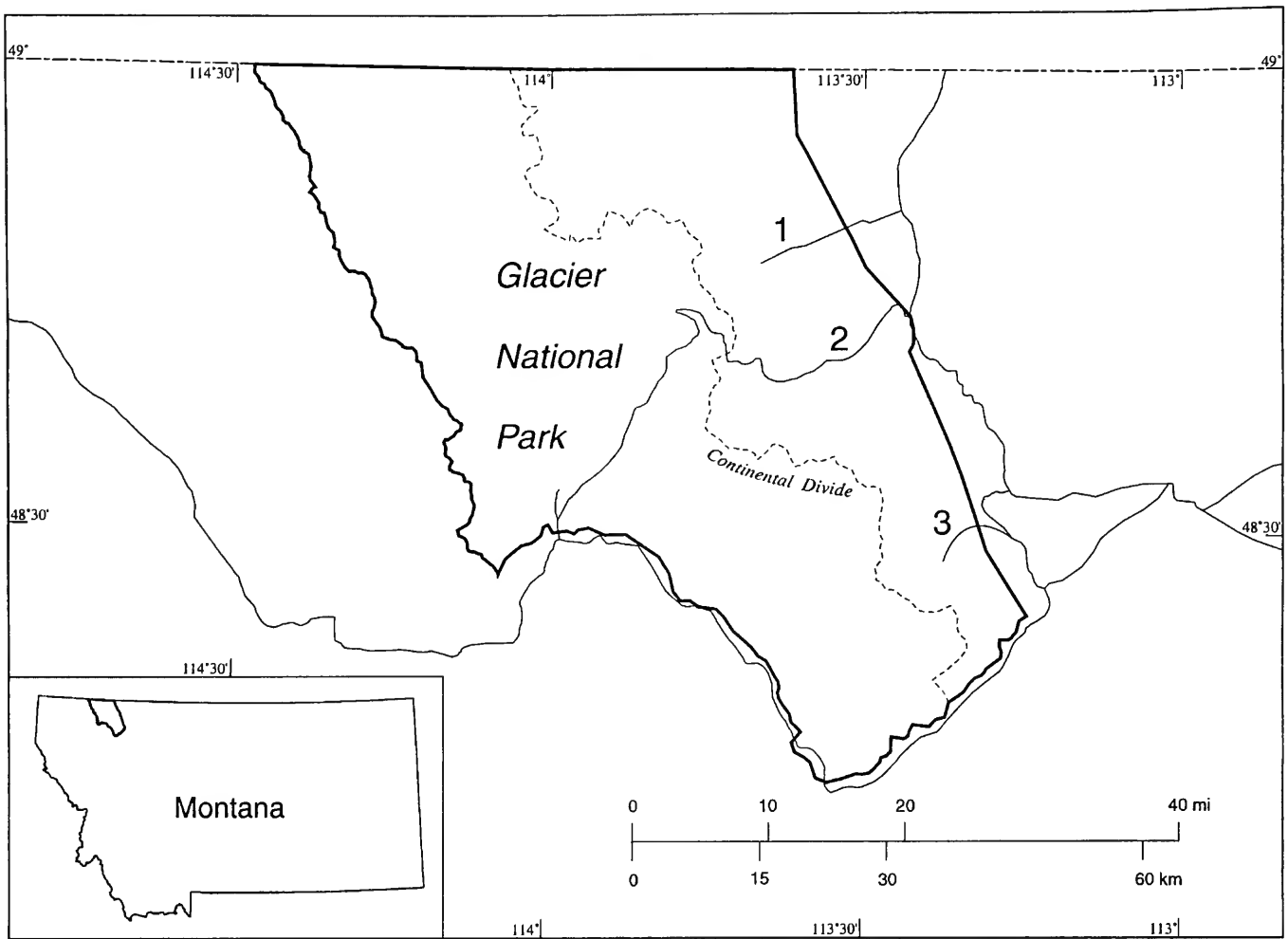


FIGURE 1.—Outline map of boundary of Glacier National Park (GNP) and principal roads. The three collecting localities are indicated: (1) Apikuni Mountain; (2) Going-to-the-Sun Road; and (3) Rising Wolf Mountain.

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We are grateful to T.A. Ivanovskaya, Geological Institute, Russian Academy of Sciences, Moscow, for her comments concerning glauconite. Eugene Jarosavich (retired), Department of Mineral Sciences, NMNH, performed microprobe analyses at our request. Donald Dean, Department of Paleobiology, NMNH, made polished and thin sections. Walter Brown, head of the Scanning Electron Microscope (SEM) Laboratory, NMNH, aided our SEM inquiries. We are particularly indebted to Victor Krantz (retired), Office of Photographic Services, NMNH, for the outstanding photographs of exceedingly difficult material. Figures 18 and 19 were prepared by E. Tokareva and S. Rozhnov, respectively, artists at the Paleontological Institute, Russian Academy of Sciences.

Early drafts were read by Donald Winston and F.M. Bayer, Department of Invertebrate Zoology, NMNH. Their suggestions improved the manuscript, which later also benefitted dra-

matically from critical reading by D. Erwin, Department of Paleobiology, NMNH, and A. Knoll, Museum of Botany, Harvard University, Cambridge Massachusetts.

Geologic Setting

The Proterozoic Belt Supergroup covers a vast region in Montana, Idaho, and Washington and is in excess of 16 km thick. Winston and Link (1993:495) summarized the regional setting and stratigraphic correlations. Glacier National Park (GNP) is at the eastern edge of the Belt outcrop. Near the northeastern GNP boundary, the oldest unit exposed is the Altyn Formation (Figure 2). That carbonate unit contains prominent and abundant stromatolites, particularly *Biacalia* Krylov (Horodyski, 1983, 1989a) in its upper portion. The Altyn is thrust eastward over Cretaceous beds; its thickness is unknown, but about 150 m are exposed at Apikuni Falls. Whipple (1992) noted the contact with the overlying Appekunny Formation is disconformable, showing up to 2 m of relief.

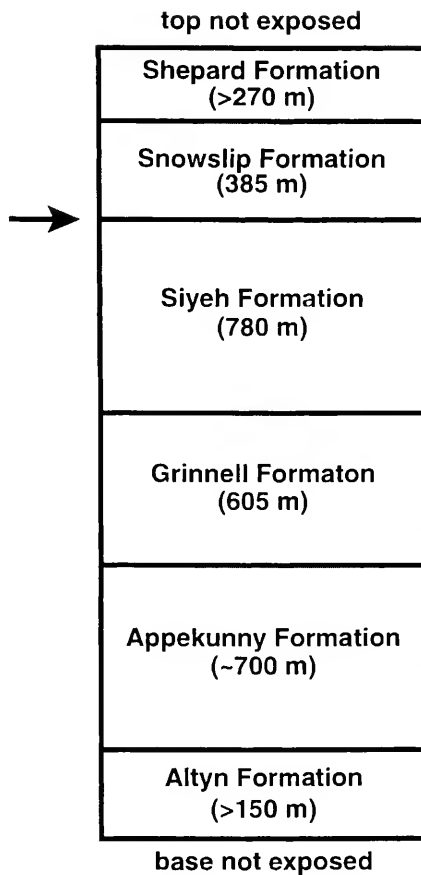


FIGURE 2.—Units of the Belt Supergroup exposed in the northwest part of GNP. Both the lower and upper parts of the section are cut off by faults. The thicknesses are taken from sections measured by others in the Swiftcurrent Valley-Logan Pass area. The position of the Pursell Lava is indicated by an arrow.

The Appekunny Formation is 530–690 m thick on the eastern edge of GNP and is divided into five informal members (Whipple et al., 1984). On the west side of GNP, the formation is thin and only the uppermost informal member can be identified; members 1–4 grade laterally into the upper part of the Pritchard Formation (Winston, in litt., 1997). The Pritchard contains microfossils, but no megafossils have been reported (Horodyski, 1993, appendix). The Appekunny Formation is the approximate temporal equivalent of the Greyson Shale in the Big Belt Mountains. There is no evidence that the two formations were interconnected, although a connection through the Highland Range is plausible (Winston, in litt., 1997); both microfossils and megafossils occur in the Greyson (Horodyski, 1993, appendix).

Overlying the Appekunny Formation within the Swiftcurrent Valley-Logan Pass area near the center of GNP are the Grinnell, Helena (=Siyeh), Snowslip, and Shepard formations, totaling about 2000 m in thickness. In the southwest part of GNP, west of the Blacktail fault, the Mt. Shield, Bonner, and McNamara formations outcrop. The Helena and Shepard are carbonate units. The Helena, like the Altn, contains stromato-

lites, being particularly noted for several cycles of alternating growths of *Biacalia* Krylov and *Conophyton* Maslov. The other formations are argillites, siltstones, and sandstones that are characteristically red-colored.

Based on the literature, Fedonkin et al. (1994:202) suggested an age of about 1.4 billion years for the Appekunny Formation. Recent age determinations (U/Pb) on the Pursell Lava, between the Snowslip and Shepard formations, range from 1508 to 1845 Ma (Aleinikoff et al., 1996:376).

The Appekunny Formation is primarily variegated siltstone, weathering into slabby layers 1–10 cm thick. As previously noted, Whipple et al. (1984:38–39) divided the formation into five informal units. The specimens of interest are in the lower portion of the section. “The lowest member, member 1, is about 450 ft thick and consists of alternate successions of pale-maroon and grayish-green siltite and minor argillite.” A key marker mentioned by Whipple (1992) is a sand-sized quartz arenite about 175 ft above the base. We did not observe it during field work; Winston (in litt., 1997) noted that most fossils occur below it.

“Member 2 closely resembles member 1, except in the absence of maroon beds, it is about 550 ft. thick. Thin beds of arenite, 1 to 3 in. thick are common in the lower part and laminae are generally thicker in member 2 than in 1” (Whipple et al., 1984). Member 3 is given as about 550 ft of interbedded pyritic arenite, grayish green siltite, and minor argillite. The poorly exposed member 4 was measured by Whipple et al. (1984) at about 450 ft of “thin to very thin laminae of olive siltite accompanied by thin lenticular beds of rusty-brown arenite.” Member 5 is a bright green argillite about 200 ft thick, containing mud-chip breccia, fluid-escape structures, and shrinkage cracks, features that occur less commonly in member 3. In brief text accompanying his GNP map, Whipple (1992) mentioned the members, but they were not mapped. Harrison et al. (1998) mentioned, but did not map, the five informal units and mentioned them intertonguing with the Pritchard Formation.

During the 1992 season, Fedonkin et al. (1994:204) arbitrarily designated three units at Apikuni Mountain on the basis of color. Examination of lithology by sawn and natural cross sections now suggests our collections and Horodyski’s may be confined to member 1 of Whipple et al. (1984), but this can only be confirmed by further field work. Distinction between members 1 and 2 is based primarily on color of the weathered rock and may not be as significant as differences in overlying units. The range of fossils through member 1 was not determined in 1992, but they are present though some meters of rock thickness.

COLLECTING LOCALITIES

A broad glacial valley occurs above the carbonate Altn Formation, the upper ledges of which form Apikuni Falls. Apikuni Mountain is the east flank of the valley, with strata of the Appekunny Formation dipping at a low angle toward the valley cen-

ter. The lower part of the mountain slope is only slightly steeper than the dip, and large rock surfaces are well exposed.

All Appekunny units weather into slabs. Slabs from members 1 and 2 commonly are 1–3 cm thick, thinner than those from higher units. Most bedding planes appear flat, but within members 1 and 2 are low, nearly imperceptible hummocks, many less than 1 cm high with 1–2 dm between hummocks (Winston et al., 1989:91) (Figure 6c). Limited field observations suggest these hummocks, which superficially resemble ripple marks, are more abundant and larger in the higher members.

In the 1992 season, specimens were collected at two other localities (Fedonkin et al., 1994:206) (Figure 1). The first is about 16 km south of Apikuni Mountain, along Going-to-the-Sun Road, U.S. Highway 89, the GNP east-west route. Outcrops only along small road cuts and a steep dip restrict collecting. Winston (in litt., 1997) noted hummocks are larger in these beds than in the equivalent member 1 at Apikuni Mountain.

The second locality is about 45 km south of Apikuni Mountain, on the southern flank of Rising Wolf Mountain near Two Medicine Campground (Figure 1). The section is primarily dark-colored strata; red or green beds are rare. Because of the steep mountain slope and the dip, only a relatively small outcrop is available, and we obtained few fossiliferous slabs. Several Horodyski slabs have a 1991 date, which is presumably when he found this locality.

Winston (pers. comm., 1996) judged that the Rising Wolf Mountain locality occurs within member 1. At Apikuni Mountain, dark-colored beds are rare, although Winston reported they are persistent. It is also possible the strata at Rising Wolf Mountain extend up into member 2, which further reinforces Winston's opinion that the differentiation of member 1 and 2 may not be significant. One small piece in the Horodyski collection is from Otokomi Mountain (Figure 14d), which is between Apikuni Mountain and Going-to-the-Sun Road. It is about 6 km north and slightly east of the highway site. We have no further information on this occurrence. In 1993, Winston and Yochelson briefly examined the Appekunny Formation near the GNP southern boundary and in Waterton Lakes National Park in southern Alberta. No indication of Proterozoic life was seen at either location.

MATERIAL AND METHODS

About 120 slabs in the Horodyski collection show specimens of interest. Almost one-third of these bear 1992 collecting dates, about one-third have a 1991 date, and seven were collected in 1993. Fifteen numbered slabs were keyed to his 1983 notebook. Most of this material is from Apikuni Mountain. Some Horodyski slabs have no associated locality data or field number. We assume these unmarked slabs probably came from Apikuni Mountain, as Horodyski's notes indicate he visited that locality most field seasons. For the illustrated specimens of uncertain provenance, the locality is given as "Apikuni Mountain" to note this minor uncertainty.

The 1992 collection of Fedonkin and Yochelson is smaller than that of Horodyski and includes material not directly germane to this investigation. We concentrated on collecting other indications of possible biogenic origin, for there was a tacit understanding that Horodyski would study this common form. Still, about 75 slabs show this fossil. Among this material, a few slabs show early growth stages, as do several specimens in the Horodyski collection. Post-larval, tiny specimens are difficult to find. Once that size range is passed, strings of smaller beads are more common on the outcrop than larger ones.

In 1993, Yochelson and Winston spent one day at Apikuni Mountain to collect a few additional slabs. Figure captions omit year and collector; this data can be obtained from museum labels.

Although specimens are abundant, good ones are not common. Mechanical weathering is severe in GNP, and few specimens show surface details. Coating with glycerine, water, or ammonium chloride were inferior to photographs of dry slabs. The illustrated slabs include a centimeter scale to show size. Several slabs are shown in entirety, but for economy most have been trimmed. Most large slabs show a number of specimens. About 5% of specimens we examined in the laboratory are illustrated herein.

Specimens have been cataloged, and their numbers are preceded by the acronym USNM (collections of the NMNH, which include those of the former United States National Museum).

Previous Investigations

Horodyski (1982:884) described and illustrated "problematic bedding-plane markings" from Apikuni Mountain. He provided no formal description and called them "string of beads" because of their appearance on the outcrop. So apt an informal descriptive term is used herein without quotation marks. Nevertheless, it is not meant to imply that the fossils were spherical.

The strings of beads were illustrated and briefly noted the following year (Horodyski, 1983:399–400). Along with a later reillustration, Horodyski (1989b:11–13) mentioned several trace fossils, but said: "The Appekunny specimens are not demonstrably biogenic. Work is in progress on studying the internal structure of these markings; but at present, the mode of formation of these structures remains uncertain. At present, they are best regarded as dubiofossils."

Horodyski's work in GNP emphasized studying stromatolites and sampling for microfossils. He took a cautious approach toward recognition of any higher life forms in the Belt Supergroup. At one time Horodyski (1986) questioned the organic nature of all forms from the Belt described as fossils by Walcott (1899).

Following report of GNP string of beads, Grey and Williams (1987) noted occurrences from Western Australian beds of about the same age. Subsequently, they illustrated material that appears remarkably similar to that described herein (Grey and Williams, 1990). Their work strongly reinforced the biologic nature of the string of beads, but despite comprehensive

description and careful analysis, they also did not provide a taxonomic name.

Photographs of Horodyski's material were published twice in *The Proterozoic Biosphere* (Schopf and Klein, 1992). Fedonkin and Runnegar (1992:394) noted them as "puzzling bedding-plane markings." Hofmann (1992a:418–419) compared them to the trace fossil *Neonereites* Seilacher, acknowledged the work of Grey and Williams, but considered them dubiofossils. The book has become a basic reference for those involved in Proterozoic studies; although the illustrations did not add new data, they introduced the strings to a wide audience of geologists who normally do not follow paleontologic literature. It may be significant that despite continued study of Precambrian sediments by many geologists, no further occurrences of the strings have been published.

Horodyski (1993:562–563) remarked that the 1990 paper by Grey and Williams led him "to conclude that the Belt specimens truly are fossils," and in a figure caption he wrote, "These structures are interpreted as megafossils, possibly having eukaryotic algal affinities." Fedonkin et al. (1994) illustrated several specimens but did not include a detailed discussion.

Early workers on the Precambrian named presumed biogenic structures that later turned out to be spurious. This "Precambrian syndrome" has properly made present-day workers skeptical of formalizing a name for a structure obtained from older Proterozoic rocks, and it may have influenced Horodyski's delay of detailed study. Proterozoic paleontologists have concentrated on carbonate rocks bearing stromatolites and on microfossils preserved in cherts. Siliclastic units have been little investigated, perhaps because Proterozoic paleontologists "know" they do not yield organic remains.

Organic Versus Inorganic Origin

Recognizing the need for caution, we judge enough information is available to confirm that the string of beads are fossils and that they are distinctive enough to be formally named. They are not dubiofossils or pseudofossils. In light of Horodyski's reluctance to name the specimens and his later concerns as to their nature, it is appropriate to explain our view from two aspects.

