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NEW MICROORGANISMS FROM THE APHEBIAN GUNFLINT IRON FORMATION, ONTARIO

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ABSTRACT—Two new algal taxa are described from the approximately 2,000 m.y. old Gunflint Iron Formation, Ontario. *Leptoteichos golubicii,* n. gen. et sp., were relatively large (5-31 μm) spherical plankters living in the water column above the central portions of the Gunflint basin. *Post-mortem* degradation processes have acted on this taxon to produce a "spot cell" organization similar to that exhibited by younger putatively eukaryotic cells; however, *L. golubicii* is here placed among the Algae *incertae sedis* and considered to be a probable cyanophyte. *Megalytrum diacenum,* n. gen. et sp., is the preserved sheath of a colonial chroococcalean blue-green alga. It constitutes an allochthonous element of the algal chert facies microbiota of the Gunflint Iron Formation.

INTRODUCTION

THE FIRST REPORT of fossil microorganisms from the iron-rich Precambrian rocks of the Lake Superior region was written by the French geologist Cayeux who, in 1911, published a brief unillustrated account of his visit to the western Great Lakes. His observations were followed by those of Moore (1918) and Gruner (1922) who figure microfossils from the Belcher Group and the Gunflint Iron Formation, respectively, but none of these discoveries was accorded more than the passing interest of curiosity at the time. Perhaps this is because the great antiquity of these rocks was not fully appreciated at the time; perhaps it is because most paleontologists of the day were biased toward megascopic evidence of early life. In any event, the prevailing attitude of earth scientists toward early reports of Precambrian microbial remains seems to be well summarized in the opinion proffered by Raymond in 1939 (p. 30): "Perhaps the most astonishing discovery in pre-Cambrian rocks was that announced by Walcott in 1915. Sections made of one of the 'calcareous algae' proved, on examination under high powers of the microscope, to have in them minute (0.95–1.3 μm in diameter) somewhat irregular rods which were identified as bacteria . . . . Walcott leaves it to be accepted on faith that an organism without hard parts, and less than 0.001 millimeter in diameter, would be preserved in identifiable condition from pre-Cambrian times to the present!" Raymond's choice of punctuation is as fully revealing as any critique he could have penned.

In 1954, a short report on Gunflint microbes published by Tyler and Barghoorn signaled the advent of an era of widespread acceptance of the existence of a Precambrian microfossil record. Over the next decade a diverse flora of Proterozoic blue-green algae and bacteria was documented from the Gunflint (Barghoorn and Tyler, 1965), and since that time a host of workers have turned their attention to the paleontological and biogeochemical examination of this formation, adding to both the breadth and the sophistication of our knowledge of Gunflint paleobiology (Cloud, 1965; Cloud and Hagen, 1965; Schopf et al., 1965; Oro et al., 1965; Hoering, 1967; Cloud and Licari, 1968; Smith et al., 1970; Hofmann, 1969, 1971; Edhorn, 1973; Darby, 1974; Kline, 1975; Awramik, 1976; Kazmierczak, 1976; Tappan, 1976; Awramik and Barghoorn, 1975, 1977; and Barghoorn et al., 1977). This paper describes two new Gunflint algal taxa which are of interest not only in terms of their additions to the fuller understanding of this particular flora, but also in their contribution to the general understanding and interpretation of the Precambrian fossil record.

GENERAL GEOLOGIC AND PALEONTOLOGICAL SETTING

The regional geology of the Gunflint Iron Formation has been known since the publi-

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cation of early works by Broderick (1920) and Gill (1924); however, much of our understanding of the facies relationships of the formation, particularly the cyclical nature of sedimentation, dates from Goodwin's analysis (Goodwin, 1956). Goodwin defined upper and lower sedimentary members having remarkably similar facies sequences characterized by a basal algal chert succeeded by shale, chert-taconite, and plane-bedded chert-carbonate units—the sequence documenting two transgressive cycles. It is primarily from the basal algal chert beds, particularly of the lower member, that the paleobiological interpretation of the formation was first established (Tyler and Barghoorn, 1954).

As a basin sequence, the Gunflint is both remarkably thin and notably persistent over its entire known length of outcrop from Gunflint Lake on the Minnesota-Ontario boundary to its points of submergence beneath Lake Superior in the Rossport-Schreiber area of Ontario, a distance of some 275 km. Regional metamorphism is low to negligible, the fortunate consequence of which is the beautiful preservation of the Gunflint microbiota. There exists some question as to whether the Gunflint sediments are lacustrine or marine. The regional geological picture is strongly suggestive of an ocean margin or platform depositional site, but certain geochemical arguments regarding the origin of the contained iron-rich sediments are more compatible with a lacustrine environment (Govett, 1966; Eugster and Chou, 1973). Stromatolites can be formed in lakes as well as lagoons, and the presence of pseudomorphs after evaporite crystals within some Gunflint samples likewise gives few clues. Hypersaline lakes have been features of the earth throughout geologic time. Among the few facts of which one can be certain is that the Gunflint sediments were deposited in a restricted basin in which stagnant conditions prevailed over large areas of the bottom. A large, saline lake such as Lake Chad (Lemoalle and Dupont, 1972) could have accounted for Gunflint deposition, as could a large but highly restricted lagoon along a continental margin, such as Lake Maracaibo, Venezuela. Reconstruction of the Gunflint basin as a somewhat hypersaline restricted lagoon marginal to true continental shelf may provide a best-fit hypothesis to accomodate existing data. Dimroth's (1977) suggestion that the southern shore of the present Persian Gulf provides a modern analogy to Precambrian shelf iron formations would be consistent with this environmental reconstruction. However, only future sedimentary and geochemical analyses of the Gunflint can hope to elucidate more precisely the true depositional environment of this formation.

Gunflint microfossils have been discovered in both the algal chert and the chert-carbonate facies. In both cases, the microbial remains are permineralized by microcrystalline silica and are preserved as organic matter, iron oxide or pyrite incrustations, or a combination of organic and inorganic constituents (Barghoorn and Tyler, 1965).

THE AGE OF THE GUNFLINT

The age of the Gunflint Iron Formation has been the subject of some disagreement for a number of years, and it seems appropriate to summarize the argument here. In 1962, Hurley et al. published data obtained by both K-Ar and Rb-Sr analyses of an illite-montmorillonite mixture occuring in bedded tuffaceous and argillaceous units within the Gunflint. Their values indicated an apparent age of 1,600 ± 70 m.y., but the authors assumed a 15–20% loss of radiogenic argon and concluded that the true age of deposition must have been closer to 1,900 ± 200 m.y. B.P. Applying whole rock Rb-Sr techniques to the same sediments, Faure and his coworkers (Faure and Kovach, 1969; Misra and Faure, 1970) obtained a similar age of 1,635 ± 24 m.y. which they interpreted as the date of sedimentation.

That low grade regional metamorphism may cause isotopic rehomogenization of strontium, leading to underestimates of sedimentation dates, was explicitly recognized by Faure and Kovach (1969), but they cited the extremely low metamorphic grade of the Gunflint as evidence militating against such a hypothesis. Goldich (1972) disagreed, stating that even such low temperature effects as might accompany epeirogenic uplift *may* lead to an isotopic open system. Interestingly enough, the resultant isochrons can still be quite linear, although they do not reflect true depositional dates (Goldich, 1972).