First, we are unfamiliar with any phenomenon of sedimentation, subsequent compaction, or lithification that might produce such a shape as the string of beads (Frontispiece, Figures 6a, 14c,d). They are not raindrop impressions, for otherwise slabs would be covered with them. The strings are not gas escape structures, for otherwise beads would be randomly distributed; the beads are not concretions or nodules. Winston (pers. comm., 1993) noted the low hummocky structures show no evidence of mud cracks or other indicators of exposure. That effectively rules out other terrestrial phenomena, such as salt crystal molds, which occur higher in the Belt.

The beads are not produced by recent weathering. Lichens are abundant on exposed surfaces, but their growth commonly

forms irregular spots larger than the largest beads. Lichen-produced patches are surface phenomena, whereas a few strings were collected from freshly split bed rock. Questionable forms, scrubbed off the rock with a stiff brush, were eliminated from this study.

Second, the definite arrangement in strings is a feature of at least some later forms of colonial life. Although the size of beads varies among strings, all beads on a single string are virtually the same size. In our interpretation, the nearly uniform spacing of beads on a string, regardless of bead size, is another indication of coherent growth (Figures 8b, 12d).

In documenting "bedding-plane markings" in Australia, Grey and Williams (1990:319–320) discussed possible inorganic origin in detail and concluded the strings of beads were probably biogenic. Hofmann (1992a) commented on similarity to strings of "millet seed" gypsum casts from the Balbirini Dolomite, MacArthur Basin, Northern Territory, Australia (Jackson et al., 1987:139) and considered them dubiofossils. From the illustrations provided, comparison to these rare secondarily silicified gypsum nodules is not convincing to us. Grey and Williams (1990) saw no need to make such a comparison in their comprehensive discussion. The Appekunny Formation shows no evidence of evaporites.

Systematic Paleontology

Domain EUCARYA

Kingdom Uncertain

Phylum Uncertain

DISCUSSION.—The classic Linnaean subdivisions of Animal, Vegetable, and Mineral are long discarded, but for much of the nineteenth century, the prevailing concept was of plant and animal as the only two kingdoms. Coordinate with ever more sophisticated microscopy, classification has expanded in the twentieth century. Taxonomic increase at high systematic levels is the order of the day. Textbooks recognize five living kingdoms: bacteria, protists, fungi, plants, and animals. Kingdoms proposed from the fossil record need not be noted here.

Some workers divide modern algae among several kingdoms. Recently, bacteria have been placed into two divisions. To a large extent these changes are based on molecular criteria rather than on the morphologic criteria traditional to paleontology.

We suggest the organism described below was a multicellular eucaryote. If its growth and other points discussed are correctly interpreted, the life cycle was far more complex than clumping of single cells, such as in the modern *Volvox*. The fossil has no obvious morphologic relationship to Phanerozoic or Vendian taxa considered to be animals. The algal record is less well known, but again there is no close comparison to any Vendian taxa. Eventually, this fossil may be recognized as distinct at the phylum level.

Horodyskia Yochelson and Fedonkin

Horodyskia Yochelson and Fedonkin, 2000:844.

TYPE SPECIES.—*Horodyskia moniliformis* Yochelson and Fedonkin.

DIAGNOSIS.—Cones spaced along a horizontal tube.

DESCRIPTION.—Presumed colonial organisms of small vertically oriented cones, hemispherical on their upper surface, growing with essentially uniform spacing from an elongated horizontal stolon.

DISCUSSION.—To our knowledge this genus does not closely resemble other living or fossil forms. Observation on taphonomy and other points bearing on morphology are discussed in other sections of this work before the general discussion.

Even by standards of the Phanerozoic, *Horodyskia* is a locally common fossil. Although negative information may be destroyed in an instant of collecting, the active investigation of Middle Proterozoic in the western United States has not yielded any other occurrences. The taxon occurs only in siliclastic rocks and is limited in time. Such restrictions support interpretation of a highly specialized life habitat.

At the time this manuscript was prepared, we had not seen any specimens reported by Grey and Williams (1990). On the basis of one color transparency, we were tempted to assign the Australian specimens to the genus, but it seemed more prudent to leave open the question of whether those forms are congeneric, let alone conspecific. That material was originally known from three localities, but it now has been found in outcrops stretching several hundred kilometers in Western Australia (Grey, in litt., 1998). Winston and Link (1993:503) showed several reconstructions of Proterozoic paleogeography, one of which would place Antarctica and Australia close to Montana.

Horodyskia moniliformis Yochelson and Fedonkin

FRONTISPICE, FIGURES 3, 4, 6–17b

Horodyskia moniliformis Yochelson and Fedonkin, 2000:844, fig. 1.

DIAGNOSIS.—Proportionally uniform spacing of cone at all growth stages.

DESCRIPTION.—A series of tiny spherical bodies growing from a thin horizontal stolon and elongating with growth. Size and spacing between bodies remaining nearly uniformly proportional for every individual series. During growth, spheroidal shape becoming ellipsoidal and oriented with the long axis vertical, while size of the bodies and spacing between them proportionally increases. Tubes relatively short, with general shape like a wide ice cream cone. Upper surface hemispherical in early stages and probably at maturity, although slight invagination cannot be ruled out.

DISCUSSION.—Horodyski (1982) suggested that distinct large and small forms occurred. We judge all specimens are one species represented by various growth stages. Horodyski also indicated that several specimens were branched. We reex-

amined his original material and a few other strings that superficially appear to branch. They are all interpreted as closely adjacent strings or, rarely, as two strings crossing.

We are satisfied that only one species is present at the three GNP localities. What differences exist are best interpreted as slightly different taphonomic histories.

The holotype selection presents some concerns. The first issue is whether a string on a bedding plane or a sole surface should be selected. A sole surface better illustrates bead spacing, yet more details of the individuals can be seen on some upper surfaces. The second issue is selection of the type locality. It is easy to obtain specimens at Apikuni Mountain if one has a collecting permit from the National Park Service. Material from Rising Wolf Mountain is scarce, but it shows more of the morphology, and in the final analysis, that is more significant. The Frontispiece illustrates most of the slab that bears the holotype.

HOLOTYPE.—USNM 508100.

PARATYPES.—USNM 508101–508131. Only the figured material is formally designated as paratypes; the bulk of the collections contributed to the interpretations given, but to declare all material as paratypes would not have been good museum policy.

ETYMOLOGY.—The generic name marks the contributions of Robert J. Horodyski to the study of Proterozoic life. The specific name alludes to the appearance of the fossils as a string of beads or a necklace.

Comparison to Trace Fossils

Several workers have compared *Horodyskia* to trace fossils, but we judge this approach to be spurious. The closest similarity in appearance is to *Hormosiroidea* Schaffer (see Häntzchel, 1975:69–71), which looks like hemispherical or spherical bodies aligned on a string, but *Hormosiroidea* does not show the mode of growth of *Horodyskia*. The mode of growth and cone-like shape of beads distinguishes *Horodyskia* from *Neonereites* Seilacher, interpreted as a string of fecal pellets. In *Phycodes* Richter, vertical outlets in the burrow system arise from a horizontal shaft, and where these shafts are preserved on an upper bedding plane they may mimic a string of beads. They are unlike traces known from the Vendian (Fedonkin, 1981).

Specimen Characteristics

ABUNDANCE AND GENERAL SHAPE

At Apikuni Mountain *Horodyskia* is extremely abundant (Figure 6a); one outcrop of about 0.5 m² includes more than 12 strings. If the restricted collecting areas on Going-to-the Sun Road and on Rising Wolf Mountain are considered, specimens may be equally common at those localities. At Rising Wolf Mountain slabs are generally small, yet several bear two strings.

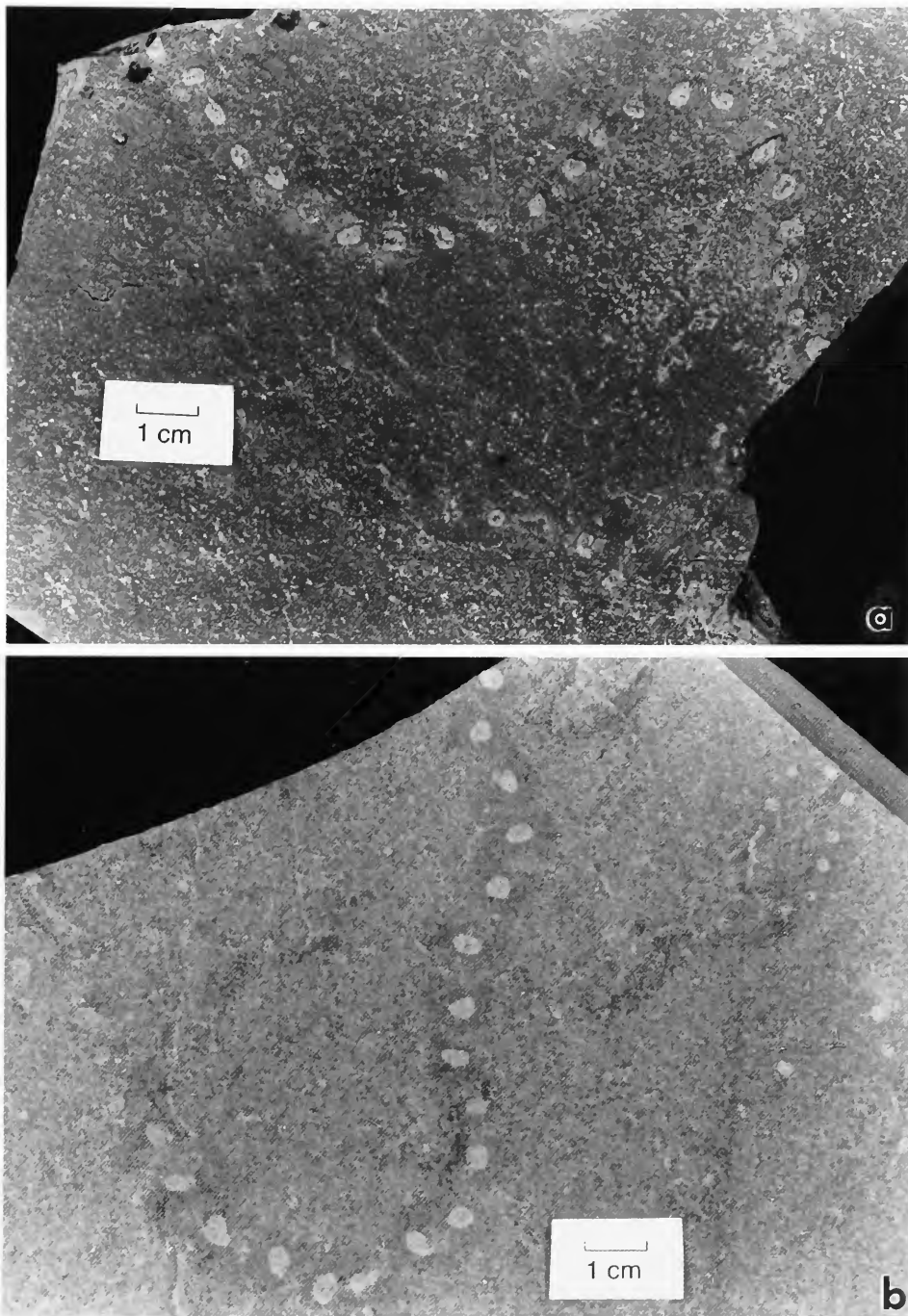


FIGURE 3.—*a*, An exceptionally long string of beads in a sigmoidal pattern on a gray sole surface, with the beads in shallow negative relief. The axes of ovals of the beads vary along the string. Several beads above the scale and to the right show a dark spot within the bead. USNM 508101; Apikuni Mountain. *b*, A long string of relatively large beads on a grayish tan sole surface of essentially no relief. A wide halo of iron oxide occurs around each bead. A shorter string of smaller beads to the upper right shows much smaller halos around several beads. Two isolated beads of the same size occur below this string. The larger beads are irregular in outline, whereas the smaller ones approach a circular shape. USNM 508102; Apikuni Mountain.

Because the sediment is arenite, any bottom may have provided a firm substrate for early growth. The rain of sediment was slow enough that many organisms were not smothered at an

early stage. Settling of an initial stage could have been more or less continuous. Adjacent occurrences of strings with different sizes of beads supports the interpretation of continuous settling.

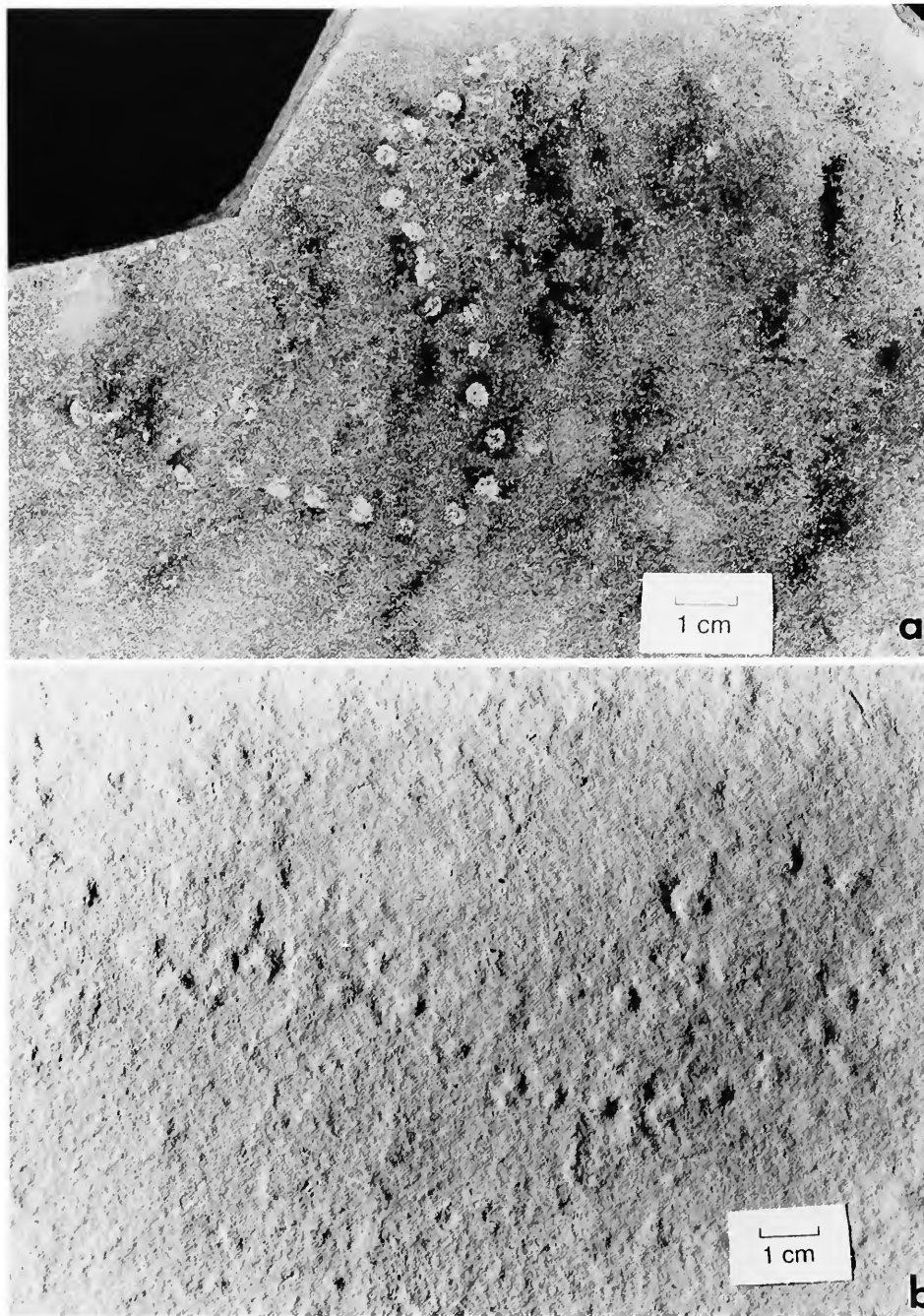


FIGURE 4.—*a*, A long string, which undergoes an abrupt bend, in slight negative relief on a gray sole surface. In color, this matrix approaches that of slabs from Rising Wolf Mountain, but these beads are of white silica and some are accentuated by small halos. USNM 508103; Apikuni Mountain. *b*, A long string in positive relief on a greenish gray upper bedding-plane surface. The curve to the right forms a shape like a reverse question mark, which is appropriate for this enigmatic fossil. USNM 508104; Apikuni Mountain.

Some strings were collected that grew on hummock surfaces (Figures 6*c*, 7*c*), and a relationship may exist between slight bedding-plane depressions and more abundant strings. It is equally possible that collecting bias is involved, for strings in prominent swales are easier to see in the field. Some

strings cross hummocks from trough to crest; others are oblique to slope.

Strings of fewer than six beads are exceedingly rare. Slabs with only one or two beads are broken across a string or have a parting plane cutting obliquely across the string. The shape of

strings varies widely. Straight or nearly straight strings are uncommon (Figure 5). Gently curved arcs (Figure 8b), distinct U shapes (Figure 3b), sigmoidal (Figure 4a), and irregular shapes (Figure 4b) all occur. We cannot find any correlation of bead size with shape of a string or number of beads. Variation in string shape and length are judged to be primary growth features.

Smaller beads are closely and uniformly spaced, and larger beads are more widely, but still uniformly, spaced (Figures 8a,b, 12c; Table 1). Horodyski (1982:887) plotted the relationship between length and spacing of beads on 10 strings. Grey and Williams (1990:312) added more data from 20 strings and produced a scatter diagram using both data sets. It confirms a relationship between bead size and spacing; no further discussion of this feature is necessary.

Grey and Williams (1990:313) used mean bead size and its standard deviation for comparison to various organisms and inorganic objects. In our view, tiny individuals are rare due to difficulty of preservation and collecting; large individuals are rare due to general considerations of population growth. Most beads are in a narrow size range, mainly because of the ease of seeing them on the outcrop. Size distribution seemingly has no deeper significance.

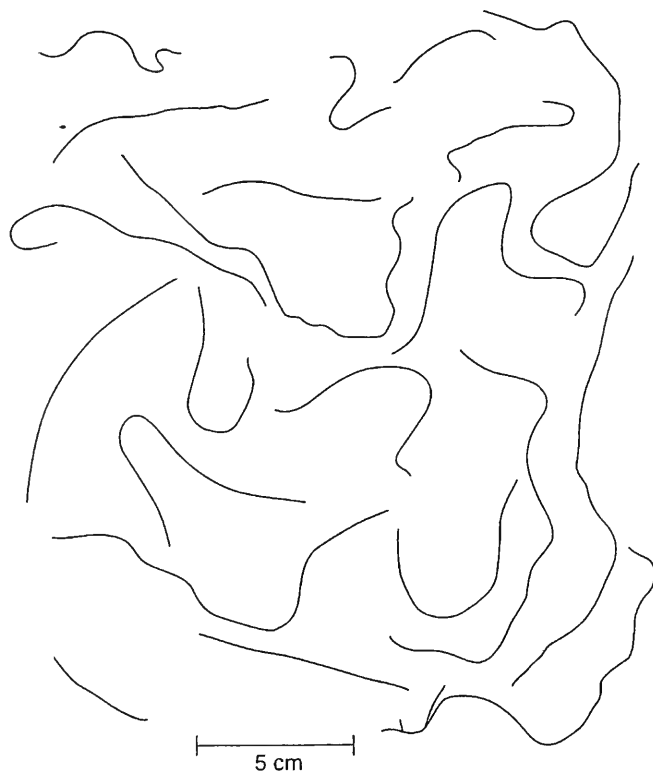


FIGURE 5.—Tracings, from a multiple number of slabs, of the course of 21 strings of beads. The strings do not touch the edges of a slab and seemingly are complete. The beads are of a variety of growth sizes, but bead size does not correlate with either string length or string orientation. Growth in a nearly straight line almost never occurred, and even slight curvature was an exception.

TABLE 1.—Measurements of selected specimens of *Horodyskia moniliformis*.

Number of beads	Average diameter of beads	Spacing of beads	Reference
5	4.5	4.6	Figure 7c
6	9.2	14.2	Figure 8a
7	5.0	4.6	Figure 12b
8	4.6	5.2	Figure 7b
8	4.9	4.3	Figure 8b
8	4.5	4.9	Frontispiece
10	6.3	3.7	Figure 11c
12	4.4	3.9	Figure 14c
21	4.1	3.8	Figure 4a
22	3.6	4.5	Figure 4b
23	2.7	2.5	Figure 8b
29	2.1	2.0	Figure 6c

BEAD SHAPE

Although a few beads, especially smaller ones, are nearly circular in outline, they are the exception. On many strings bead shape changes along the length. Bead outlines may be elongated ovals or, especially larger ones, irregular. This observation seems consistent with mechanical properties of objects under compaction—the smaller the diameter, the greater the durability. Beads surrounded by an aureole show a greater diversity of shape. On slabs that show current shadows or scour patterns, change in shape is more consistent; this is interpreted as specimens having been tilted slightly by a unidirectional current.

Hemispheres on bedding-plane surfaces are essentially circular in outline and reflect the upper portion of vertical tubes, which is further support that during life the cross section was nearly circular. The negative impressions seen rarely on both the bedding-plane and sole surfaces are triangular to quadrangular. We interpret them as an approximate impression of the lengthened bead. We reconstruct the shape as similar to a low, quite wide cone with a rounded scoop of ice cream on top. Original tube length cannot be determined, but we surmise from observing both lower and upper layers of integument on the sole surface that there was little shortening by compaction. Our best guess is that the tallest beads grew about 1 cm.

ASSOCIATED BIOTA

Sphaeromorphs in the Appekunny (Horodyski, 1993) are too poor for any generic assignment, but their range of cell size is within that of procaryotes. Horodyski (1993) also indicated the formation contained spiral impressions up to 10 cm in diameter and oval depressions about 2 cm in diameter bordered by elevated rims; both may be inorganic structures. Fedonkin et al. (1994) reported a variety of bedding-plane traces from member 1. We now interpret “tiny trails” as stolons of *Horodyskia*. Several other traces have been ruled out as sedimentological phenomenon or fragments of bacterial film. Reexamination of this material still suggests that other biota may have been present. Good specimens of faint traces are rare and are subject to different interpretations.

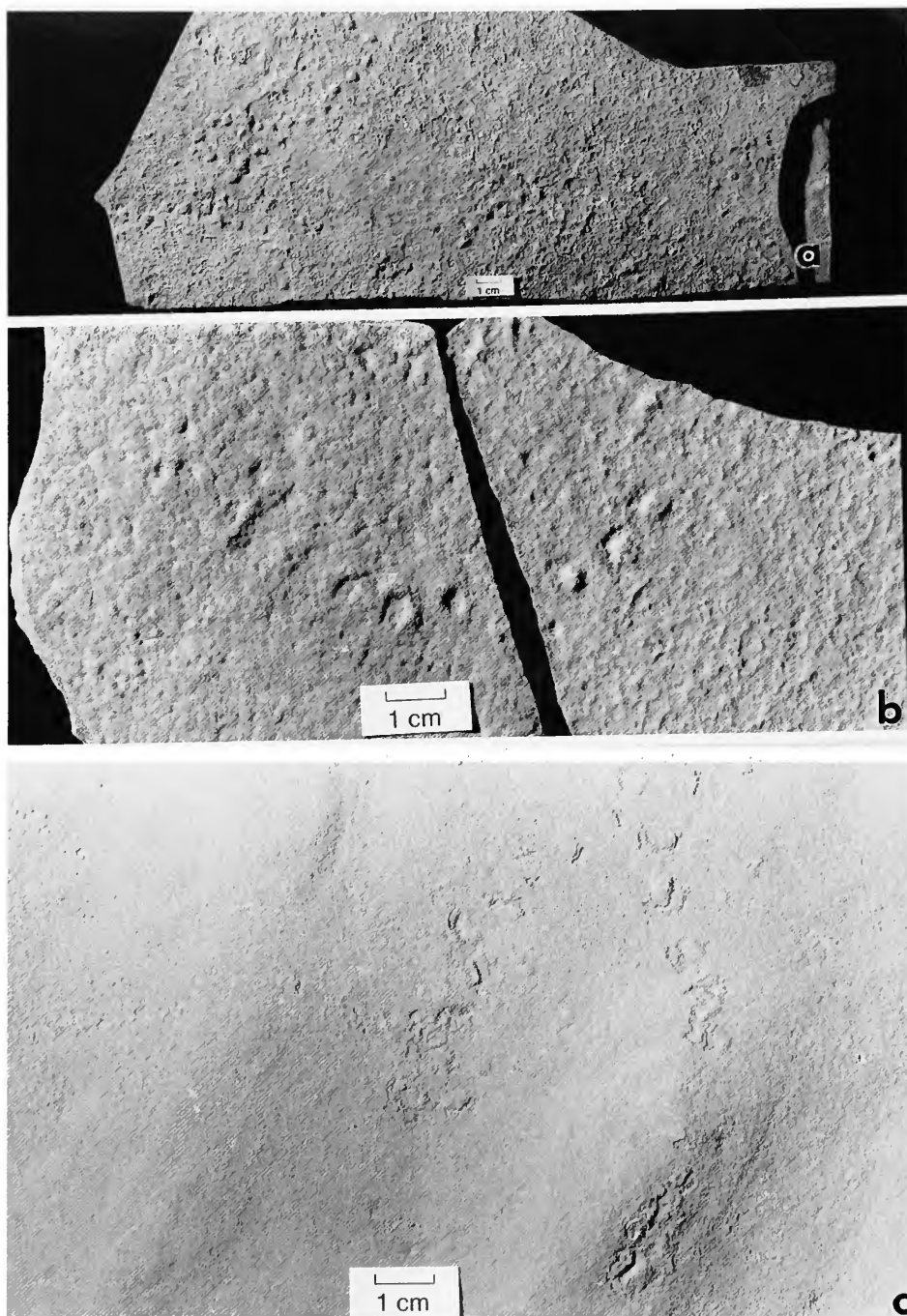


FIGURE 6.—*a*, Several strings, all with beads of nearly the same size, in positive relief on a greenish gray upper bedding-plane surface. All beads are nearly the same size, and the differences in string length and curvature suggest random orientation of the earliest growth stages. USNM 508105; Apikuni Mountain. *b*, Part and counterpart of a string of beads broken off at both ends. To the left is the gray sole surface, with the upper bedding-plane surface to the right. The beads preserved in negative relief on the sole surface are accentuated by infilled current crescents standing in relief as arcuate ridges. This specimen confirms the surface assignment for most of the loose slabs. USNM 508106; Apikuni Mountain. *c*, A hummocky surface bearing several strings of beads. To the right of the scale, a short string of beads occupies a depression in the center of the photograph, and a string of larger beads

is above them; because of the lighting, the surface topography appears in reverse relief. Above the scale is another string of poorly preserved beads on a crest, trending more or less parallel to the others. To the left, nearly at right angles to the strings of larger beads, a long string of very small beads crosses the crest of a hummock and a trough. Current crescents are well developed around some of the larger beads. The more obscure crescents associated with smaller strings suggest that bead size was a factor in the formation of these features. The degree of development of the crescents also may reflect various declinations of individuals originally in vertical position within the sediment, but shifted slightly because of the irregular surface of the hummock and, perhaps, may reflect slight differential compaction of the sediment. USNM 508107; Apikuni Mountain.

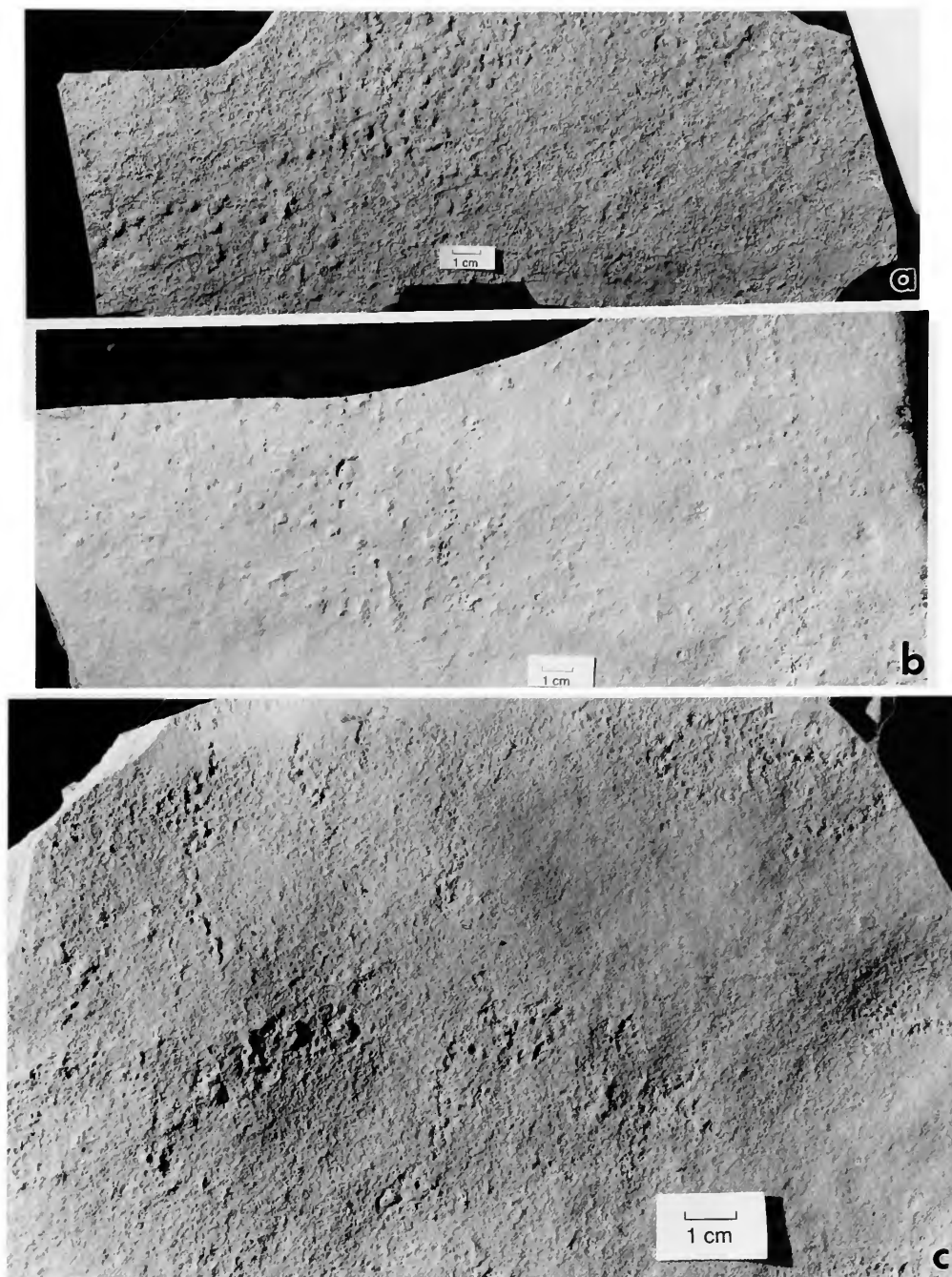


FIGURE 7.—*a*, Large beads preserved in positive relief on a grayish green upper bedding-plane surface. The large concentration of beads demonstrates high population density and makes the various strings difficult to differentiate. Beads vary in shape, but many are oval. USNM 508108; Apikuni Mountain. *b*, Strings preserved in positive relief, like a series of rounded knolls, on a dark green upper bedding-plane surface. Several sizes are present: large beads to the left are in two strings, each curved at the end and nearly touching so as to appear as a U within a shallow trough; small beads to the center trend across a hummock and trough; to the upper right are beads intermediate in size between those on the other two strings. At the upper right one string trends more or less horizontally with a “kink” near the center; above it is another string, which thereby gives a superficial impression of branching. USNM 508109; “Apikuni Mountain.” *c*, A hummocky, green upper bedding-plane surface showing numerous strings in positive relief. The few large beads to the left trend obliquely up the crest of a low hummock. The string of smaller beads directly above it go through a trough and up toward a crest. There are a variety of sizes, lengths, and orientations among the other strings, all of which show essentially uniform proportional spacing. USNM 508110; Apikuni Mountain.

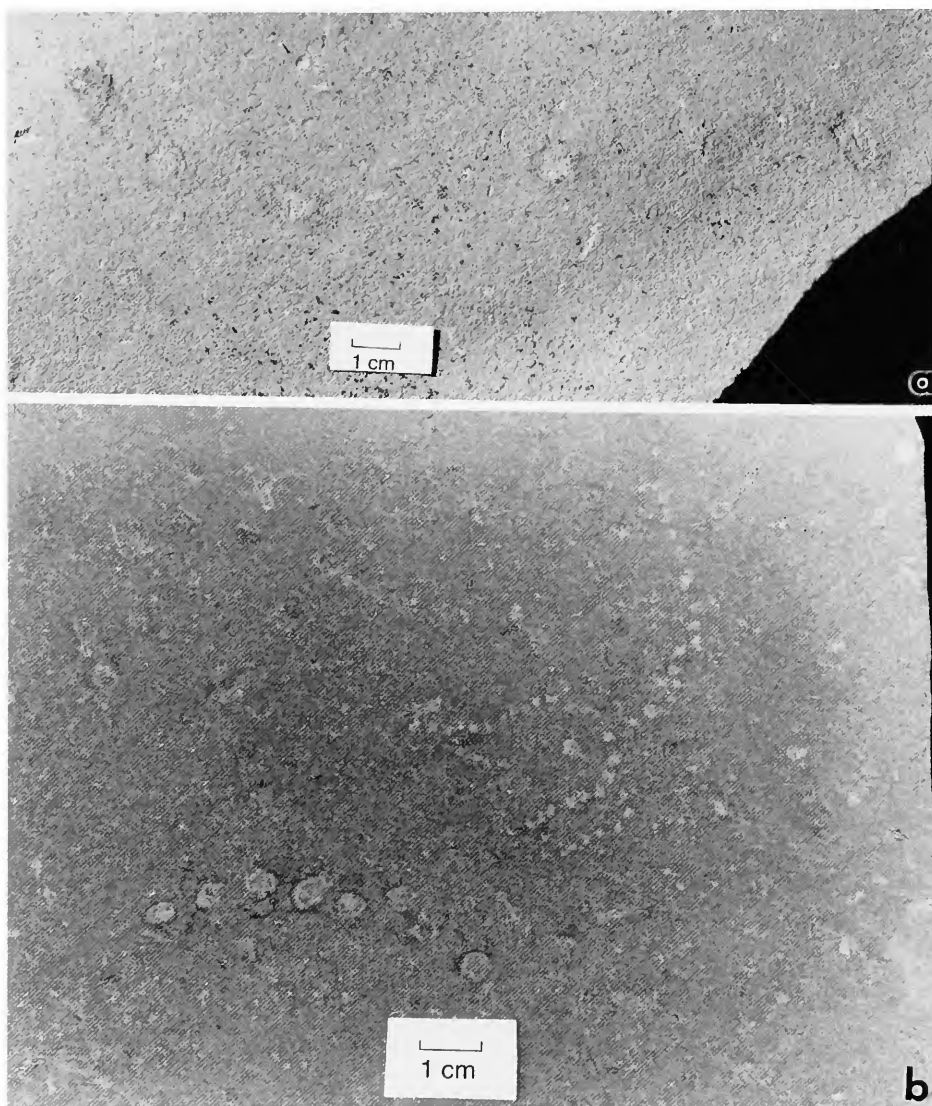


FIGURE 8.—*a*, A string of the largest beads known to date, with the widest spacing between beads. Above the scale is a bead so faint that it hardly appears on the photograph; another faint bead is between the two that are to the right. USNM 508111; Apikuni Mountain. *b*, Strings of several sizes on a dark green sole surface. The large beads above the scale show very shallow current crescents preserved as ridges; they mimic the outlines of halos. To the center right, two strings of smaller beads cross. Still smaller beads occur to the lower right of the crossed strings. USNM 508112; Apikuni Mountain.