In an analysis of Animikie equivalents in Minnesota, Peterman (1966) had earlier demonstrated that oxidation of sedimentary rocks

by hydrothermal or weathering solutions can cause isotopic alteration. Dating the Mahomen Formation of the Cuyuna Group (correlated by Schmidt [1963] with the Animikie Kakabeka Conglomerate), he obtained Rb-Sr whole rock ages of 1,850 m.y. (all of Peterman's dates have been recalculated by Faure and Kovach [1969] using a Rb^{87} decay constant of $1.39 \times 10^{11}yr^{-1}$) for twelve unoxidized specimens, while six red and brown argillite samples from the same horizon yielded ages averaging 1,540 m.y. (K-Ar dates for the same formation ranged from 1,470 to 1,670 m.y. [avg. = 1,580 m.y.].) Peterman also analyzed samples from the correlative Rove, Virginia, and Thomson formations and reported a combined isochron of 1,660 m.y. which he considered to represent the timing of folding and metamorphism. Faure and Kovach (1969) disputed this interpretation.

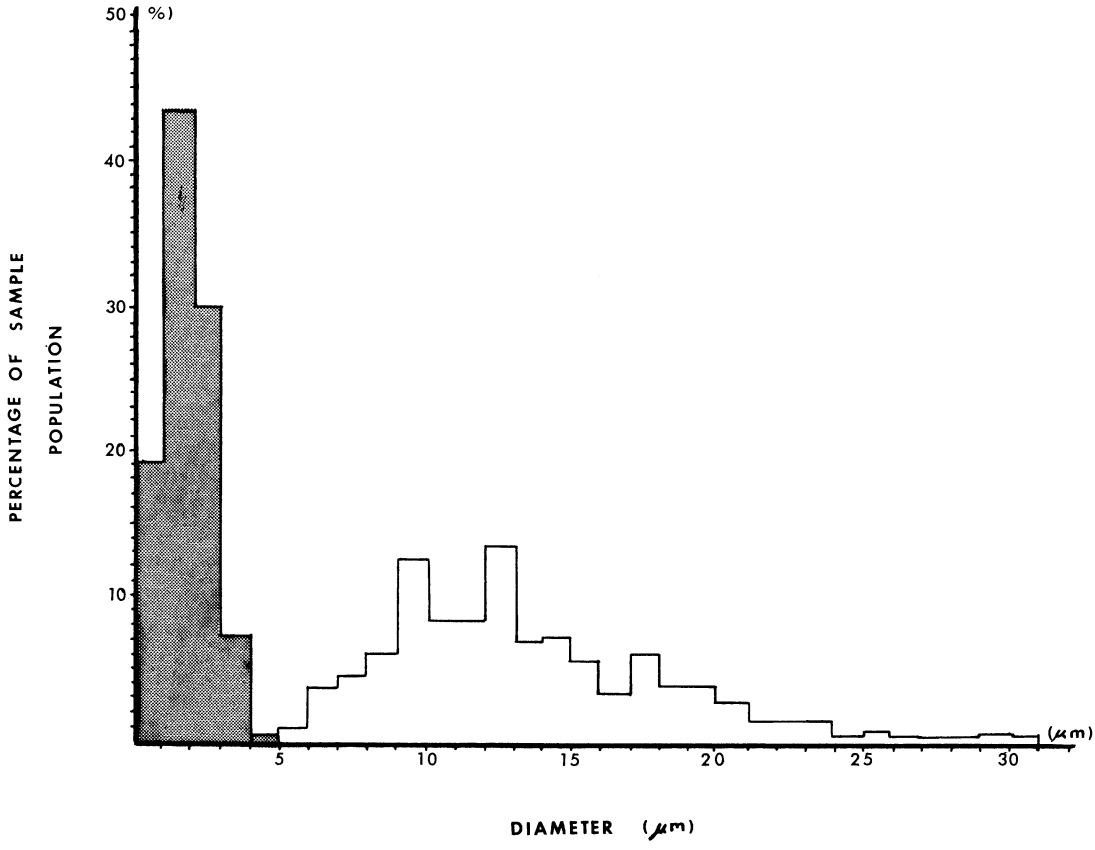
Studies conducted over the past few years indicate that indeed a low temperature metamorphic and geochemical regional event did affect the entire Lake Superior area some 1,650 m.y. ago (Van Schmus et al., 1975). Unfortunately, the nature of this event and the manner in which it reequilibrated Sr-bearing rocks remains poorly known, but the existence of this episode does explain why so many workers have obtained 1,600–1,700 m.y. dates for Gunflint and equivalent sediments. U-Pb ages from zircons contained in volcanic and plutonic rocks representing an orogenic phase which post-dated Animikie sedimentation give ages of 1,800–1,900 m.y. (Banks and Cain, 1969; Banks and Rebello, 1969; Van Schmus, 1974; Van Schmus et al., 1975). Thus, as Goldich (1973) has suggested, 1,900 m.y. B.P. is probably a minimum age for Gunflint sedimentation. We accept Goldich's view that the deposition of the Gunflint Iron Formation occured during the interval 2,000–1,900 m.y. B.P., and that the organisms here described flourished approximately two billion years ago.

Leptoteichos golubicii

Leptoteichos golubicii (formally described at the conclusion of this paper) is the taxonomic designation applied to a large population of spherical unicells contained in carbon-rich black cherts of the chert-carbonate facies of the Gunflint Formation (upper member) from the northernmost shores of Thunder Bay, Ontario. The cells are preserved as hyaline to finely granular light brown organic walls approximately 1 μm in thickness (the textural variations apparently reflecting differences in *post-mortem* degradation) which may retain their sphericity, be collapsed on one side, or occasionally, be completely flattened (Plate 1). These algal remains generally occur as solitary unicells, but also can be found in aggregations of a few to well over 100 cells held together by a thin layer of what in life was an amorphous mucilage.

The size frequency distribution of 800 measured individuals of *L. golubicii* is shown in Text-fig. 1. Cells were measured using an optical micrometer, and the values obtained are accurate to within 0.5 μm. Mean cell diameter is 13.5 μm. The sample range is large (5–31 μm) and so, correspondingly, is the standard deviation of cell size (4.5 μm or 33% of the mean diameter). The distribution is broadly unimodal and is moderately skewed to the right. Such a skewness is common among algal distributions (Prakash et al., 1973), and according to Simpson et al. (1960, p. 144), "this may be a general tendency of morphological characters in zoology." The question of modality is perhaps more intriguing. Although the overall trend of the distribution seems unimodal, three distinct peaks are superimposed onto the general sense of the curve. The two highest frequencies fall at 10 μm and 13 μm, while a third, less pronounced, peak can be seen at 18 μm. In light of the large size of the sample population, it is unlikely that the plotted distribution is an artifact of sampling. The next question is whether or not the several maxima indicate that the sample population was drawn from a heterogeneous biological assemblage. That is, do the frequency peaks correspond to the modes of three distinct species whose size ranges overlap?