One organic form that is not so open to argument is bacterial mats. These produce a crinkled surface on bedding planes, aptly described informally as “elephant skin” texture. The wrinkles may represent upper-surface relief of a mat after degradation under a layer of sediment (Figure 9*b,d*). Evidence of some mats at Apikuni Mountain was documented by Fedonkin et al. (1994), and at least one specimen of *Horodyskia* was covered by a mat (Figure 9*b*).

Having mentioned that, it must be noted that such mats are an exception, and few specimens were found at Apikuni Mountain. The sediment below modern mats is strongly anaerobic.

The paucity of mats in the formation might be related to greater depths rather than to shallower water.

Details of Matrix

LITHOLOGY

At Apikuni Mountain, individual beds weather to red, green, tan, or gray. Specimens of *Horodyskia moniliformis* occur in all rock colors with no differences in morphology. Sawn cross sections show no obvious differences among the different colored siltstones, and they show that most of the grays, browns, and

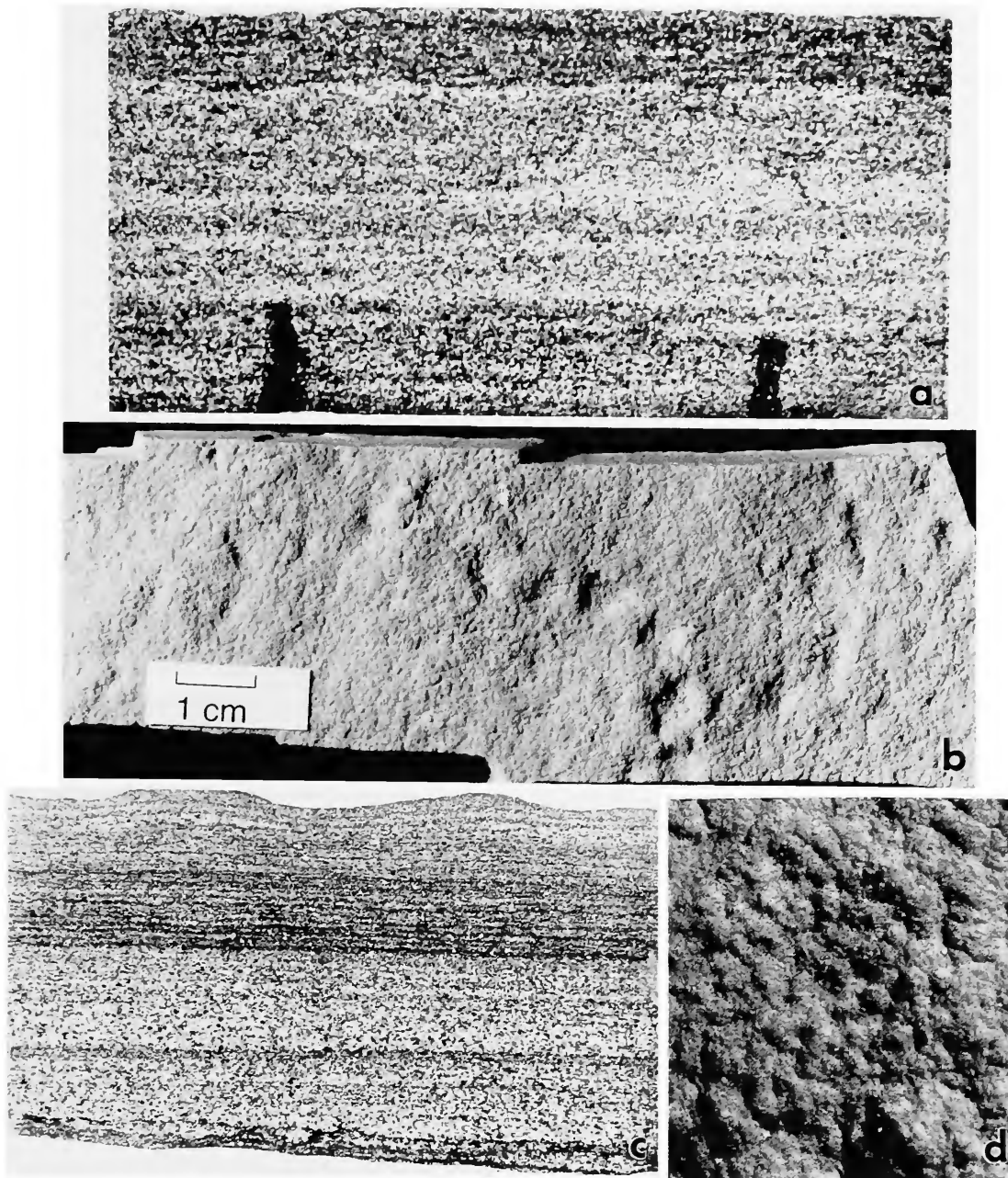


FIGURE 9.—*a*, Thin section through the impression of a flattened, white-colored bead marked on the sole surface by two lines. USNM 508113 ($\times 7.5$); Apikuni Mountain. *b*, A string of large beads preserved in negative relief on a presumed sole surface. The microrelief of the surface is interpreted as the impression of a bacterial mat that grew over the beads. USNM 508114; Apikuni Mountain. *c*, Thin section across at least three cycles of graded bedding. At the base and near the top of the thin section are microripples. The fine lamination could reflect participation of bacterial films in binding of sediment surfaces under conditions of very low sedimentation rate. USNM 508115 ($\times 5$); Apikuni Mountain. *d*, Enlargement of a portion of *b* to show the “elephant skin” texture of the bacterial mat ($\times 4$).

greens are a result of surface weathering. Most fossiliferous slabs from this locality are green to greenish gray. Most of the material from Going-to-the-Sun Road is in a dark red matrix, but the strings are no different. The surface color at all locali-

ties is mentioned in the figure captions, primarily because the color of the matrix affects the quality of the illustrations.

As shown well in thin sections, the rock is laminated on a delicate scale (Figure 9*a,c*). Commonly four to six laminae oc-

cur within 1 mm, yet all show graded bedding of silt-sized to clay-sized particles. Very low-angle cross bedding on a 1–2 mm scale occurs in some layers and is so slight as to be hardly apparent to the naked eye (Figure 9c).

Petrographic examination indicates that the rocks are composed almost entirely of angular grains of quartz and smaller amounts of angular feldspar. Extremely rare black grains showing right angles are iron oxide, but they originally may have been disseminated pyrite. If any clay minerals were present, they are not obvious. No mica or glauconite was observed.

One tan weathering bed was examined by microprobe. Analysis made with a 20 micron-wide beam and 100 microns spacing was run parallel to the laminae. The results, normalized to 100% for each spot analyzed and averaged, are as follows: SiO₂, 73.03%; Al₂O₃, 12.76%; FeO, 2.87%; MgO, 2.55%; CaO, 1.93%; K₂O, 4.51%; TiO₂, 0.57%; MnO, 0.05%; Na₂O, 1.46%. A run across coarser and finer laminae at the same spacing gave similar results: SiO₂, 74.53%; Al₂O₃, 9.60%; FeO, 3.08%; MgO, 3.72%; CaO, 4.11%; K₂O, 3.03%; TiO₂, 0.98%; MnO, 0.07%; Na₂O, 0.85%. A third probe, also at right angles to laminations, through a shorter distance with a 10 micron beam at 40 microns spacing, produced virtually the same results: SiO₂, 72.96%; Al₂O₃, 12.73%; FeO, 3.91%; MgO, 3.91%; CaO, 2.99%; K₂O, 3.95%; TiO₂, 0.50%; MnO, 0.03%; Na₂O, 0.4%. These analyses support the results of the petrographic determination that the grains are silica and feldspar. Iron and manganese oxides may come mainly from coatings on silica grains.

Microprobe analysis showed no obvious differences between beads and matrix. Beads examined from Apikuni Mountain are now formed of white silica (Figure 13b). Beads from Rising Wolf Mountain are black on a dark gray matrix (Figure 13a). This rock is also finely laminated, but material is limited, and we have not sacrificed any for more detailed study. Whether the dark color represents organic components originally present is a problem for future study.

DEPOSITIONAL ENVIRONMENT

Key lithologic features in member 1 of the Appekunny are the microscopically thin laminations and the tiny size of grains constituting them. This ultrafine lamination appears unique within the Belt Supergroup (Winston, in litt., 1997). The "microlamination sediment type" described by Winston (1989:53) from the Belt is different and is an alternation of silt and clay on a millimeter scale.

It is not clear how these delicate laminations formed. Whether an external mechanism, such as diurnal or lunar, influenced formation is uncertain. Glacial varves is an unlikely mechanism, and there is no evidence of glaciation within the Belt. The episodic lamination resembles modern sedimentation in the central basin of large lakes (Reineck and Singh, 1980:250–251).

In our view, the sediment source was probably wind-borne dust. Darwin (1962:5) commented on a dust cloud far at sea during his first few days on *H.M.S. Beagle*. In that example, the

dust was composed primarily of microscopic-sized organisms, but fine volcanic ash has been documented on ships far from a volcano. Differential settling of larger and smaller particles would provide graded bedding on a microscopic scale. Huebschman (1973:697) proposed that silt in the Pritchard Formation was wind-blown in origin.

Intermittent wind provides an ideal mechanism for fine-scale, graded bedding. Even a gentle breeze would have stirred shallow water enough to insure laminae were widespread. Most sediment settled below the fair-weather wave base. The regional distribution of the Appekunny Formation implies it was on a shelf rather than at great depth, but there is no evidence of emergence. Thus, a depth range of more than 2–3 m, and less than 100 m, is a reasonable guess. The fine laminations and small grain size indicate low energy conditions at the basin floor and thereby support an implication of greater rather than shallower depth.

Member 1 of the Appekunny Formation shows another novel sedimentological feature in that individual grains are coated with hematite (Winston, in litt., 1997). Red color occurs through the Belt, especially in some younger units, but those beds show mud cracks, salt crystal molds, and other indicators of terrestrial deposition. This is the only subaqueous red unit within the Belt Supergroup.

Since the pioneering efforts of Walcott (1899), arguments have raged over whether portions of the Belt were deposited in marine waters or were deposited in lakes. One may interpret the depositional environment as analogous to a modern playa lake having a slight bathymetric gradient (Winston and Link, 1993:505–506). The adjacent terrestrial sediment-source area was low-lying on a stable platform; most sediment was produced mechanically. In the absence of land vegetation, eolian erosion and eolian transport were significant and were augmented by unconfined and sheet-like flow of water (Winston and Link, 1993:503). Proterozoic paleogeographic reconstructions are less certain than those for the Phanerozoic, but some schemes place the Belt depositional basin near the equator. Such a warmer region would accelerate formation of hematite and would have a climate in which variable winds would be common.

In the fossiliferous part of member 1, most slabs are 2 to 3 cm thick; bedding planes may imply episodic sedimentation. It is plausible that each slab represents a major storm that formed the low hummocks, although any relationship between hummocks and bedding planes remains to be studied. If intermittent, gentle winds followed, the stirring water would have formed many cycles of graded bedding. At a final, extremely quiet stage, the finest clay-sized particles would have settled out to form a plane of weakness, before another storm ensued.

"Clay" as used herein indicates size and not mineralogical composition. The clay material on the bedding planes and elsewhere in the Belt is sericite (D. Winston, pers. comm., 1996). It may have been derived from a smectite-bearing illite (Maxwell and Hower, 1967) by low-grade metamorphism. Most fossils abound at and just above or just below the bedding planes, on

naturally separated surfaces (Figures 6b, 7a). Evidence of sediment starvation and low energy conditions of bottom water would seem to exclude catastrophic burial of organisms, but that is a function of scale. Even a slight increase in sedimentation rate could have smothered the organisms, for the beads stood only millimeters above the substrate (Figure 11c).

Few strings were found within medial portions of the slabs, although many slabs were split in the field. Put in other terms, the silt layers were closely packed angular grains and were essentially uncompacted. We recognize a unit of clay-sized arenite compacts much less than the same original thickness composed of clay minerals, and we guess that bedding planes, before compaction, represent a few millimeters of clay-sized arenite particles.

Thin sections of the Appekunny were examined by T.A. Ivanovskaya, a specialist on glauconite, to search particularly for that mineral; it was not identified. Glauconite indicates marine deposition and/or low sedimentation rates (Gary et al., 1972:40) (a more recent glossary (Jackson, 1997:272) defined the mineral but noted that “mode of origin is not a criterion”). Grey and Williams (1990:309) mentioned glauconite in the Middle Proterozoic Manganese Subgroup, Western Australia. Their account suggests a geologic setting in water shallower than in the Appekunny.

Winston and Link (1993:516) presented a diagram depicting the older Belt rocks as deposited within a giant lake. The model of a modern playa is helpful, but the Appekunny Formation was not formed in a fully enclosed body of water, for it interfingers westward with the Pritchard Formation. We are satisfied that the evidence for “lake-like” deposition of the Appekunny Formation is compelling. A plausible setting is lagoonal or estuarine, where relatively quiet water might prevail for long periods. In such an environment salinity might also have varied and affected settling rates of fine particles.

Although we reject a strict modern lake model, there is merit in comparisons. In contrast to eutrophic lakes, a playa may be an oligotrophic basin with low input of nutrients and low primary bioproductivity. The Appekunny basin may have been oligotrophic partly because of weak ventilation of the bottom by currents. Another consideration is the relatively low concentration of free oxygen in the Middle Proterozoic atmosphere so that the water column would not have contained as much oxygen as in present-day aquatic conditions. There are many gradations between freshwater lakes and normal marine waters, but there are too few constraints to be more specific. Zavarzin (1993) discussed some implications of atypical alkaline water bodies in the development of life.

PRESERVATION

Specimens of *Horodyskia moniliformis* are on both upper bedding plane and sole surfaces. The bulk of the material is loose slabs, but a few pieces are from outcrop with top and bottom marked; these confirm our orientation of fossiliferous surfaces. For illustrated specimens where there is uncertainty, we

have deliberately omitted any comment on orientation from the figure caption.

Specimens on both surfaces show a variety of taphonomic effects. Slabs are nearly flat, and, commonly, beads are nearly flat. Most strings, by far, are on sole surfaces where beads differ in color from matrix and are readily collected.

Upper bedding-surface specimens are commonly preserved as low hemispheres in positive relief. Unless light is strongly oblique, they are more difficult to see. Impressions of specimens—negative relief—are quite rare on upper bedding planes. Tiny specimens are on bedding-plane surfaces where a thin layer of clay-sized particles is preserved.

TAPHONOMY OF UPPER BEDDING-PLANE SURFACES.—On upper bedding surfaces, strings of hemispheres (Figure 7a) are common on both red and green colored rocks, with those on tan to gray rocks being less common. Red hemispheres are more prominent to the eye than those in other colors of matrix. The hemispheres show less size distribution of the individual beads than do beads on sole surfaces, and beads tend toward a larger size. This is a collecting artifact, as smaller specimens are obscure, except under ideal lighting conditions.

The hemispheres show no internal details in thin, polished, and fractured sections (Figure 10a–c). The hemispherical surfaces show occasional black flecks with right angles; these may have originally been pyrite crystals formed during decay of the integument. Another source of a central dark spot is exfoliation (Figures 10b, 13b). In detail, beads may be rounded (Figure 7b) or flattened (Figure 10a), which we attribute to compaction. Some flattened beads have rays extending outward, which are variable in length, number, and position around the bead. We interpret the rays as compaction structures and have not bothered to illustrate them.

Allen (1982:173–205) discussed in detail the formation of “obstacle marks” resulting from water movement. One slab shows lineation, referred to as “current shadows” (Figure 12a). Some strings show “current crescents” of coarser grains commonly around one-fourth to one-half of bead circumference; this is particularly striking when coarser material is a different color than the matrix (Figures 11c, 12b). Other beads show a faint depression on one side, although it may be a modern phenomenon of weathering away of coarser grains rather than scour. A few strings show a scour-remnant ridge surrounding beads (Figure 11b). We interpret the beads as resistant structures standing a short distance, a few millimeters or less, above the substrate and therefore affecting a directional current.

Furthermore, based on these observations, it is likely that the cone-shaped beads decayed slowly, for the hemispheres approximate the negative impressions of the sole surface. The upper part of a cone was more likely to have been cemented earlier than parts further within the sediment. Partially compressed and decayed beads were resistant enough to form a “buried hill” topography.

The few examples of bedding-plane negative relief are a series of quite shallow pits, showing little detail of the form

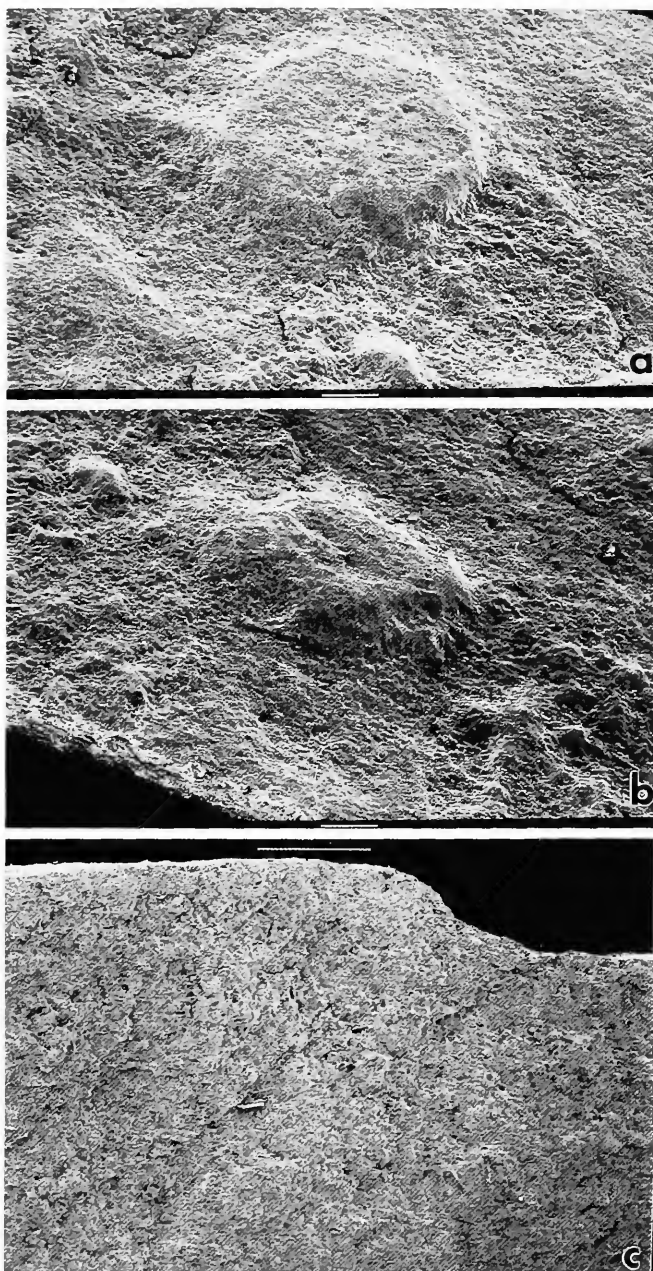


FIGURE 10.—*a*, Slightly oblique view of a flat-topped, nearly circular bead on an upper bedding-plane surface. USNM 508116 (scale=1 mm); “Apikuni Mountain.” *b*, Slightly oblique view of an elongated bead on an upper bedding-plane surface; the central depression may result from exfoliation. This bead is on the same string and is next to the one shown in *a*. USNM 508116 (scale=1 mm). *c*, Fracture surface through a bead preserved in positive relief on an upper bedding-plane surface. An exceedingly thin layer marks the surface of the bead. USNM 508117 (scale=1 mm); Apikuni Mountain.

plucked from the hole. Negative relief results from replacement of body volume by sediment from above during the process of decomposition and subsequent loss of the differentially cemented filling.

TAPHONOMY OF SOLE SURFACES.—Characteristically, strings on sole surfaces at Apikuni Mountain are easy to see because they are white beads in matrix of a different color. The hemispherical shape on bedding planes is reflected in the slight inward curvature of beads. On some strings, nearly all the bead is eroded, but the depression retains a thin white residue sufficient to reflect light (Figure 13*b*).

The material now forming the beads is silica, which is apparently amorphous. We attribute this to replacement of the original bead surface. Presumably, organisms died in situ, were smothered by sediment, and became partially compressed, but the covering matrix was porous enough to allow penetration of silica-rich waters; in Phanerozoic rocks, organic matter may assist the replacement process (Fedonkin, 1987). It is less likely that decay products might have locally hardened the sediment and silica filled a void.

Thin sections across these silica plates confirm they are limited to the sole surface and are less than 1 mm thick. Indeed, when a section is cut through these structures, they cannot be identified without prior knowledge of where a bead was located (Figure 9*a*).

Occasional beads show a central dot or two of silt matrix, which are prominent because of color difference. When the compressed lower surface is present, no matrix is seen, but when the lower “layer” is absent, one observes the inner surface of the hemisphere or a break in it. A central spot of matrix is seen in beads of varying sizes. Its random presence among the beads of a string is probably a taphonomic effect.

We suggest that at early growth stages a hemispherical upper surface was present on a bead. We cannot rule out that at maturity this area might have become slightly invaginated. If so, as the organisms were killed by sediment influx, this depression collected a few larger grains.

A different interpretation of this silt speck is that it marks an opening at the top of the hemisphere. In that scenario, when the cone-like tube was overwhelmed by sediment influx, several grains entered a central opening and survived silicification. We cannot prove either interpretation, nor can we rule out any others, but we are convinced that a central spot is secondary and not an opening in the living organism.

Examined in detail, the silica plates provide little more data. The rock does not split around the fossils but cuts across them (Figure 14*c*). As a result, bead size is not only related to growth, but it is also a function of where the parting plane intersects them. Smaller beads tend to be closer spaced than larger ones, yet we have examples of seemingly small beads widely spaced; these are readily interpreted as the consequence of the parting plane cutting relatively high across the hemisphere of larger beads.

In about one-third of the strings, a brown aureole occurs around beads; when present, most or all beads in a string show this feature. Commonly, the aureole is wider on one side (Figure 14*b*). There may be a correlation between oval shape and aureole width, but too few samples show both features to draw

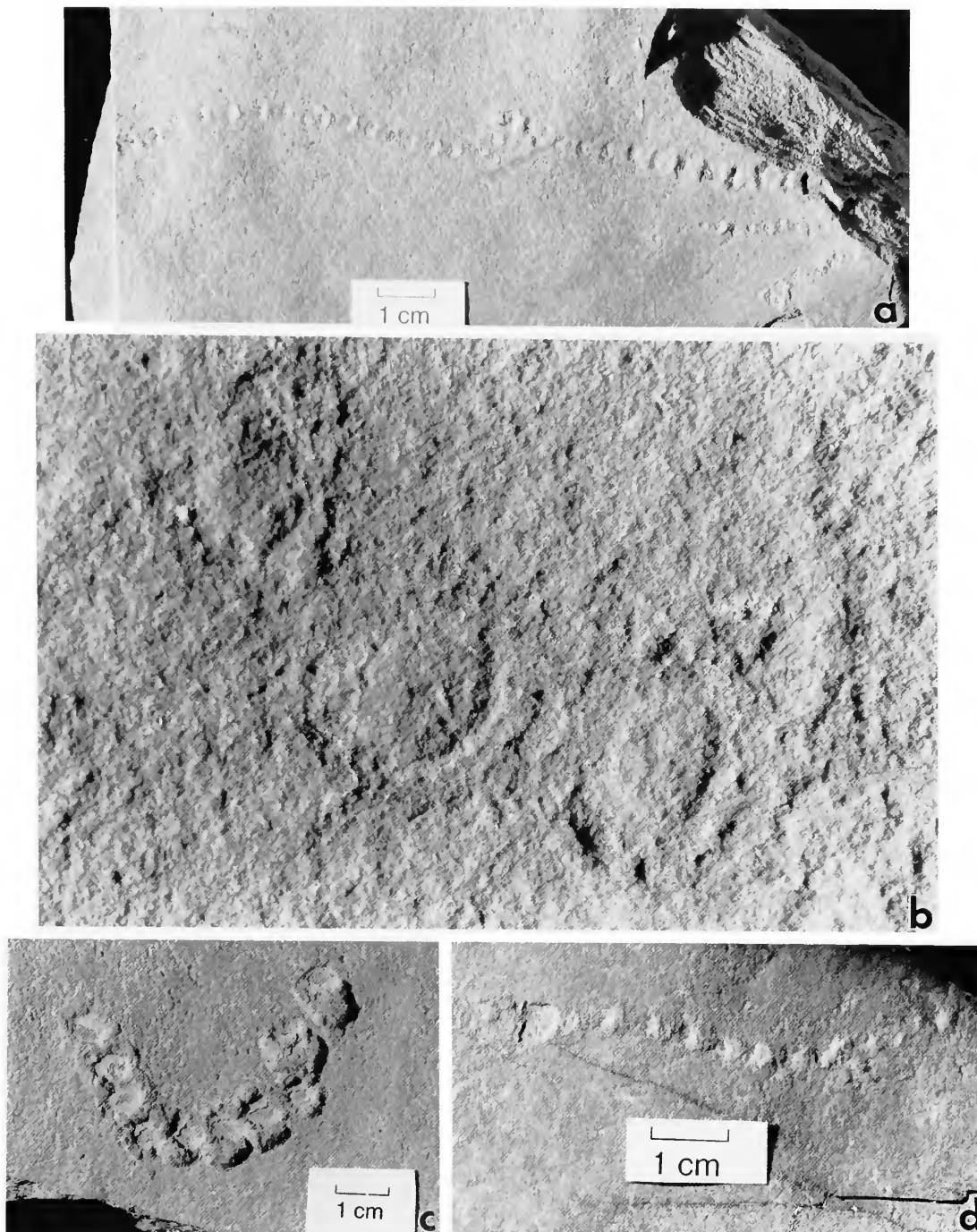


FIGURE 11.—*a*, Chevron-like impression of three strings of beads. The inclination of the smaller set of grooves below the right is opposite that of the slightly larger grooves above. A short, even smaller set is to the right of the larger grooves. This specimen was previous figured by Fedonkin et al. (1994, fig. 22). USNM 468250; Apikuni Mountain. *b*, Individual beads on a dark brown, upper bedding-plane surface preserved in negative relief. The asymmetrically expressed depressions adjacent to the beads are scour marks, a form of current crescents. The upper left bead is affected by slight spalling of the surface; the middle bead shows a slight central protuberance. As a result of the extremely low angle of the light, the crescent on one bead appears as a

moat and on another as a ridge. USNM 508118 ($\times 4$); Apikuni Mountain. *c*, A string of beads in negative relief on a green sole surface. Each bead is surrounded by an infilled scour mark of coarser material that stands in relief. The infilled scour marks rise at least 3 mm and suggest a minimum height of the bead of more than 1 cm. USNM 508119; "Apikuni Mountain." *d*, Chevron-like impressions of a string on a dark green sole surface. They are consistently inclined, being deeper toward the left. These are interpreted as the impression of individual beads, and the depth gives an indication of their relative height. The sediment retains some impression, which indicates the stiff character of the individual beads. USNM 508120; Apikuni Mountain.

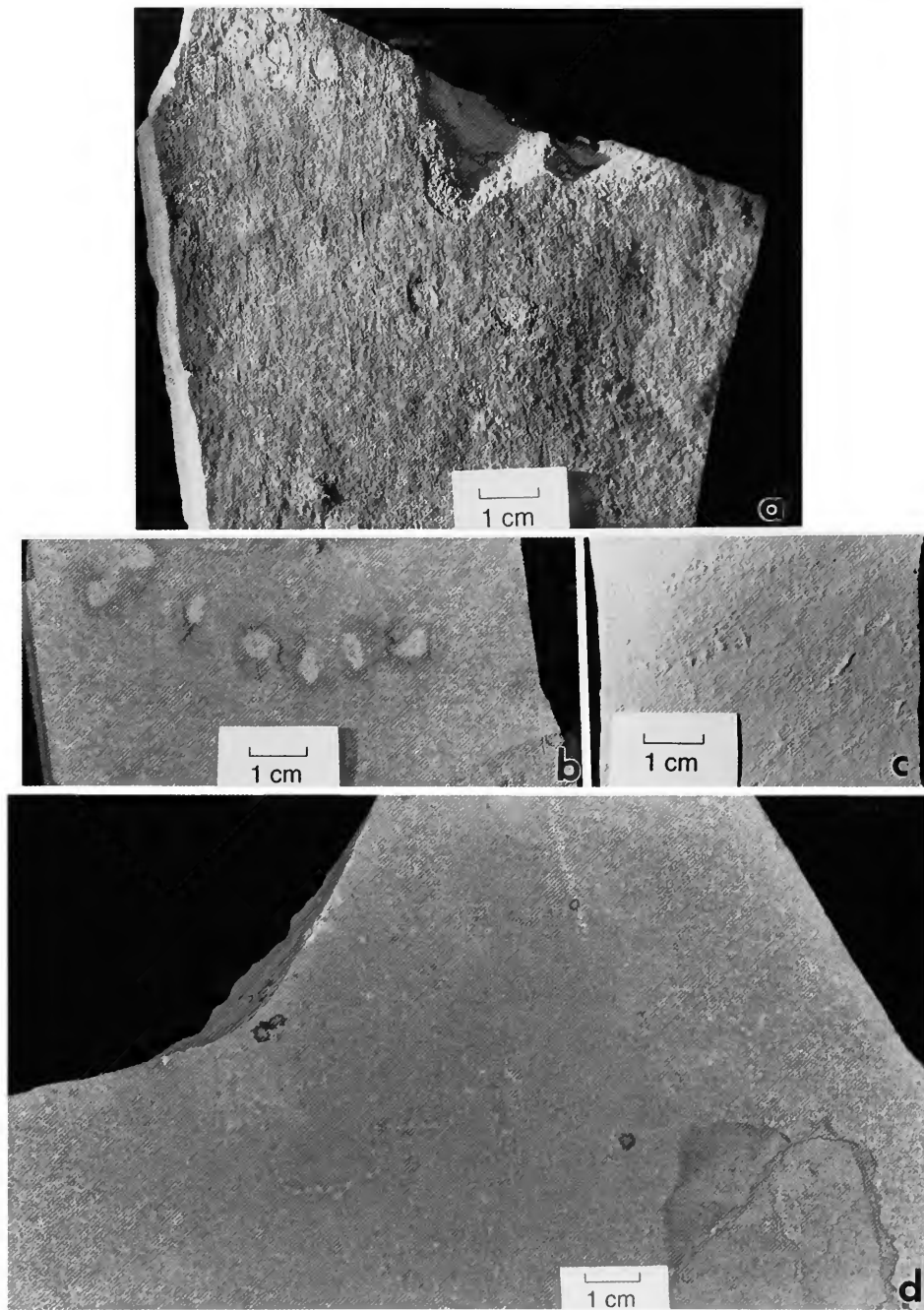


FIGURE 12.—*a*, A dark gray sole surface showing elongate current shadows running the length of the slab, plus current crescents associated with beads. USNM 508121; “Apikuni Mountain.” *b*, A short string of beads on a light tan sole surface. The apparent halo around the beads is a slightly raised current crescent infilled with lighter colored grains. The irregular shape of the various beads may have resulted from deformation by compaction. USNM 508122; Apikuni Mountain. *c*, A string of quite small beads in positive relief on a grayish green upper bedding-plane surface. Several beads show ridges, presumably caused by compaction. USNM 508123; Apikuni Mountain. *d*, A long string of closely spaced tiny beads on a gray upper bedding-plane surface is shown to the left, below an irregular lichen patch. This colony, at an early growth stage, shows the fine thread, or stolon, connecting the beads. The string is mainly a trough parallel to the edge of a hummock, but at the “kink” it trends up the slope of the hummock. A shorter string is to the right above a place where matrix has spalled away. USNM 508124; Apikuni Mountain.

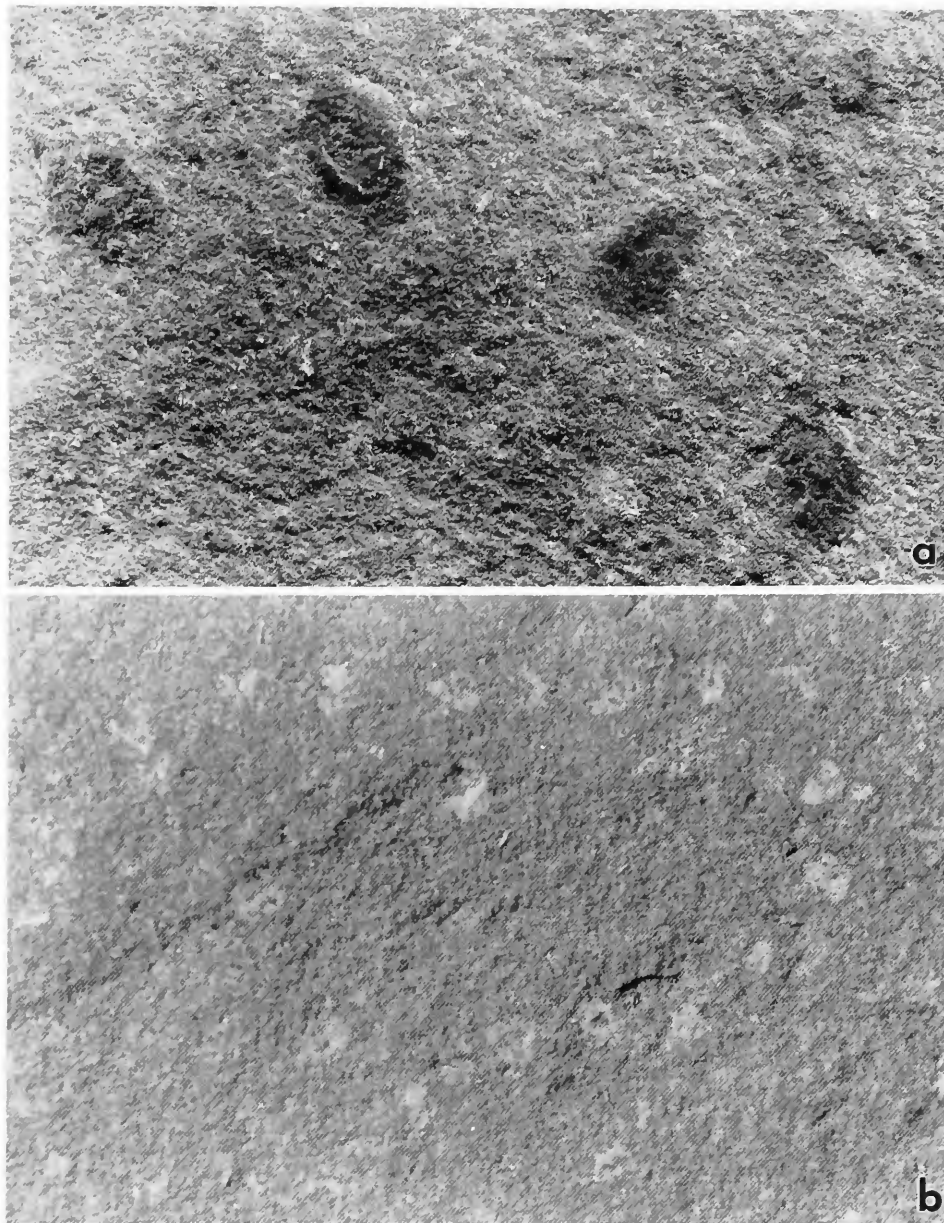


FIGURE 13.—*a*, Part of a string of black beads on a dark gray sole surface. The different orientation of the axes of the ovals may indicate inclination of the individuals as a post-mortem effect, but there is no deformation of shape to support this interpretation. There are no halos around the beads. USNM 508130 ($\times 4$); Rising Wolf Mountain. *b*, A number of tiny beads preserved as flat patches of white silica on a reddish brown matrix. Some beads have a dark central spot resulting from flaking away of part of the thin silica layer. USNM 508131 ($\times 4$); Apikuni Mountain.