That such an interpretation is unlikely can be ascertained by examination of the size frequency distribution of several individual clusters of *L. golubicii* (Text-fig. 2A–D). Presumably, each cluster consists of genetically similar cells belonging to a single algal species. In terms of their mean, standard deviation, and range of diameters, these clusters have a distribution quite similar to that of the sample population as a whole (Table 1). The similarities include frequency peaks at approximately 10–11 μm, 13–14 μm, and 17–18 μm. This



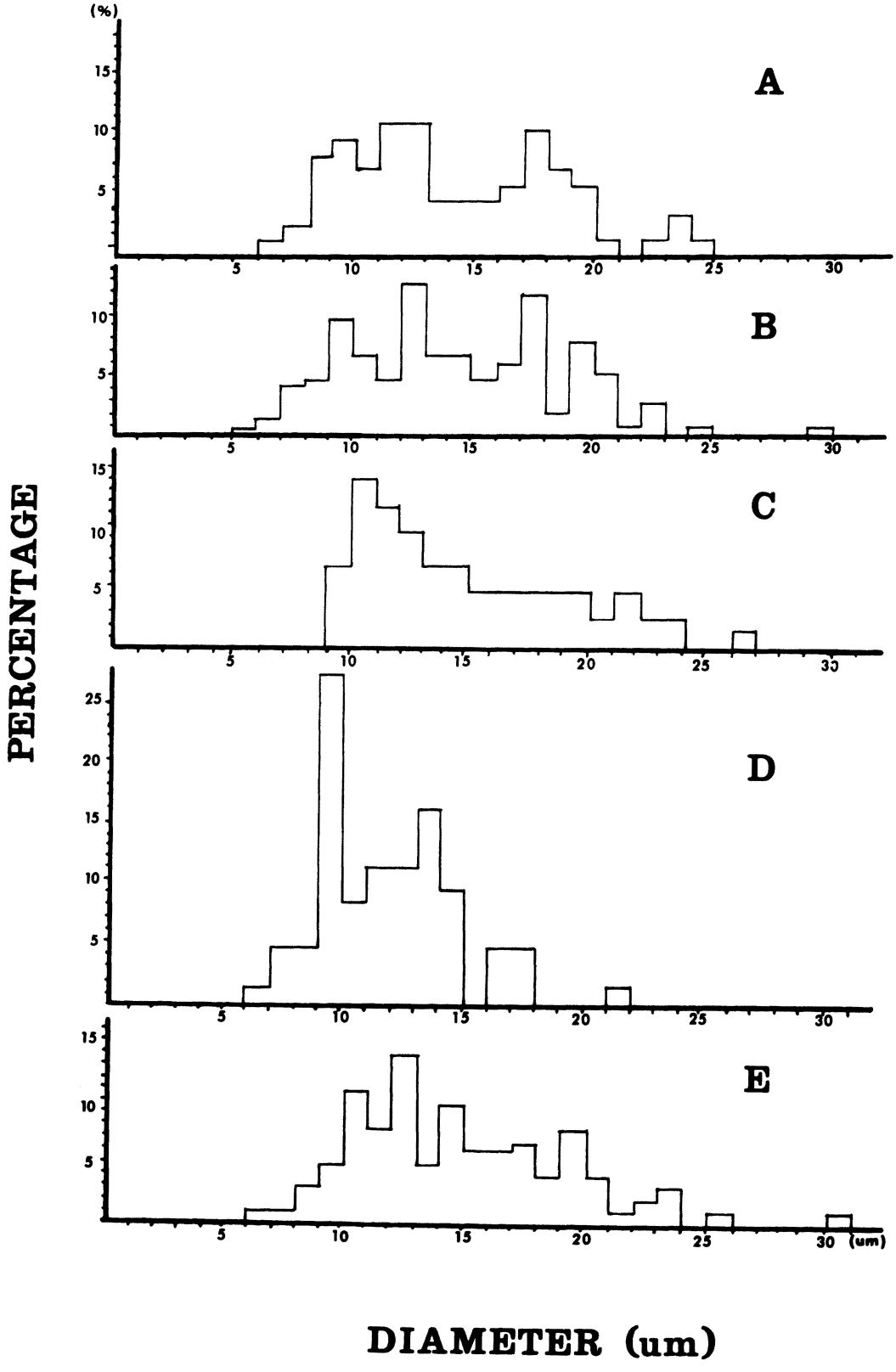
TEXT-FIG. 1—Size frequency of *Leptoteichos golubicii* (N = 800). Open histogram refers to cell diameters; stippled histogram indicates size distribution of organic contents.

indicates that we are not dealing with a series of discrete, albeit morphologically similar taxa, but rather with a single, highly variable species.

Application of such statistical evaluations as Student's *t*-test or the Kolmogorov-Smirnov test confirms the hypothesis that the clusters belong to a homogenous population. A randomly chosen sample of 100 isolated individuals (Text-fig. 2E) demonstrates that solitary unicells of *L. golubicii* can also be considered as part of the same population. The only cluster that fails these comparative tests is the one shown in Text-fig. 2D. This grouping fails because it has six too many 10 μm diameter cells; however, in light of the relatively small num-

TABLE 1—Size distributional data for subpopulations of *Leptoteichos golubicii*. Designation of subpopulations corresponds to the histograms in Text-fig. 2. The asterisk at cluster 2B indicates that this grouping has been chosen as the type for the species.

	N	MEAN DIAMETER (μm)	STANDARD DEVIATION (μm, % of mean)	SIZE RANGE (μm)
Total Sample Population	800	13.5	4.5 (33%)	5–31
Subpopulations:				
Cluster 2A	74	14.3	4.4 (33%)	7–25
Cluster 2B*	133	14.2	3.8 (33%)	5–30
Cluster 2C	42	14.6	3.2 (22%)	9.5–27
Cluster 2D	64	12.7	2.9 (24%)	7–22
Solitary Individuals (2E)	100	15.2	5.6 (37%)	6.5–31


(%)
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ber of individuals in the cluster, and taking into consideration the fact that cluster 2D is in all other ways morphologically, degradationally, and statistically identical to the population as a whole, we find no grounds for segregating this aggregation into a second species.

If one accepts the premise that we are dealing with a single species, it is then reasonable to hypothesize that the three frequency peaks in the distribution of *L. golubicii* diameters reflect some measure of periodicity in the life cycle of this alga. Unfortunately, we have no clear understanding of the cause or causes of such a pattern.

In another way of looking at size distributional data, Schopf (1976) has defined the Divisional Dispersion Index (DDI) as the number of equal binary divisions required to produce the smallest cell in a population from the largest—assuming no growth between fissions or mitoses. DDI's for a variety of modern blue-green and green algal cultures fall between 2 and 8. Among fossil populations, "spot cell" assemblages from the Bitter Springs Formation (considered by Schopf to represent a homogeneous population perhaps encompassing two species) and *Huroniospora* unicells from the Gunflint Formation (considered as a heterogeneous grouping of three or more biological species) have DDI's of 5 and 12, respectively. Abiotic organized spheroids from the Orgueil Meteorite have a value of 13. From these calculations, Schopf has estimated that a high DDI—perhaps 9, 10, or more—constitutes evidence for a biologically heterogeneous or abiological population, while lower DDI's are consistent with the assumption of biological (taxonomic) homogeneity. The DDI calculated for *L. golubicii* is 8, which places it at the outside fringe of monospecific populations, as estimated by this method. Although a much weaker line of evidence than that afforded by the comparison of size distributions of selected subpopulations of cells, the calculation of the DDI provides further support for the contention that the cells assigned to *L. golubicii* comprise a single taxonomic entity.

Leptoteichos golubicii is not found among the well known algal chert facies communities described by Barghoorn and Tyler (1965) but rather occurs in the abundantly fossiliferous cherts of the chert-carbonate facies. According to Goodwin (1956), the sediments of this facies were deposited in shallow, somewhat stagnant lagoons having limited exchange with the open sea. The presence of siderite, pyrite, and abundant reduced carbon (as opposed to the oxidized iron found in the algal chert facies) supports this interpretation. Clastic grains and typical near-shore sedimentary structures are absent, indicating that these beds accumulated in the central portions of the basin where they were precipitated from very quiet waters. Brecciated chert layers do occur and may indicate occasional subaerial erosion, but some of these breccias were apparently formed by the flowing and recrystallization of interbedded carbonate units (Moorhouse, 1960).

The flora of the chert-carbonate facies is biologically distinct from that of the stromatolitic cherts. It is dominated by trichospheric colonial microbes morphologically identical to the extant Mn-oxidizing bacterium *Metallogenium personatum* Perfil'ev (Cloud, 1965, 1976; Kline, 1975), as well as associated 3–15 μm sac-like unicells of uncertain affinities assigned the name *Galaxiopsis melanocentra* Awramik and Barghoorn (1977). Within this facies, these organisms occur in loosely defined layers, but do not form distinct laminae of the type characterizing algal mats. This distribution within the cherts, as well as the density of the population ($\delta = 10^7$ individuals/cm^3) suggests that these microbes formed a bottom community in the oxygen-poor Gunflint siliceous mud, an interpretation consistent with observations of modern *Metallogenium* (Dubinina et al., 1973; Bolotina, 1976). In contrast, *L. golubicii* occurs spottily, but is neither more nor less abundant in the *Eoastrion*-rich bands. This distribution, as well as the morphology and the apparently random solitary or clumping patterns of the population, suggests that *Leptoteichos* was not part of the bottom community, but rather was plankton-

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TEXT-FIG. 2—Size frequency of subpopulations of *Leptoteichos golubicii*. Histograms *2A–D* show size distribution within individual clusters of 74 (*A*), 133 (*B*), 42 (*C*), and 66 (*D*) cells. *2E* indicates the size frequency distribution of 100 randomly chosen solitary *L. golubicii* unicells. See Table *1* for numerical data on these subpopulations.

ic. Individuals died, sank, and were preserved in the siliceous bottom sediments. Planktonic organisms are not well documented from Aphebian rocks because most of our paleontological information comes from mineralized algal mats. *Eosphaera tyleri* Barghoorn (Barghoorn and Tyler, 1965), discovered in the algal chert facies of the Gunflint, may also have been planktonic, agreeing with *L. golubicii* in its spherical morphology and its independence of the distribution of known benthonic microbes in its facies. Of course, by late Precambrian times the planktonic realm had been invaded by numerous taxa (Timofeev, 1966; Downie, 1973; Vidal, 1976), but this proliferation appears to have been a decidedly post-Gunflint event related to the diversification of eukaryotic stocks.

A major question concerning *L. golubicii* is its biological affinities. This is of particular interest because of a single prominent feature common to most specimens examined—a small, eccentrically located, organic bleb internal to the preserved wall structure (Plate 1). Seventy-nine percent of the cells counted possessed this character, whereas the remaining 21% were completely empty. In only two cases were relatively large internal blebs observed. Such a state of preservation—and this feature is indicative of degradational state, not taxonomic affinity—obviously brings to mind the well known "spot cells" found in the one billion year younger Bitter Springs Formation of Australia (Barghoorn and Schopf, 1965; Schopf, 1968, 1974). Comparison of Text-fig. 1, showing the relative size distributions of *L. golubicii* cells and their contents, with a corresponding histogram constructed by Schopf (1974) for the Bitter Springs cells demonstrates the marked similarity of the two populations in terms of the relative size of perserved cell contents. The Bitter Springs "spots" have been taken as strong evidence for the eukaryotic level of organization, both because of their interpretation as cell organelles—either nuclei (Schopf, 1968, 1974) or pyrenoids (Oehler, 1976, 1977)—and because of their consistently small size and eccentric position (Schopf and Oehler, 1976; Oehler, 1977). If such an interpretation can be validly extrapolated, the Gunflint unicells in question represent early eukaryotes. The question, then, clearly becomes how good a criterion for the eukaryotic level of evolution is the "spot cell" morphology?

Rephrased, this question might well be stated: can prokaryotic organisms degrade to produce "spot cells"? If they can, then one must look beyond the "spots" themsleves to answer questions of biological affinities. Awramik et al., (1972) first explored the relevance of blue-green algal cell degradation to the Precambrian fossil record, and this theme has since been applied successfully to specific microfossil assemblages by several workers (Knoll et al., 1975; Knoll and Barghoorn, 1975; Golubic and Hofmann, 1976; Hofmann, 1976; and Golubic and Barghoorn, 1977). In all of these cases the cyanophytes studied possessed firm sheaths, and as pointed out by Oehler (1977), degraded cell contents were often of variable size and central position. Our own observations on both laboratory cultures and naturally occuring muds show that this is also true for many eukaryotic algae. However, bacterial degradation of cyanophytes that lack strong sheaths can and does produce populations which have consistently small and eccentrically placed cytoplasmic remains. This can be seen in the photographs of degraded *Cylindrospermum* sp. (IU 942) shown in Plate 2, figs. 12–14. *Cylindrospermum* is a filamentous blue-green alga belonging to the order Nostocales. During the process of *post-mortem* deg-