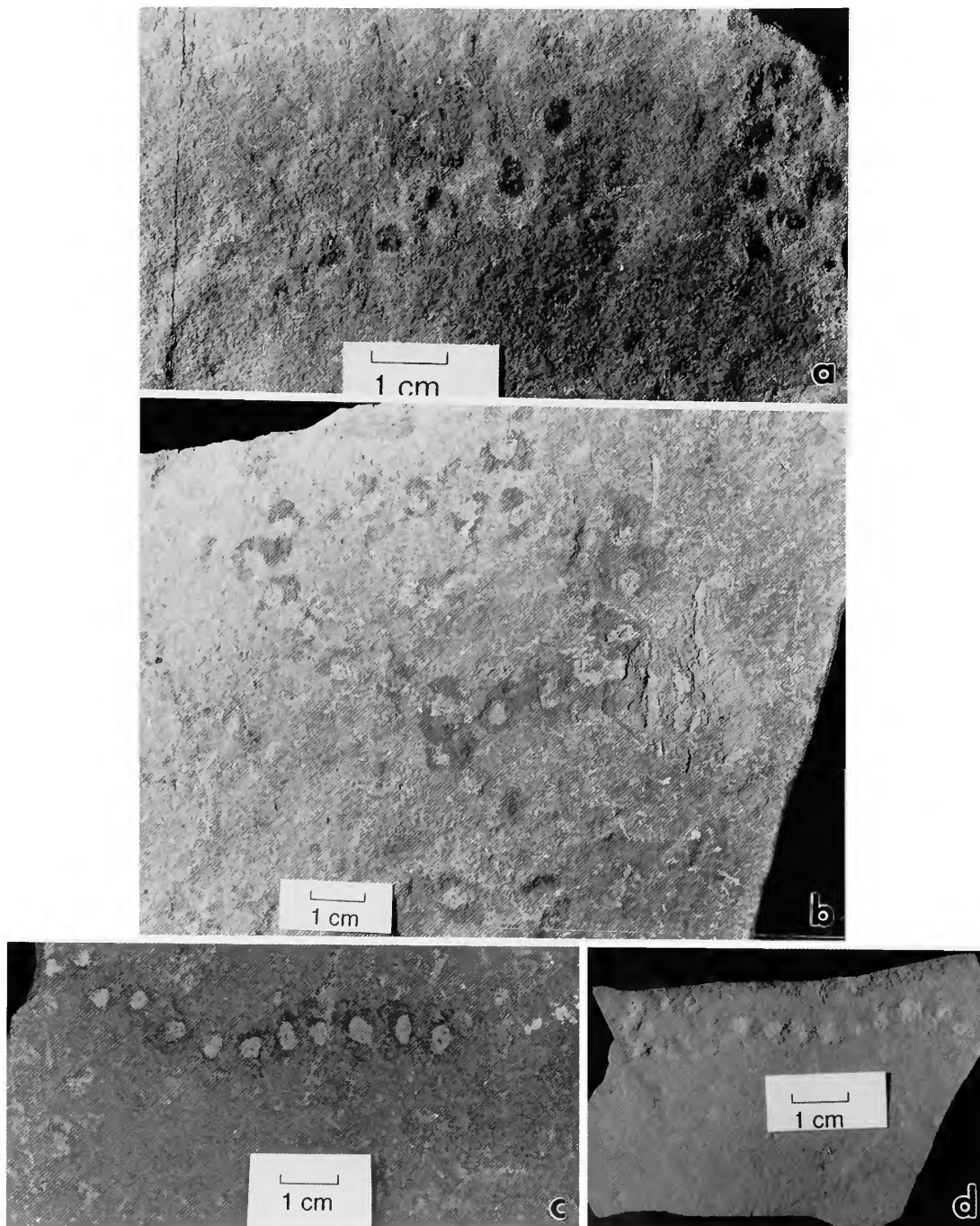


FIGURE 14.—*a*, Two strings of different curvature, one across the sole surface of a dark gray slab and one on the right edge. The black, flattened beads are surrounded by lighter colored halos that vary widely in size. On the string to the upper right, the halos are narrower and less prominent. USNM 468248; Rising Wolf Mountain. The specimen was illustrated by Fedonkin et al. (1994, fig. 21). *b*, Several strings of large beads on a light gray slab; this may be a sole surface. The large beads have extensive halos of iron oxide, and those in the slightly smaller string to the upper left have slightly smaller halos. USNM 508127; Apikuni Mountain. *c*, A string on a gray sole surface showing an apparent slight size gradient, with larger beads to the right. The false gradient is the result of the sole surface not being completely flat, as a

thin layer was spalled away on the left side. The beads to the right are in very slight positive relief, and several show a central dark spot; beads to the left are in slight negative relief. The different cross sections vary from nearly circular through elliptical to nearly triangular; this may be a taphonomic effect. Several smaller strings are on the lower part of the slab, which is not illustrated. USNM 508128; Apikuni Mountain. *d*, The only known specimen from Otokomi Mountain. The beads are preserved in slight negative relief on the dark green sole surface. One string of beads trends horizontal near the upper edge of the small slab. A second string is broken by the upper edge of the slab, and a third is to the upper left and is in the shape of an irregular oval. USNM 508129; Otokomi Mountain.

a firm conclusion. Likely, the color is an oxidation product from pyrite, which, in turn, may be related to decay of integument and inner cells. A logical interpretation is fast burial and decomposition under low permeability, preventing aeration and escape of degradation products.

Strings that show sediment piled on one side of a bead or other evidence of current activity are far less common than those showing an aureole, although they are better developed on the sole surface than on the upper bedding planes. These two forms of taphonomic change, scour and aureole, appear to be mutually exclusive because they reflect different conditions of aeration of the sediment.

Some strings on the sole surface are preserved in negative relief. In general, these depressions are in the form of acute triangles (Figure 11a,d). In both positive and negative relief the cross section does not show any internal structures preserved, for the whole volume of the body was replaced.

Beads from Rising Wolf Mountain are black rather than white (Frontispiece, Figure 14a). We have not investigated the nature of the color because of the small number of specimens available, but we suspect there originally was a higher carbon content in the rock, along with deposition of manganese.

Hypotheses

PALEOENVIRONMENTAL CONSIDERATIONS

Experience with Phanerozoic paleoecology demonstrates the effectiveness of an actualistic approach by analysis and comparison to present-day biota. For example, the presence of echinoderms indicates salinity was that of a normal marine environment, and a fossil coral reef suggests growing conditions similar to those of modern reef communities. It is a plausible approach to interpreting Proterozoic procaryotic ecosystems of cyanobacterial communities. Unfortunately, this approach is not always obvious or even helpful in considering Proterozoic eucaryotic organisms. The uncertain systematic position of many older eucaryotic organisms of both microscopic and megascopic size does not permit interpretation of the environment as in Phanerozoic paleoecologic study. When some of the unfamiliar morphologies of Late Proterozoic (Vendian) fossils are taken into account, the situation may be more dramatic, and strange morphologies might actually correlate with unfamiliar or extinct physiologies. In the still older Middle Proterozoic there may well be peculiar relations between organisms and their environment that have no recent counterparts.

Deposition of banded iron provides support for this notion. Early in earth history, conditions were appropriate for development of that rock and other "extinct deposits" (Fedonkin, 1996a). Conditions later changed and such material was no longer deposited. One cannot be certain of the systematic placement of *Horodyskia* because no obvious similarities indicate either homology or analogy, and one cannot be confident

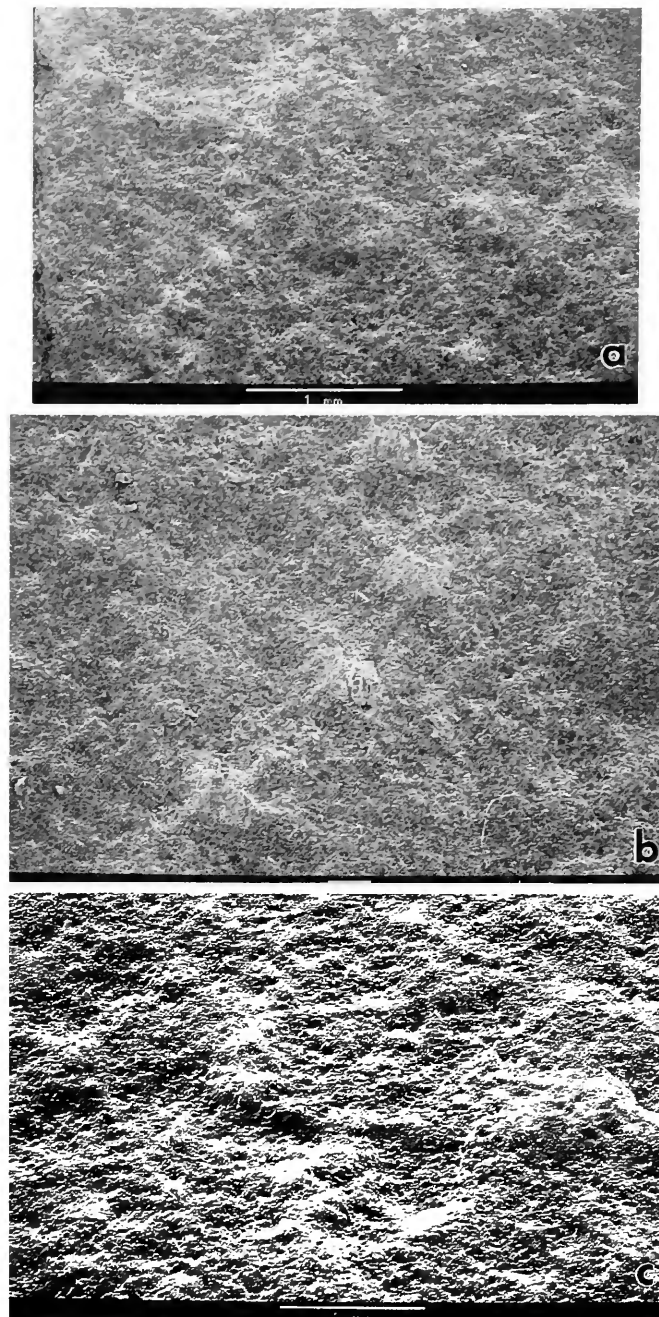


FIGURE 15.—a, A string of tiny beads on an upper bedding-plane surface, trending diagonally upward from the lower left and turning toward the right. The ridge of uniform width between the beads is interpreted as a stolon. USNM 508125 (scale=1 mm); Apikuni Mountain. b, Enlargement of three of the beads illustrated in a. The beads are connected by a stolon. The rays and projections from the beads are judged to be a result of compression. USNM 508125 (scale=100 μ m). c, Oblique view of a curved stolon on an upper bedding-plane surface. Several swellings occur on the lower limb of the U-shaped structure. USNM 508126 (scale=1 mm); Apikuni Mountain.

of its environment. Like any rule, actualism should be treated with caution. *Horodyskia* may have lived in an environment

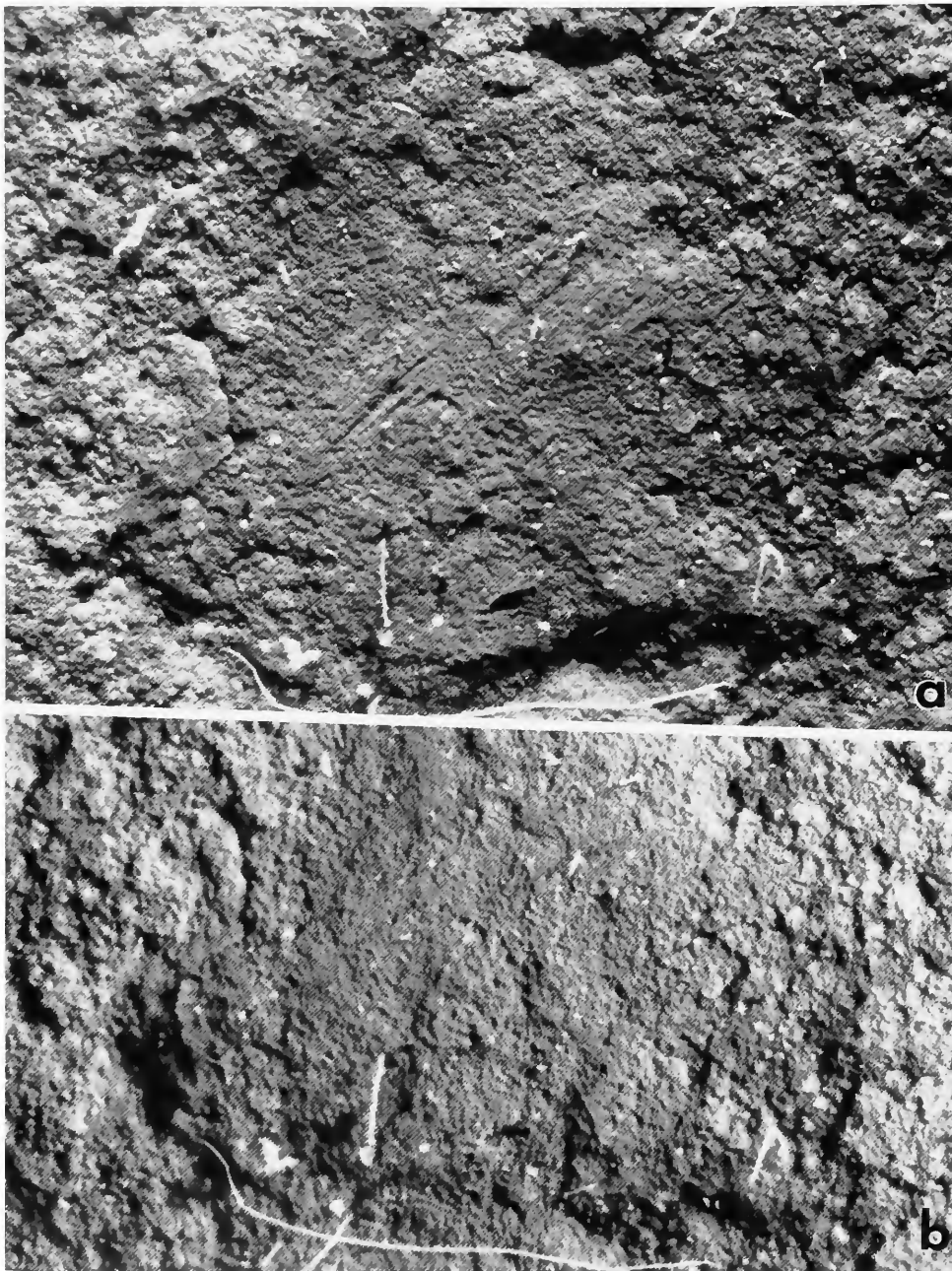


FIGURE 16.—*a*, Enlargement of a bead, not shown on Figure 13*a* but directly below the one to the lower right. The oblique markings across the bead are clear. USNM 508130 ($\times 20$). *b*, The same specimen taken with different lighting. Curved marking may be seen on the surface of the bead ($\times 20$).

more like that of the Phanerozoic than like that of the Archean, but details cannot be stated.

Timofeev et al. (1988) suggested that during the earlier part of earth history, the hypsometric contrast between shelves and ocean basins was less pronounced, the rate of sedimentation was lower, and the lateral differentiation of clastic sediments was less significant, relative to conditions in the Phanerozoic.

MODE OF LIFE

Three theoretical modes of life should be considered for *Hordyskia*: pelagic, infaunal, or epifaunal. Although the last two terms imply animal, they are used in an ecological sense only.

Grey and Williams (1990:322–323) compared their strings to various pelagic algae, particularly the brown alga *Hormosira* (Endlicher) Meneghini. One might then view individual beads

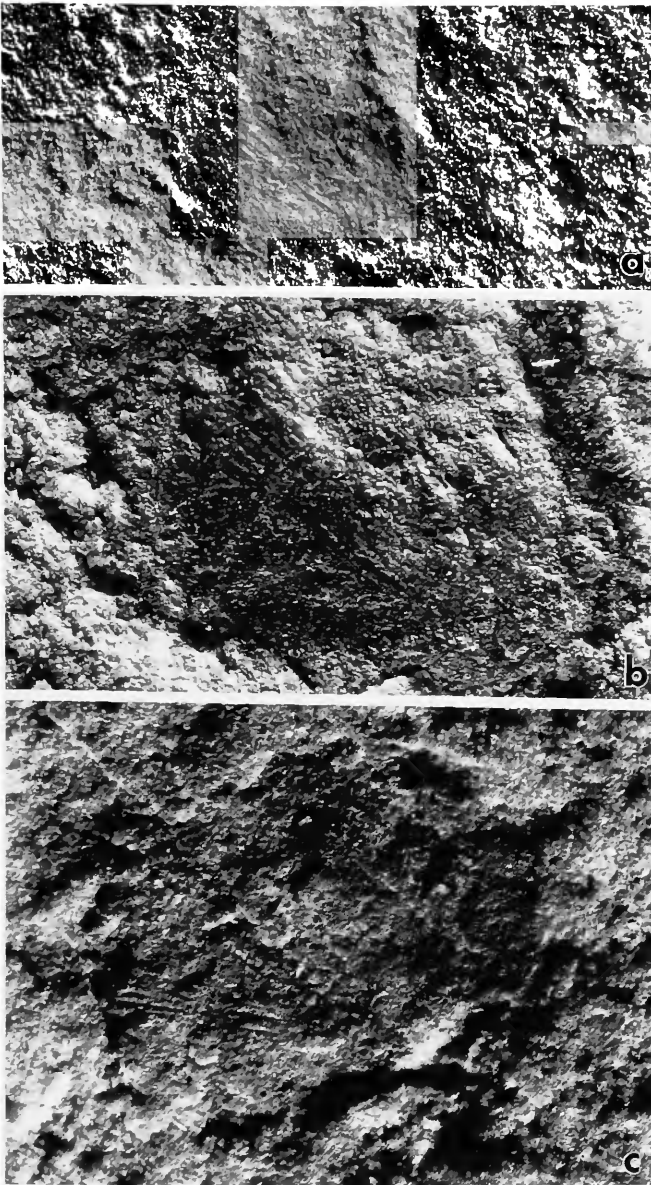


FIGURE 17.—*a*, Enlargement of a bead on the far right of Figure 13*a*. Elongate markings may be seen. USNM 508130 ($\times 10$). *b*, The same bead further enlarged and with different lighting. Lines in the lower part of the bead area are at an angle to those above them ($\times 20$). *c*, A bead from a string on the same slab that bears the holotype; it is indicated on the frontispiece by an arrow. Markings across the bead at two different angles may be seen. USNM 508100 ($\times 20$).

as air bladders, allowing the string to float. This interpretation has merit and cannot be ignored.