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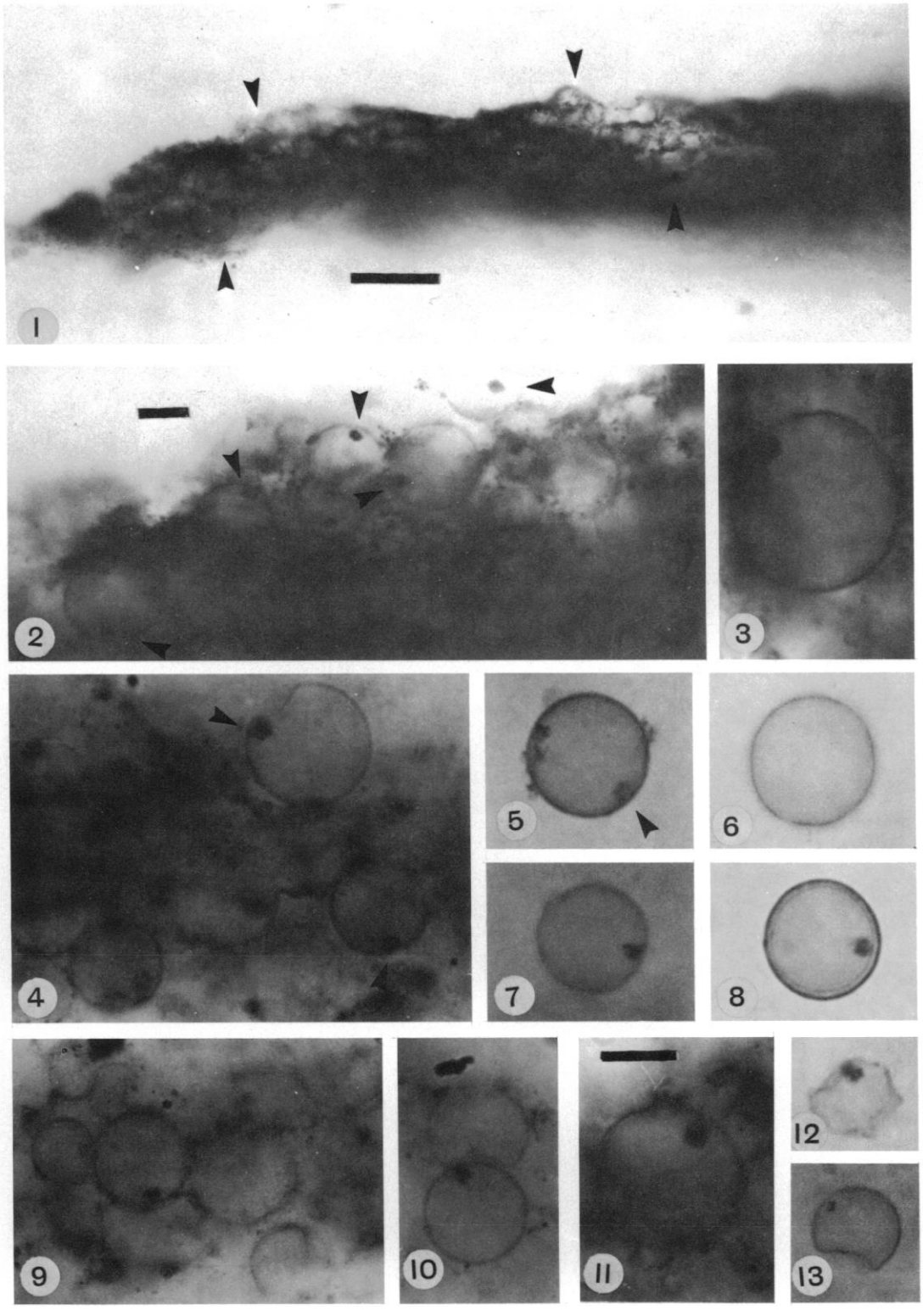
EXPLANATION OF PLATE 1

Leptoteichos golubicii n. gen. et sp. from the chert-carbonate facies of the Gunflint Iron Formation. Arrows point to internal organic residues. Slide and coordinate numbers are given for each photograph. (Bar = 50 μm in Fig. 1, 10 μm in Figs. 2 and 11. The bar in Fig. 11 pertains to Figs. 3–13.)

FIGS. *1–3,11*—Type cluster of *Leptoteichos golubicii* n. gen. et sp. FB10a2 (H.U. 60274), 45 × 109.8.
4,9,10—Views of a second cluster of *L. golubicii* cells. FB10a3b (H.U. 60178), 39.8 × 117.7.
5–8,12,13—Isolated individuals of *L. golubicii*, illustrating various aspects of its morphology. *5*, 10a3b (H.U. 60278) 16 × 102.9. *6*, FB74-12a (H.U. 60277), 49 × 113.2. *7*, 10a3 (H.U. 60284), 39 × 111.2. *8*, FB10a3b (H.U. 60278), 43.2 × 108.2. *12*, 10a3b (H.U. 60278), 27.2 × 116.8. *13*, FB74-12a (H.U. 60279), 49.2 × 117.1.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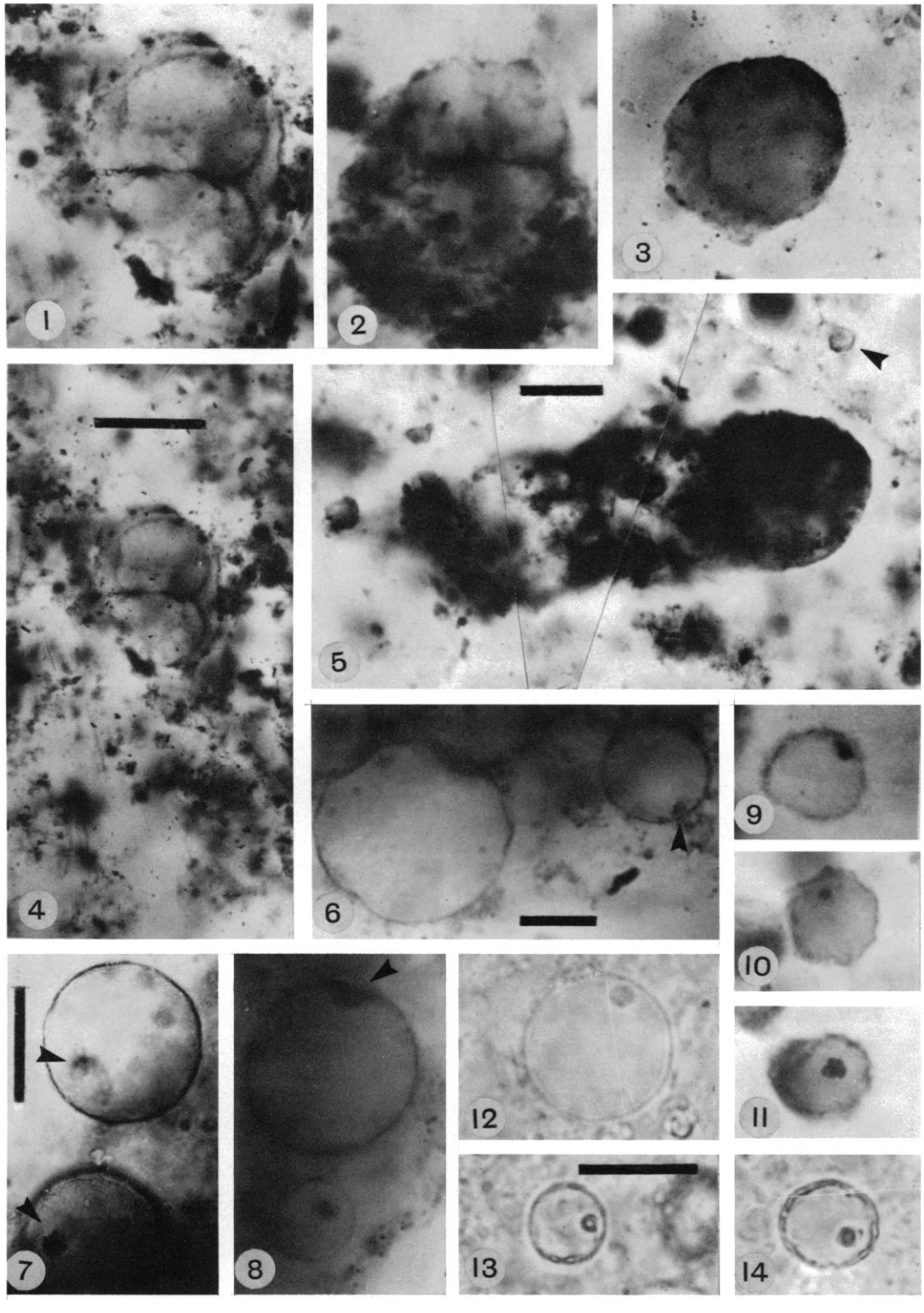
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radation, the filaments often break apart, and the originally barrel-shaped individual cells become rounded. The cytoplasm coalesces into the small blebs illustrated in Plate 2. We do not mean to suggest here that *Cylindrospermum* provides a close analog for any specific Precambrian cell population. We merely wish to demonstrate the capacity of certain cyanophytes to form degradational features similar to those found in *Leptoteichos*. It should be noted that neither the Gunflint cells nor the degraded modern prokaryotes commonly exhibit the internal membranous structures characteristic of some of the Bitter Springs "spot cells" (Oehler, 1976, 1977), and this may be an important factor in determining the taxonomic affinities of fossil unicells. As Golubic and Barghoorn (1977) have pointed out, we still have a great deal to learn about the diagenetic breakdown of algal cell interiors.

"Spot cell" organization is not unique to the Bitter Springs algae and *Leptoteichos golubicii*. On the contrary, spot cells have been observed in Devonian algal assemblages from cherty Helderberg limestones of Virginia and West Virginia (Knoll, unpublished data), in the Proterozoic Bitter Springs (900 m.y.), Galeros (850 m.y.), Minyar (750 m.y.), Shorikha (900 m.y.), Dismal Lakes (1,200 m.y.), Beck Springs (1,350 m.y.), Bungle Bungle (1,500 m.y.), Amelia (1,600 m.y.), and Belcher (1,900 m.y.) biotas (Schopf, 1975; Schopf et al., 1977), and even among populations of *Huroniospora* Barghoorn from the stromatolitic cherts of the Gunflint Formation (Plate 2, figs. 9–11). Hofmann (1976) has described a variety of cells from the Belcher biota that exhibit "spot cell" organization. One can infer from this either that eukaryotes flourished throughout the time span represented by the above formations or that such preservation may not be unusual in environments where rapid silicification is possible. Of course, the veracity of the second possibility does not rule out the possible correctness of the first.

In short, the presence or absence of an internal "spot," particularly in the absence of additional cytoplasmic residue, does not allow unequivocal differentiation between fossil prokaryotes and eukaryotes. The corollary to this, as expressed by Tappan (1976), is equally true. A microfossil that lacks such internal structure is not necessarily prokaryotic. Nor is it necessarily taxonomically distinct from other cells in the same or a different horizon which do have this organization.

As internal contents fail to elucidate the taxonomic affinities of *Leptoteichos,* one might look into the size and ecologic niche of *L. golubicii*. This taxon is larger than many extant blue-green algae (see compilation of Schopf and Oehler, 1976), but even the largest cells observed in the population are well within the known size-range of cyanophytes. Evidence of reproductive patterns is also absent. Thus, one is again left with few clues to the assignment of *L. golubicii* to even the broadest of taxonomic categories.

Overall considerations of the morphology, size, and mode of life of *L. golubicii* do indeed make the hypothesis of eukaryotic affinities attractive; there are no modern blue-green al-

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EXPLANATION OF PLATE 2

Algal microfossils from the Gunflint Iron Formation, Ontario, and modern degradational analogs. Slide and coordinate numbers given for fossil specimens.

FIGS. *1–5*—*Megalytrum diacenum* n. gen. et sp. The dyad illustrated in Figs. *1* and *4* has been designated the type of the new species. *1,4,* Sch46W-BA (H.U. 60275), 12 × 11.5. *2,* Sch46W-BA (H.U. 60275), 23.3 × 105.6. *3,* Sch57-27 (H.U. 60281), 23 × 116.6. *5,* Sch46W-BA (H.U. 60275), 29 × 105.5. (Bar = 25 μm for Figs. *1–3* and *5,* 50 μm for Fig. 4.)

6–8—*Leptoteichos golubicii* n. gen. et sp. Arrows point to internal organic contents. (Bars = 10 μm, bar in Fig. *6* also applies to Fig. *8.*) *6* and *8,* Type cluster. FB10a2 (H.U. 60274), 45 × 109.8. *7,* FB1 (H.U. 60280), 32.3 × 116.2.

9–11—*Huroniospora* Barghoorn from the algal chert facies of the Gunflint Iron Formation, exhibiting "spot cell" morphology. *9,* K-4-Z (H.U. 60282), 23 × 112.4. *10,* K-4-Z (H.U. 60282), 20.6 × 99.4. *11,* Sch56 (H.U. 60283), 11 × 100.4. (Bar in Fig. *13* = 10 μm and applies to Figs. *9–11.*)

12–14—Experimentally degraded cells of the extant cyanophyte *Cylindrospermum* sp. (IU 942) showing a pattern of internal degradation similar to that of *L. golubicii*. (Bar in Fig. *13* = *10* μm and applies to Figs. *12–14.*)

gae that closely resemble this taxon in all of its salient characteristics. However, we acknowledge a reluctance, in part subjective, to conclude that higher algae arose prior to two billion years ago. The suggestion that eukaryotes evolved about this time is not new, although most speculation has been without the benefit of strong supporting evidence from the fossil record. Fundamental to these considerations is the realization that the evolution of the nucleated cell required an oxygenic atmosphere (Cloud, 1968; Margulis et al., 1976), and that once this condition was met, no other chemical bars precluded protist evolution. The temporal distribution of the earth's iron formations, detrital uraninite, and continental redbeds have led some geologists to the conclusion that the widespread appearance of relatively high concentrations of free oxygen in the atmosphere occured approximately two billion years ago (Cloud, 1972, 1974), thus setting an upper limit on the timing of eukaryote evolution (Cloud, 1976). In a recent analysis of rock sequences antedating two aeons, Dimroth and Kimberley (1976) presented evidence for the contention that at least some free oxygen was present in the atmosphere at a much earlier date, perhaps even prior to the deposition of the earth's oldest known supracrustals some 3.8 billion years ago. Whether concentrations of atmospheric oxygen sufficient to account for the observed sedimentary record were also high enough to permit the emergence of eukaryotes (which are almost universally fully aerobic) is doubtful, but the possibility does exist that environmental constraints against the evolution of higher organisms were removed earlier than Gunflint time. *If* this is so, then theoretically at least, eukaryotes could have inhabited the Gunflint basin; *whether* it is so remains to be elucidated.

Recently, several scientists have reinterpreted previously existing microfossil evidence to suggest the presence of higher algae in the Gunflint biota. Kazmierczak (1976) and Tappan (1976) have both placed the problematical microbe *Eosphaera tyleri* Barghoorn (Barghoorn and Tyler, 1965) among the ranks of the higher algae, although their interpretations are at variance with each other. Darby (1974) and Tappan (1976) have also suggested that the taxon *Huroniospora* Barghoorn (Barghoorn and Tyler, 1965) was also nucleated.