The strings show a variety of shapes. If they settled from the water column under extremely quiet water conditions, as deduced from the sediment laminations, one might expect some uniformity in shape. We have no strings that are tangled, or any instances in which one specimen lies directly across another of the same growth size, phenomena to be expected with strings

falling to the bottom. Dead pelagic organisms lying on the bottom surface might produce drag marks on the bedding plane, but such marks have not been observed. As noted, delicate sedimentary structures of obstacle marks, or “current shadows,” and scour do occur. In *Hormoseria*, the connection between true spheres is horizontal, yet no impressions linking beads beyond the earliest stages have been observed. We find little to support the comparison and, equally, for an interpretation of a pelagic life mode.

A modification of pelagic life would be if a string were anchored at one end. We presume that if the beads acted as floats, they would show a size gradient. The stem might be imprinted on the sediment along with the beads. Neither has been observed, and we rule out this interpretation.

At an early life stage, it is far easier for a tube of microscopic cross section to grow on the sediment surface than within sediment, an argument against continuous covering. None of the sawn cross sections, polished sections, or thin sections show any significant change in the delicate graded bedding. On virtually all slabs, specimens are limited to bedding-plane and sole surfaces. We cannot exclude the possibility of a small, shallowly buried tube-like organ occasionally giving rise to beads or short vertical tubes that thrust up through the sediment, although we judge this to be most unlikely. There is no evidence of disturbance of laminae.

Current crescents and scour around beads indicate they stood above the bottom during life or were partially uncovered by water movement before being smothered by sediment. This vertical component of growth seems a powerful argument for life extending upward from the bottom. Morphology of the strings also supports a benthic mode of life. Unbroken strings are six or more beads long. Both very small beads of millimeter size and strings of large beads are often preserved on the same bedding plane. No evidence of size sorting or dominant orientation has been found.

We interpret life position as benthonic, and it was a combination of extremely shallow infaunal and epifaunal position as the organism grew upward to avoid being buried. The vast majority of these organisms were buried in situ by a sediment influx deeper than that through which the organism could grow; therefore, the number of strings reflects an extremely high population density. Mode and time of reproduction, details of substrate and microenvironment favorable for settling, and growth and subsequent preservation of organisms are among the major elements controlling the local mass occurrence of *Horodyskia*, but we are unable to quantify any of these factors. An artistic rendering of our interpretation is shown in Figure 18.

GROWTH

At least three theoretical models of growth are possible: uniform (coherent) growth of stolon length and bead size; growth of some beads and inhibition of others in the process of maturation; and growth of some larger beads and regressive development of other smaller ones.

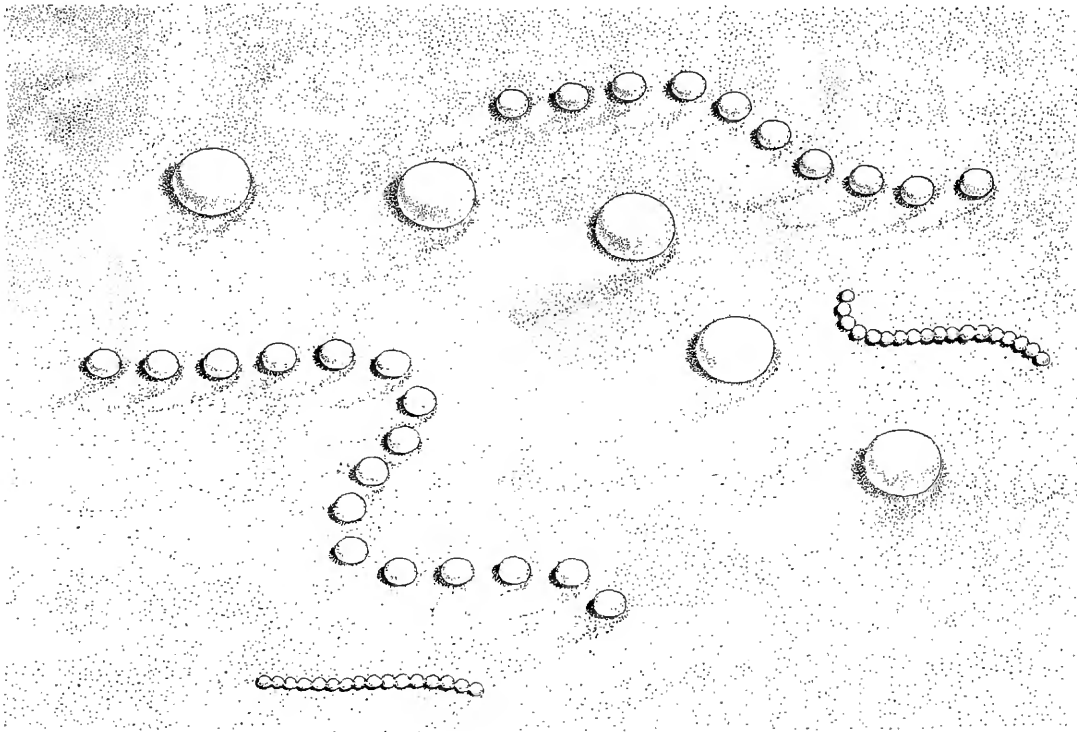


FIGURE 18.—Reconstruction of several strings of *Horodyskia* of different growth stages living on a fine-grain arenite bottom. The specimens are partially covered by sediment so that the “string of beads” effect is obvious. Current shadows and infillings associated with the beads are in the lee of the current direction. These features are more apparent for the larger and older string than for the smaller beads.

The first model may imply the stolons grew to their full length and then gave rise to beads of different size. If upward extensions appeared as a stolon elongated, beads would be of varying lengths. Either case would not produce proportional bead spacing; therefore, we reject this model.

There is little obvious difference between the second and third models. The former implies passivity and therefore more opportunity for irregularity. We prefer the third model, in which loss of intermediate beads is an active, regulated process. To facilitate discussion, beads continuing to grow are termed “acceptors” and those ceasing growth are termed “donors.”

Although the sedimentation rate was slow, the organism had to grow fast enough to either keep the upper portion of beads above the bottom or keep them from being buried too deeply. If the colony were episodically thinly covered by sediment, donor cells would provide nutrients for further upward growth of adjacent acceptors. As bizarre as this speculation may be, it is the only one we have been able to envision for the proportionality of spacing in *Horodyskia*. We know of no close modern analogues, although colonial hydrozoans show redistribution of cellular material through a colony.

We presume *Horodyskia* began growth from one cell settling to the bottom. Initial stolon growth may have been unidirectional rather than in both directions from a center, but there is no evidence for either possibility. We have reconstructed a life

cycle partly based on taphonomic interpretations to conclude that *Horodyskia* was sessile and benthonic. It is presented as a series of stages, and for ease of understanding, we have eliminated repetition of earlier points, as well as appropriate cautionary comments. An artistic summary has been prepared (Figure 19).

Stage 1. A thin thread grows to some length, but both length and orientation seems to be random (Figure 15c). We are now convinced that at least some of the tiny trails described by Fedonkin et al. (1994:216–218, figs. 28, 29) may be the first growth stage of *Horodyskia*. Probably a slightly thicker clay-sized sediment film was preferred for this stage, but intermixing of sizes suggests larval settlement may have been nearly continuous.

Stage 2. The thread expands regularly, developing tiny bead-like swellings close to one another (Figure 15a,b). In one specimen, swellings appear ellipsoidal rather than spherical, but this may be a result of compaction modifying the shape.

Stage 3. Alternate swellings disappear, and those remaining develop to slightly larger and more widely spaced spheres.

Stage 4. Spherical shape changes to slightly elongated tapering tubes, the upper surface of which is hemispherical (Figure 7c). Alternate beads, the early donors, decrease in size, but the uniformly spaced acceptors enlarge. The donor/acceptor switch

may be triggered by a thin cover of sediment one or two grains in thickness.

Stage 5. More alternate beads cease growth and become donors; acceptors, still proportionally spaced, become wider and longer, in part by transfer of donor material and in part from their own metabolism. Estimating from the number of smallest beads on a string to the largest, suppression of donors may occur at least three to five times, or more.

Stage 6. An invagination of the upper surface may occur, or, far less likely, a small opening may develop in the hemisphere at the top of the cone. We have not observed any feature leading to either interpretation on beads smaller than about 3 mm.

Stage 7. Upward growth is at a decreasing rate and eventually stops.

A general rule among fossil collections, regardless of the group, is that large individuals are rare. For sessile organisms where sedimentation events are a matter of life or death, relationship of size to abundance is obvious. Judging from the fine laminations, episodes of graded bedded lasted for long intervals.

Nevertheless, transfer of material must have had limitations, particularly for a relatively simple organism. Eventually the metabolic cost of this transfer would have become too large, thereby putting an upper limit on the size of the beads. The largest diameter beads suggest a maximum cone length of about 1 cm, but it may have been less. The bead diameter approximated its height above the initial stolon and below the curvature of the upper surface.

In this interpretation of life shape, the ratio of volume within the cone to surface area of the hemispherical top is nearly constant. By measuring the length of strings and the total surface area of the number of beads in the string, we estimate that surface area remained nearly constant and may actually have increased slightly as the number of beads decreased.

SINGLE ORGANISM VERSUS COLONIAL ORGANISM

The most remarkable peculiarity of growth in *Horodyskia* is the proportionality of bead size and spacing. As beads grow larger, the spacing between beads becomes wider; proportions remain nearly constant within the limits to be expected in biologic variation. Because of the interrelationship among beads of one string, we judge *Horodyskia* was a colonial organism. That term is used several ways in the literature, but it need not mean that many different kinds of cells were present in the colony. For a modern analogy, we consider the organism more comparable to a simple hydroid colony than to a complex sea pen.

INTEGUMENT

Horodyski (1981; 1993, appendix 10) reported microfossils, carbonaceous sphaeromorphs that measured 17–82 μm (mkm) across, from the Appekunny Formation. The very low degree of metamorphism in the formation allowed those fossils to survive. Inasmuch as these microorganisms are preserved, their walls might have been a cellulose-like compound resistant to

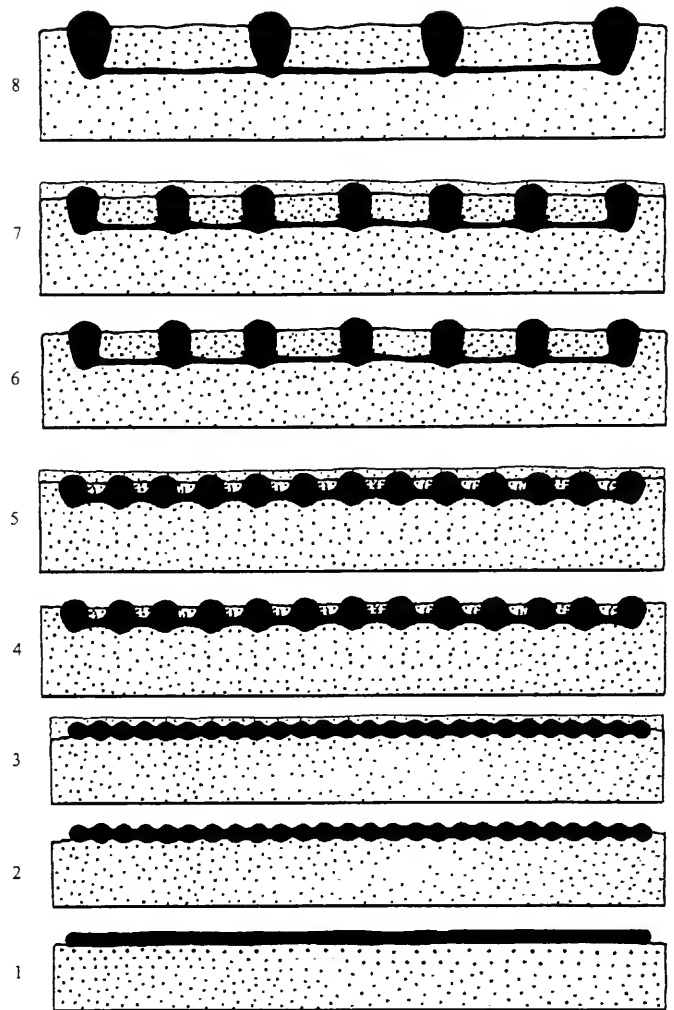


FIGURE 19.—Schematic representation to show the growth of *Horodyskia moniliformis* Yokelson and Fedonkin. A stolon (1) on the bottom develops tiny, closely spaced beads (2) before being covered by sediment (3). As a result of the cover, alternating "donor" beads transfer material to "acceptors," which then grow upward through the thin sediment cover (4) before being lightly covered again (5). Alternating donor beads again contribute to acceptors, permitting more upward growth (6) before yet another thin covering of sediment covers the string (7). With the loss of another set of alternating donor beads, upward growth continues and a conical shape of individual beads develops (8).

rapid oxidation and biochemical degradation. Accordingly, larger organisms of similar organic composition had a chance of being preserved. Proterozoic *Chuarua* Walcott and *Grypania* Walter, Oehler, and Oehler, locally common in other areas, are now carbonaceous films. Similar preservation is typical for Late Proterozoic algae, such as *Tawuia* Hofmann (1992b) and *Vendotaenia* Gnilovskaya (1992). The absence of any fragments of organic films within the Appekunny may mean that *Horodyskia* was not formed of a cellulose-like compound.

Beads from Rising Wolf Mountain are black, similar in color to the Proterozoic algal(?) taxa mentioned above, but there is a greater thickness to the flattened beads than to carbonaceous

films. A few beads show another feature, that of low ridges closely spaced on the inner surface. The concept of compression of an upper and lower surface is reinforced by several beads that show ridges trending one direction on the interior of an upper layer and trending in another direction on a layer below. On one bead, curved traces occur. Large *Chuarina* of comparable size from the Grand Canyon are strongly wrinkled, much like a raisin, whereas beads do not show such irregularities. Close, regular spacing of ridges within the few beads that preserve them is further indication of a stiff integument less affected by compaction than a sphere. We suggest that these may have been primary structures for strengthening the wall of the cone. Some laniations may be the result of tectonism, but these are limited to the diameter of the bead, and several show these features with different orientations (Figures 16a-c, 17a-c).

These observations hint that cellulose material was not present in the beads; admittedly it is far from any proof. If nothing else, the presence of the delicate ridges supports replacement of an integument by silica rather than void infilling. Cellulose is more stable than protein in the face of agents such as oxidation, biochemical degradation, and heating. Paradoxically, fast decomposition of protein may facilitate fossilization of buried soft-bodied organisms, for it leads to a geochemical shift of the local microenvironment towards temporary anoxia and early sediment diagenesis around a decaying organism (Fedonkin, 1987). Halos around beads imply low permeability and fast decomposition. Possibly proteinaceous matter rather than cellulose-like material was also significant in decay.

FEEDING AND POSSIBLE FOOD SUPPLY

We judge the presence of a central hole on the top of a cone as quite unlikely. Assuming reconstruction of the environment is reasonably accurate, it carries the concept of nutrient-poor water, which, in turn, translates to few microorganisms as a food source and less of a prospect for direct feeding. Were a central opening present, sediment might drift into the interior, unless one postulates a ciliated exterior of the tube actively beating to move away small particles, an activity counterproductive for an organism feeding through a mouth.

If the upper surface of the cone was closed, the organism could not have been a suspension feeder. From the standpoint of geometry, a hemispherical shape provides a large surface area. As noted, although the number of beads in a string decreases through time, the surface area of each remaining bead becomes larger. At a late growth stage, minor invagination would yield more surface area.

Photosynthesis as a food source cannot be ruled out and may be more plausible than any other suggestion. It presupposes such environmental parameters as well-oxygenated bottom water and reasonably clear water for sunlight penetration. An episodic rain of fine arenite particles might inhibit photosynthesis, as would low oxygen levels in the water column.

As an alternative, chemosynthesis should be considered. The concept has been well known to generations of bacteriologists, although it is only coming into prominence with the discovery of deep-sea vent faunas. In general, chemosynthesis is exploited by bacteria, and these in turn are exploited by more complex organisms.

Chemosynthesis requires a redox gradient. Some beds are variegated, and many are green; incipient reducing conditions may have been present early. We do not know whether the iron and manganese coating of arenite grains might be a result of bacterial activity, but it is within the realm of possibility that the hematite coating could have served as an ultimate energy source. It has also been suggested that bacteria play a role in binding the individual grains forming the delicate laminae.

Discussion

In preceding sections we have attempted to present a reasoned case that *Horodyskia moniliformis* is an organism that should be formally named. Our hope is that this action will lead to more paleontological study of siliclastic units. This study has also led us to notions that are not rigorously supported, but they provide a framework of larger implications concerning this fossil. To insure that speculations do not weaken the primary focus of this work, they are discussed below rather than in the main body of the text.

To recapitulate the occurrence of *Horodyskia*, Winston (in litt., 1997) noted that the lower part of the Appekunny Formation has three novel aspects: the extremely well-sorted nature of the sediment; the subaqueous depositional environment; and the hematite coating on the arenite grains. Thus, the Appekunny is the only fine-grained, subaqueous red unit in the entire Belt Supergroup.

Study of ecological aspects of the emergence of eucaryotes (Rozanov and Fedonkin, 1994) has led to a conclusion that those more complex life forms should have occupied a limited space in the early Proterozoic biosphere. For much of the early history of life, environments were dominated by prokaryotic organisms. During the Proterozoic, cyanobacterial communities formed relatively stable ecosystems of stromatolites and mats on a global scale. A bacterial community derives two important advantages from stromatolitic structures, a large surface area to be populated plus substrate stability, and these provide stability for any colonizing population.