The *Huroniospora* question is perhaps more easily explained and so is considered first. Darby's and Tappan's interpretations are based on common *Huroniospora* morphologies that are suggestive of reproduction by budding. Budding is unknown among modern cyanophytes, but can be observed in extant fungi and higher algae. However, a similar morphology also results from the local weakening followed by expansion or rupture of cyanophyte sheaths during *post-mortem* degradation. This phenomenon is clearly shown by certain degraded blue-green algae in the Bitter Springs Formation (Schopf and Blacic, 1971, Plate 111, figs. 8–13). Further, the relationship between the Gunflint *Huroniospora* cells and the algal mats and stromatolites in which they are found is more than casual. These organisms were not planktonic, nor were they washed into the Gunflint basin from an external environment. They were restricted to stromatolitic laminae and as such were probably an integral part of the mat building community (Awramik, 1976). Such an ecologic niche is not compatible with the suggested budding eukaryotic analogs. Thus, although the true affinities of *Huroniospora* remain less than clearly understood, we can find little strong evidence to suggest that it was eukaryotic.

The hypotheses concerning *Eosphaera* are more intriguing. Kazmierczak (1976) likened it to his Devonian alga *Eovolvox* (Kazmierczak, 1975) which, as its name implies, has been compared to the modern Volvocales of the Chlorophyta. Resemblances between *Eosphaera* and *Eovolvox* seem superficial. As Cloud (1976) and Awramik and Barghoorn (1977) have pointed out, the taxa differ markedly in size, and the distributions of small spheroids about the periphery of the central cells are quite different. Most crucial, it is difficult to derive the double concentric walled structure of *Eosphaera* from the architecture of volvocalean algae. Tappan (1976), on the other hand, compared *Eosphaera* to members of the extant Rhodophyte order Porphyridiales. The red algae are generally much smaller than *Eosphaera,* but may sometimes attain the size of the Gunflint problematicum. The planktonic marine habitat presumed for *Eosphaera* is also consistent with Tappan's interpretation. Finally, members of the extant genus *Porphyridium* are capable of reproduction via peripheral buds that are held in close proximity to the parent cell by a thin outer

sheath—a pattern which could account for the singular morphology of *Eosphaera*. Still, this interpretation is not without problems. In addition to this budding morphology, modern porphyridialean algae exhibit a variety of other shapes related to vegetative existence and binary fission. None of these morphologies has yet been recognized in the Gunflint fossil record. Tappan's (1976) hypothesis has been rejected by Cloud (1976) and Awramik and Barghoorn (1977), both of whom envision the Gunflint biota as wholly prokaryotic. Unfortunately, at present there exists no positive evidence bearing on the true affinities of the organism. Thus, the taxonomic position of *Eosphaera* remains obscure, and it cannot be considered demonstrably prokaryotic or eukaryotic.

Although Gunflint age floras are now known from several additional areas of the world (Hofmann, 1976; Walter et al., 1976; Knoll and Barghoorn, 1976) none of these biotas contains any forms which can be interpreted as the remains of nucleated cells. Other evidence for the presence of eukaryotic algae, however arguable it may be, is not found in the Precambrian record prior to 1,400 m.y. B.P. or later. Degradationally resistent-walled acritarchs, which are commonly preserved in Late Precambrian detrital deposits, are not encountered in Gunflint-age shales. Thus, it is deemed likely that nucleated cells did not exist two billion years ago, implying that the *Leptoteichos* was prokaryotic.

A third, intermediate possibility does, however, exist and should be explored. The evolutionary transition from prokaryote to eukaryote was a complex process, involving fundamental changes in both ultra-structure and physiology (Margulis, 1970). Such a change must have taken a long time to be accomplished, regardless of how the changes occurred (Margulis et al., 1976). It is also likely that many characters that today are considered to be essentially eukaryotic arose at quite different times and in a variety of independent groups. For example, the relatively large size found among some higher algal unicells could have evolved well before the segregation of genetic material into a membrane-bound nucleus; the reverse could as easily be true. What is important is that most of these fundamental changes would not be observable in the paleontological record and that some problematical microfossils could in fact represent transitional stages in the evolution of the nucleated cell. While the logic of this proposition is sound, empirical evidence is difficult to obtain; thus, the hypothesis must needs remain speculative. Nevertheless, it should be kept in mind as possibly being relevant to the interpretation of *L. golubicii,* as well as a number of younger Precambrian microbes whose affinities are not decipherable.

Having weighed the above arguments, we have elected to place *Leptoteichos golubicii* among the ranks of the Algae *incertae sedis,* while tacitly assuming that this taxon did not have eukaryotic organization. This is not circumventing the question; it is an honest reflection of the nature and limitations of the Precambrian fossil record.

In its size, morphology, and habitat, *L. golubicii* differs from all previously described Precambrian taxa and therefore deserves distinct generic status. Its closest comparisons are to *Glenobotrydion majorinum* Schopf and Blacic (1971) and *Myxococcoides* sp. Schopf (1968), particularly as these names have been applied to microbes from the 2,000 m.y. old Belcher Group of Hudson's Bay, Canada (Hofmann, 1976). However, *L. golubicii* differs from the aforementioned taxa in its larger size range, its common aggregation into clusters of cells held together by a thin amorphous coat of mucilage, and in its interpreted depositional environment—a planktonic form deposited in the central portions of a restricted basin versus algal mat dwellers (Hofmann, 1975, 1976). Spheroidal unicells possibly referable to *L. golubicii* occur in the carbonaceous cherts of the coeval Duck Creek Formation of northwestern Australia (Knoll and Barghoorn, 1976).

Megalytrum diacenum

The stromatolitic cherts of the algal chert facies of the Gunflint Formation contain numerous organic sacs of varying sizes. Although some of these appear to be sedimentary products of coalesced organic detritus, others are strongly delimited and closely resemble the sheaths of blue-green algae. Particularly in the size range of 30–100 μm, these hollow carbonaceous bodies strongly suggest algal origins. From among the various morphologies represented in this size class, we have chosen a distinct subclass for inclusion in the new genus

and species *Megalytrum diacenum*. *Megalytrum diacenum* consists of spherical to ellipsoidal, thin, but clearly defined, organic sheaths, ranging in size from 33 × 33 μm to 48 × 47 and 52 × 36 μm. (Measurements on 12 individuals yield average dimensions of 47 × 38 μm.) Specimens occur singly or in linearly arranged groups (Plate 2); pairs may be encompassed by an outer envelope of the same constitution (Plate 2, figs. 1, 4). Indeed, it is this occasional presence of identical inner and outer boundary layers that permits the interpretation of *Megalytrum* as sheath remains. Algae possessing two nested walls of identical structure are unknown, but cyanophytes that have multiple sheaths are not uncommon. *Megalytrum diacenum* differs from other organic sacs in the formation not only in its occasional tendency to form groups, but also in the fact that these sheaths retain their well rounded turgid shape and are not collapsed. As in the case of *Leptoteichos,* specimens of *M. diacenum* examined are dark amber to brown in color and have a finely granular surface texture, probably a product of iron chelation at loci within the sheath. Internal cell contents are not known.