Stromatolites are specialized developments of the general ecological group of cyanobacteria. Much of the thickness of carbonates deposited in the Newland, Altyn, Helena, and Shepard formations of the Belt Supergroup is devoid of stromatolites. Cyanobacterial mats in these units were concentrated at nearshore environments where waves broke along the shores and flats (Winston, in litt., 1997). A point of significance is that mats were not confined to carbonates. Schieber (1986) emphasized the importance of mat formation on Middle Proterozoic carbonaceous shales.

One consequence of Proterozoic bacterial activity may have been that shallow-water benthic habitats, which for that early time were well oxidized and well illuminated by sunlight, were, in a sense, a “prohibited zone” for eucaryotic organisms. Mat growth might not have allowed space for competitors, partly by using available nutrients and partly by producing by-products harmful to other organisms. A mat would have increased substrate stability and simultaneously isolated subsurface sediment, which in turn would have limited sediment aeration. Under conditions of low sedimentation rate, substrate stability, and absence of bioturbators, bacterial mats could have negatively affected larger benthonic organisms.

Modern analogues of these ecosystems, cyanobacterial mats of hypersaline lagoons, marshes, and sabkhas, should be considered as relics of the archaic Precambrian world (Awramik, 1984; Knoll, 1985; Zavarzin, 1993). (Some stromatolites in Shark Bay are draped with sea weed, but it is not certain these are growing with the mounds.) The mat ecosystems today do not leave much ecological space for eucaryotic organisms. We would expect the same for the Proterozoic world with the understanding that similar communities controlled far wider areas of the shallow-water habitats. Thus, in moving back retrospectively through time, the biotopes or habitats of benthic eucaryotes would have shrunk, and the chance to find their fossil remains decreased accordingly.

Whereas this point has general applicability, its antithesis may be more significant. The Appekunny Formation might have been deposited where cyanobacterial communities could not dominate the environment. Within member 1, bacterial mats are present but are quite rare. Their paucity might be a factor that allowed *Horodyskia* to thrive. Notwithstanding that view, one of us (MAF) suggests that the delicate lamination of the formation was formed in part under the stabilizing control of benthonic bacterial communities. Contrarily, one of us (ELY) is impressed with how rare the evidence of mats is among the numerous slabs collected.

To consider occurrence from another aspect, one ecological model for the origin and early evolution of Metazoa (Fedonkin, 1995, 1996b) claims that the habitats of the first metazoans may have been limited to cold-water basins, well beyond the carbonate belt. During most of the Proterozoic, the carbonate belt might have been wide as a result of both relatively high temperature and carbonate saturation of sea water (Lowe, 1994). Relatively cold-water basins could have occurred in temperate zones or even in polar regions, as these were ice free during most of the Proterozoic.

In temperate or cool-water basins, loose sediment and a flat sandy bottom inhibit upward growth of bacterial communities, but inhibition by sand would apply equally well to warmer waters. The presence of hematite in the Appekunny, however, tends to tip the balance of interpretation toward warmer rather than cooler conditions.

Moving from ecology to evolution, it is our opinion that diversity within a major taxon or clade is secondary in importance to the distinctiveness of one major taxon from another.

We think, with many exceptions, that from about the middle Paleozoic to the Holocene, distinctiveness decreased and diversity increased. From about the middle to early Paleozoic backward in time, diversity decreased in the fossil record, but distinctiveness increased. If the generalization has any validity, still greater disparity of grades of organization and even less diversity would be expected within the Proterozoic. The age and morphology of *Horodyskia* fit this theoretical model.

Animal body fossils and trace fossils are well known in the Vendian Period, about 600 Ma old. Their phylogenetic roots must go back much further in the Proterozoic as confirmed by the high degree of faunal differentiation at the beginning of the Vendian. Various retrospective paleontological models of metazoan evolution (Durham, 1970; Sepkoski, 1992; Valentine, 1991, 1994) provide a variety of suggested dates for the origin of animals. Data from molecular phylogenetics give other dates (Wray et al., 1996; Vermeij, 1996). Assumption of constancy for a molecular clock is a potential weakness because although numbers derived from molecular studies are helpful, in our view that method may supplement, but never supplant, discovery of authentic fossils. The fact is that *Horodyskia* appeared about 1.5 billion years ago. The speculations that may be derived from this one fact are many and varied.

To leave evolutionary concepts and consider specimens, it is obvious that soft-part morphology and metabolism of fossils almost never leave any clues, and speculation may be unbounded. Even though a Holocene cell may be larger than a grape, the length of strings and number of beads strongly imply *Horodyskia* was multicellular. Details of tissues are unknown except that the exterior was a stiff integument; a surmise is that several kinds of internal tissues were present to aid respiration and to transport nutrients. We state only that *Horodyskia* was an early organism, “different” from any younger form. In our view, terms such as “primitive” and “advanced” carry too much intellectual baggage.

In a sense, ideas of primitive and advanced are also involved with food chains. With exceptions, the longer the food chain, the more complex—advanced—the organism. In whatever way *Horodyskia* may have lived, there is no evidence of a long food chain. If the highly speculative concept of chemosynthesis as a life style can be confirmed, *Horodyskia* may represent a major evolutionary group that is neither plant nor animal. It is far more likely that somehow it ingested bacteria involved in chemosynthetic activity.

Rather than phrasing the systematic position of *Horodyskia* as a purely taxonomic question, it may be more helpful to consider it in terms of autotrophic versus heterotrophic lifestyle. The former allows us to better integrate paleoenvironmental data with morphologic criteria. This study has led us to the conclusion that *Horodyskia* was an early autotroph, which developed megascopic size. The large size in turn led to multicellularity and to tissue-grade anatomy. Whether this organism was an environmental “dead end” or a precursor of later forms remains a question for the future.

Literature Cited

- Alenikoff, J.N., K.V. Evans, C.M. Fannin, J.D. Obradovich, E.T. Ruppel, and J.A. Zieg
 1996. Shrimp U-Pb Ages of Felsic Rocks, Belt Supergroup, Western Montana. *Geological Society of America, Abstracts with Program*, 28: A-376.
- Allen, J.R.L.
 1982. *Sedimentary Structures: Their Character and Physical Basis*. Volume 2, 663 pages. Amsterdam: Elsevier Scientific Publishing Company.
- Awramik, S.M.
 1984. Ancient Stromatolites and Microbial Mats. In Y. Cohen, R.W. Castenholz, and H.O. Halvorson, editors, *Microbial Mats: Stromatolites*, pages 1–22. New York: A.R. Liss.
- Darwin, C.
 1962. *The Voyage of the Beagle; Annotated and with an Introduction by Leonard Engel*. 524 pages. New York: Anchor Books, Doubleday & Company. [First published in 1839 under the title “Journal of Researches into the Geology and Natural History of the Various Countries Visited by the H.M.S. Beagle.”]
- Durham, J.W.
 1970. The Fossil Record and the Origin of the Deuterostoma. In E.L. Yochelson, editor, *Proceedings of the North American Paleontological Convention*, pages 1104–1132. Lawrence, Kansas: Allen Press.
- Fedonkin, M.A.
 1981. Belomorskaya biota venda: Dokembriiskaya besskeletnaya fauna severa Russkoi platformy. [White Sea Biota of the Vendian: Precambrian Non-Skeletal Fauna of the Northern Part of the Russian Platform.] *Trudy Geologicheskogo Instituta Akademii Nauk SSSR*, 342: 100 pages.
 1987. [Non-skeletal Fauna of the Vendian and Its Place in the Evolution of Metazoans]. *Transactions of the Paleontological Institute*, 226: 175 pages. Moscow: Nauka. [In Russian.]
 1994. Vendian Body Fossils and Trace Fossils. In S. Bengtson, editor, *Early Life on Earth* (Nobel symposium 84), pages 370–388. New York: Columbia University Press.
 1995. Cold Water Cradle of Animal Life. In V.A. Krasilov and A. Yu. Rosanov, editors, *Ecosystem Evolution. Abstracts of International Symposium, September 26–30, 1995, Moscow*, pages 123–124. Moscow: Paleontological Institute, Russian Academy of Sciences.
 1996a. Geobiological Trends and Events in the Precambrian Biosphere. In O.H. Walliser, editor, *Global Events and Event Stratigraphy in the Phanerozoic: Results of International Interdisciplinary Cooperation in the IGCP Project 216 “Global Events in Earth History,”* pages 89–112. Berlin: Springer-Verlag.
 1996b. Cold Water Cradle of Animal Life. *Paleontological Journal*, 30(6): 671–675. [Translated from *Paleontologicheskii Zhurnal*, 4.]
- Fedonkin, M.A., and B.N. Runnegar
 1992. Proterozoic Metazoan Trace Fossils. In J.W. Schopf and C. Klein, editors, *The Proterozoic Biosphere: A Multidisciplinary Study*, pages 389–395. Cambridge, England, and New York: Cambridge University Press.
- Fedonkin, M.A., E.L. Yochelson, and R.J. Horodyski
 1994. Ancient Metazoa. *National Geographic Research and Exploration*, 10:200–223.
- Gary, M., R. McAfee, and C. Wolf, editors
 1972. *Glossary of Geology*. Volume 2. Alexandria, Virginia: American Geological Institute.
- Gnilovskaya, M.B.
 1992. Vendotaenids—Vendian Metaphytes. In B.S. Sokolov and M.A. Fedonkin, editors, *The Vendian System, 1: Paleontology*, pages 138–147. Berlin: Springer-Verlag.
- Grey, K., and I.R. Williams
 1987. Possible Megascopic Algae from the Middle Proterozoic Mangane Group, Bangemall Basin, Western Australia. In S. Beadle, editor, Abstracts, 4th International Symposium on Fossil Algae. *Friends of Algae Newsletter*, 8:36–37.
 1990. Problematic Bedding-Plane Markings from the Middle Proterozoic Manganese Subgroup, Bangemall Basin, Western Australia. *Precambrian Research*, 46:307–327.
- Häntzchel, W.
 1975. Trace Fossils and Problematica. In Curt Teichert, editor, *Treatise on Invertebrate Paleontology*, part W (Miscellanea), supplement 1. Lawrence, Kansas: Geological Society of America and University of Kansas Press.
- Harrison, J.E., J.W. Whittle, and D.J. Lidke
 1998. Geologic Map of the Western Part of the Cut Bank 1° x 2° Quadrangle, Northwestern Montana. *United States Geological Survey, Geologic Investigation Series*, I-2593.
- Hofmann, H.J.
 1992a. Megascopic Dubiofossils. In J.W. Schopf and C. Klein, editors, *The Proterozoic Biosphere; A Multidisciplinary Study*, pages 413–419. Cambridge, England, and New York: Cambridge University Press.
 1992b. Proterozoic Carbonaceous Films. In J.W. Schopf and C. Klein, editors, *The Proterozoic Biosphere; A Multidisciplinary Study*, pages 349–357. Cambridge, England, and New York: Cambridge University Press.
- Horodyski, R.J.
 1981. Pseudomicrofossils and Altered Microfossils from a Middle Proterozoic Shale, Belt Supergroup, Montana. *Precambrian Research*, 16:143–154.
 1982. Problematic Bedding-Plane Markings from the Middle Proterozoic Appekunny Argillite, Belt Supergroup, Northwestern Montana. *Journal of Paleontology*, 56:882–889.
 1983. Sedimentary Geology and Stromatolites of the Middle Proterozoic Belt Supergroup, Glacier National Park, Montana. *Precambrian Research*, 20:391–425.
 1986. Walcott's *Helminthoidichnites* Assemblage from the Middle Proterozoic Belt Supergroup. *Geological Society of America, Abstracts with Program*, 18:640.
 1989a. Stromatolites of the Belt Supergroup, Glacier National Park, Montana. In D. Winston, R.J. Horodyski, and J.W. Whipple, editors, Middle Proterozoic Belt Supergroup, Western Montana. *28th International Geological Congress, Field Trip Guidebook*, T-334, pages 27–42.
 1989b. Paleontology of the Middle Proterozoic Belt Supergroup. In D. Winston, R.J. Horodyski, and J.W. Whipple, editors, Middle Proterozoic Belt Supergroup, Western Montana. *28th International Geological Congress, Field Trip Guidebook*, T-334, pages 7–26.
 1993. Precambrian Paleontology of the Western Conterminous United States and Northwestern Mexico. In J.C. Reed et al., editors, Precambrian of the Conterminous United States. *Geology of North America*, volume C-2, pages 558–565, and microfiche appendix of 77 pages. Boulder, Colorado: Geological Society of America.
- Huebschman, R.P.
 1973. Correlation of Fine Carbonaceous Bands Across a Precambrian Stagnant Basin. *Journal of Sedimentary Petrology*, 43:688–699.
- Jackson, J.A., editor
 1987. *Glossary of Geology*. Fourth edition. Alexandria, Virginia: American Geological Institute.

- Jackson, M.S., M.P. Muir, and K.A. Plumb
1987. Geology of the Southern McArthur Basin, Northern Territory. *Bulletin of the Bureau of Mineral Resources, Geology, and Geophysics*, 200: viii+173 pages.
- Knoll, A.H.
1985. A Paleobiological Perspective on Sabkas. In G.M. Friedman and W.E. Krombein, editors, *Hypersaline Ecosystems*, pages 407–427. Berlin: Springer-Verlag.
- Lowe, D.R.
1994. Early Environments: Constraints and Opportunities for Early Evolution. In S. Bengtson, editor, *Early Life on Earth. Nobel Symposium*, 84:24–35. New York: Columbia University Press.
- Maxwell, D.T., and J. Hower
1967. High-Grade Diagenesis and Low-Grade Metamorphism of Illite in the Precambrian Belt Series. *American Mineralogist*, 52:843–857.
- Reineck, H.-E., and I.B. Singh
1980. *Depositional Sedimentary Environments*. Second edition, 549 pages. Berlin: Springer-Verlag.
- Rozanov, A. Yu., and M.A. Fedonkin
1994. [The Problem of the Primary Biotope of the Eukaryotes.] In A. Yu. Rozanov and M.A. Semikhatov, editors, *Ecosystem Restructuring and the Evolution of the Biosphere*, pages 25–32. Moscow: Nedra. [In Russian.]
- Schieber, J.
1986. The Possible Role of Benthic Microbial Mats during the Formation of Carbonaceous Shale in Shallow Mid-Proterozoic Basins. *Sedimentology*, 33:521–536.
- Schopf, J.W., and C. Klein
1992. *The Proterozoic Biosphere: A Multidisciplinary Study*. 1348 pages. Cambridge, England, and New York: Cambridge University Press.
- Sepkowski, J.J., Jr.
1992. Proterozoic-Early Cambrian Diversification of Metazoans and Metaphyes. In J.W. Schopf and C. Klein, editors, *The Proterozoic Biosphere: A Multidisciplinary Approach*, pages 553–561. Cambridge, England, and New York: Cambridge University Press.
- Timofeev, P.P., V.N. Kholodov, and V.P. Zverev
1988. [Hydrosphere and Evolution of Earth.] *Izvestiya AN SSSR, geology series*, 5:3–19. [In Russian.]
- Valentine, J.W.
1991. Major Factors in the Rapidity and Extent of the Metazoan Radiation during the Proterozoic-Phanerozoic Transition. In A.M. Simonetta and S. Conway Morris, editors, *The Early Evolution of Metazoa and the Significance of Problematic Taxa*, pages 11–13. Cambridge, England: Cambridge University Press.
1994. The Cambrian Explosion. In S. Bengtson, editor, *Early Life on Earth* (Nobel Symposium 84), pages 401–411. New York: Columbia University Press.
- Vermeij, G.J.
1996. Animal Origins. *Science*, 274:525–526.
- Walcott, C.D.
1899. Precambrian Fossiliferous Formations. *Bulletin of the Geological Society of America*, 10:199–214.
- Whipple, J.W.
1992. Geologic Map of Glacier National Park, Montana; Scale 1:100,000. *United States Geological Survey, Miscellaneous Investigations Series*, MI-1508F.
- Whipple, J.W., J.J. Connor, O.B. Raup, and R.G. McGimsey
1984. Preliminary Report on the Stratigraphy of the Belt Supergroup, Glacier National Park and Adjacent Whitefish Range, Montana. In J.D. McBane and P.B. Garrison, editors, *Northwest Montana and Adjacent Canada: Montana Geological Society 1984 Field Conference and Symposium*. Billings, Montana: Montana Geological Society.
- Winston, D.
1989. A Sedimentologic and Tectonic Interpretation of the Belt Supergroup. In D. Winston, R.J. Horodyski, and J.W. Whipple, editors, *Middle Proterozoic Belt Supergroup, Western Montana. 28th International Geological Congress, Field Trip Guidebook*, T-334, pages 47–70.
- Winston, D., and P.K. Link
1993. Middle Proterozoic Rocks of Montana, Idaho and Eastern Washington: The Belt Supergroup. In J.C. Reed et al., editors, *Precambrian of the Conterminous United States. Geology of North America*, Volume C-2, pages 487–517. Boulder, Colorado: Geological Society of America.
- Winston, D., J.W. Whipple, and R.J. Horodyski
1989. Field Trip Road Log. In D. Winston, R.J. Horodyski, and J.W. Whipple, editors, *Middle Proterozoic Belt Supergroup, Western Montana. 28th International Geological Congress, Field Trip Guidebook*, T-334, pages 71–103.
- Wray, G.A., J.S. Leviton, and L.H. Shapiro
1996. Molecular Evidence for Deep Precambrian Divergences among Metazoa Phyla. *Science*, 274:568–573.
- Yochelson, E.L., and M.A. Fedonkin
2000. A New Tissue-Grade Organism 1.5 Billion Years Old from Montana. *Proceedings of the Biological Society of Washington*, 113(3):843–847.
- Zavarzin, G.A.
1993. [Epicontinental Alkaline Water Bodies as Relict Biotopes for the Development of Terrestrial Biota.] *Mikrobiologiya*, 62(5):789–800. [In Russian.]

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