Specimens of *Megalytrum* are found among stromatolites, occurring both between lamellae within the mat structure and in spaces between stromatolite columns. This organism is rather rare and clearly did not assume an active role in the build-up of algal mats. It appears that the sheaths were carried to their site of deposition from an unknown location and thus are allochthonous elements of the algal mat assemblage. Although it is impossible to ascertain the environment in which these organisms lived, their presence in the Gunflint rocks does provide additional evidence for the diversity of life in the vicinity of the Gunflint basin two billion years ago.

Unlike some similarly large spheroidal sacs found in Late Precambrian and Phanerozoic rocks, *Megalytrum* was not an endosporangium—it lacks associated endospores and the ruptural wall or lid characteristic of such structures.

Megalytrum diacenum is here interpreted as the sheath of a blue-green alga, probably one closely related to members of the extant order Chroococcales. Within this modern group, several genera are capable of secreting structures similar to *Megalytrum*. For example, some species of *Microcystis* form large spherical sheaths that contain numerous small cells. On the other hand the equally large sheath of *Chroococcus macrococcus* encloses but one to four cells. In *Gomphosphaeria,* large spheroidal sheaths protect numerous individual cells, but unlike *Microcystis,* these cells are arranged in a radially symmetrical pattern. Clearly, precise taxonomic relationships cannot be established in the absence of information on contained cells; however, the very knowledge that more or less modern colonial sheath-forming chroococcoid algae flourished in the vicinity of the Gunflint stromatolites justifies the description of these forms. These sheaths constitute the only known evidence for the presence of such algae in the Gunflint environment.

Among previously reported Precambrian taxa, *Megalytrum* has no close analog. *Phaneroshaerops capitaneus* Schopf and Blacic (1971), a putative chroococcacean cyanophyte described from the 800–900 m.y. old Bitter Springs Formation, Australia, is broadly similar to *M. diacenum* in that the two taxa are similar in size and are equally devoid of identifying elaborations. They differ in that *P. capitaneus* has a thick brittle wall that is prone to cracking and in that *Megalytrum* has the capacity to aggregate into groups which can have a common external envelope. Lopuchin (1971, 1974) has described, under the name *Menneria,* sac-like organic bodies found in macerals from rocks ranging in age from the earliest Archean of the Aldan Shield to the Carboniferous. He applied the name *M. levis* to specimens identified from the Gunflint. Although the all-encompassing definition of *Menneria* might conceivably be applicable to certain individuals of *Megalytrum,* we feel that the differing concepts of these taxa, and indeed the somewhat questionable biogenicity of many of the forms assigned to *Menneria,* require the distinction of the genus *Megalytrum*. Whereas the name *Menneria* was applied to sacs spanning a time period of nearly three billion years and which are of diverse morphologies and origins, some of them perhaps abiological (Awramik and Barghoorn, 1977), *Megalytrum* represents a population having a discrete morphology and living during a distinct time period.

The description of *M. diacenum* as sheath devoid of contents suggests the concept of the

form genus—a fossil that represents only a portion of the original organism, but which is classified according to the same rules as whole individuals even though the identity of the complete organism may not be known with any degree of certainty (Gary et al., 1972, p. 274). Differential preservation of sheath material is not uncommon among Precambrian microfloras, and a number of essentially form taxa have previously been erected on the basis of sheath remains in Proterozoic cherts. Examples include *Animikiea* from the Gunflint Iron Formation (Barghoorn and Tyler, 1965), *Archaeotrichion* and *Eomycetopsis* from the Belcher Islands (Hofmann, 1976), *Paleopleurocapsa* from the Skillogalee Formation of South Australia (Knoll et al., 1975), and *Siphonophycus* and *Eomycetopsis* from the Australian Bitter Springs Formation (Schopf, 1968; Schopf and Blacic, 1971). Experimental evidence demonstrating that in modern cyanophytes sheath material often resists *post-mortem* degradation better than the protoplasm of the cell itself has been produced largely through the work of Golubic (Awramik et al., 1972; Golubic and Barghoorn, 1977). Horodyski and von der Haar (1976) have also noted this phenomenon in recent algal mats from Baja California and have pointed out the potential hazards of mistaking firm sheaths for large cells in the Precambrian record.

SYSTEMATIC PALEONTOLOGY

Division CYANOPHYTA
Class CYANOPHYCEAE
Order CHROOCOCCALES
Genus MEGALYTRUM n. gen.

Type species.—Megalytrum diacenum n. sp.

Diagnosis.—Large spherical to ellipsoidal sharply delineated organic sacs, occuring singly or in linearly arranged groups of two or three together. An outer envelope may encompass two individuals in a dyad. Walls well delimited, retaining regular, well-rounded morphology and not irregularly folded or collapsed. Wall hyaline to finely granular. Size of individual sheaths 33 to 50 μm in diameter, averaging 47 × 38 μm (12 specimens measured). A single well-formed individual measured 80 × 80 μm. Internal cell contents unknown.

Etymology.—From Greek, meaning "large sheath."

MEGALYTRUM DIACENUM, n. sp.
Plate 2, figs. 1–5

Diagnosis.—As for genus.

Etymology.—From the Greek, meaning "empty."

Type locality.—In carbonaceous cherts of the basal algal chert facies of the Gunflint Iron Formation exposed along the beach, 6.4 km west of Schreiber, Ontario.

Type specimen.—The specimen pictured in Plate 2, fig. 1 has been designated as the type for this new species. Slide No. Sch W46-BA, Paleobotanical Collections Harvard University No. 60275, stage coordinates 12.8 × 101.2 (coordinates of X in lower left corner of slide = 32 × 97.8).

ALGAE INCERTAE SEDIS
Genus LEPTOTEICHOS n. gen.

Type species.—Leptoteichos golubicii n. sp.

Diagnosis.—Cells spherical, generally solitary, but also occuring in irregular clumps of a few to more than 100 individuals held together by a diaphanous layer of amorphous mucilage. Surface texture hyaline to finely granular, the latter most likely reflecting retention of wall iron compounds during *post-mortem* degradation. Diameter varies from 5 μm to 31 μm, averaging 13.5 μm (800 cells measured, see Text-fig. 1). Wall thickness from 0.5 to 1.0 μm. Cells occasionally flattened as a deflated ball.

Etymology.—From the Greek, meaning "thin wall."

LEPTOTEICHOS GOLUBICII n. sp.
Plate 1, figs. 1–13; and Plate 2, figs. 6–8

Diagnosis.—As for genus.

Etymology.—In honor of Dr. Stjepko Golubić of Boston University.

Type locality.—Carbonaceous cherts in the chert-carbonate facies of the Upper Member, Gunflint Iron Formation; 1 km west of the mouth of the Blende River (Sibley Peninsula) along the north shore of Lake Superior, Canada.

Type specimen.—The cluster of cells pictured in Plate 1, figs. 1, 2, 3, and 11, and in Plate 2, figs. 6 and 8 illustrates well the salient characters and variability of the taxon and so has been designated as the type. Thin section no. FB10a2, Paleobotanical Collections, Harvard University, No. 60274, stage coordinates

45 × 109.8 (coordinates of X in lower left corner of slide = 69.5 × 97.9).

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