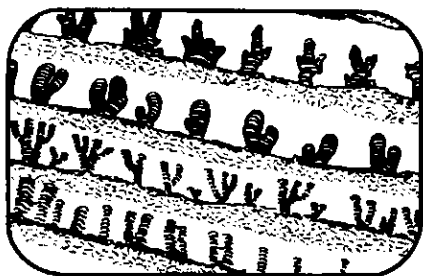


Articles



PALEOSCENE #7. Precambrian Biostratigraphy

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Introduction

Biostratigraphy is stratigraphy based on the paleontologic aspects of rocks, or stratigraphy with paleontologic methods. Although the term was apparently introduced only in 1904 in its present sense, by the Belgian paleontologist Louis Dollo (Bates and Jackson, 1980, p. 67), the practice of using fossils to characterize sedimentary packages and to subdivide geologic history dates back about 200 years. Its early development is usually associated with the work of pioneers such as Jean Baptiste de Monet Lamarck (1744-1829), Georges Cuvier (1769-1832), and particularly William Smith (the "Father of stratigraphy"; 1769-1839) (Adams, 1954, p. 268, 275). Most of the major divisions now in use (periods/systems) originated in the period 1822-1841, with the exception of the Tertiary (1760), Jurassic (1795), and Ordovician (1879). The hierarchically higher era-level terms Paleozoic, Mesozoic and Kainozoic (Cenozoic) were introduced by J. Phillips (1840), Archean by J.D. Dana (1872), and Proterozoic by S.F. Emmons (1888) (Wilmarth, 1925). The designations Phanerozoic and Cryptozoic for eons, the largest subdivisions, are of relatively recent vintage, having been introduced by G.H. Chadwick in 1930. For the finer divisions, the concept of stages was developed in 1842 by Alcide d'Orbigny (called the "Father of biostratigraphy" by Boucot (1985)),

and that of paleontologic zones by Albert Oppel (in 1856), both concepts predating the publication of Darwin's *Origin of Species* published in 1859.

Many other names have been proposed for the intervals whose rocks represent the overwhelming portion of geologic time referred to as pre-Cambrian (or by the unfortunate, but universally used, term Precambrian), rocks whose fossils had been unknown, unacknowledged, or disputed for a long time. Terms such as Agnotozoic, Archaeozoic, Azoic, Collozoic, Eobiotic, Eozoic, Hypozoic, Lipozoic, Paleophytic, Progonozoic, Proterophytic, Protozoic, and Prozoic all refer to the presumed nonexistent or primitive paleontologic character of Precambrian rocks (see Wilmarth, 1925). As the biotic diversity and fossil abundance in the rocks became better documented, first through the work of C.D. Walcott (1899, 1914), but particularly by an increasing number of others in the past 50 years, it also became possible to apply classic biostratigraphic methods to some of them. The use of terms like Sinian, Vendian, and Ediacaran (or Ediacarian) for a paleontologically characterized interval of geologic history preceding the Cambrian is gaining favour, although no single term has yet received formal approval by an international regulatory body of geology. Nor, indeed, do we know exactly where to put the base of the Cambrian and thus the top of the Precambrian. For the purpose of this review, and because of a lack of formal agreement of the position of the boundary, the top of the interval here considered to be pre-Cambrian is the base of the Rovno and the Nemakit-Daldyn (Manykay) Formations (Baltic Stage of Sokolov and Fedonkin, 1984) and similar units containing shelly fossils or "Cambrian-type" trace- and microfossils.

Paleontological objects of even older sequences are used to identify Lower, Middle, and Upper Riphean divisions (e.g., see Keller, 1982), with yet still older ones characteristic of the Early Proterozoic. All such biostratigraphic units represent very broad time intervals, of the order of hundreds of millions of years long, as a rule, in contrast to Paleozoic or younger zones, which sometimes encompass less than 1 million years. There also is no unanimity as to the placement of boundaries of some of these major divisions

(e.g., compare one placement of the basal limit of the Kudash unit (at the top of the Riphean) based on oncolites and catagraphs, and another on organic-walled microfossils, in the book on the Riphean stratotype (Keller, 1982, p. 68-70 and 94)).

In parallel with efforts by paleontologically oriented groups to develop a biostratigraphic scheme for the Precambrian, the IUGS Subcommission on Precambrian Stratigraphy has been working toward an acceptable general subdivision of Precambrian time. The latest subdivision that has evolved (Plumb and James, 1986) is said to reflect the significant events of Earth history. The major divisional boundaries are placed at round figures in such a way as to provide the most acceptable groupings of geologic events in large parts of the world, and split as few as possible of the known principal cycles of sedimentation, magmatism, and orogeny. The boundaries are defined in years without specific reference to any rock sequences. This approach complements the classical stratigraphic method based on the stratotype concept, and may even be preferable in certain respects, because it can readily accommodate data from all fields of geology from all continents within a single universal framework. Moreover, improvements in the precision of radiometric age determinations and the application of new isotope methods to calibrate geologic events look promising for the future of the geochronometric time scale favoured by the IUGS Subcommission. This scale will find wide use, certainly for most of the pre-Ediacaran interval, as long as biostratigraphic scales based on very slowly evolving life-forms remain imprecise. Nevertheless, the fossil record exists in sedimentary sequences (and even in high-grade metasediments, such as in the Grenville structural province) dating back to at least 3.5 Ga. It is therefore imperative that it be thoroughly studied for a better understanding of biospheric evolution, for making use of it in establishing biostratigraphic schemes, and to make correlations between distant successions of rocks.

What are these organic remains that make broad subdivision of the old sequences possible? How reliable and workable is Precambrian biostratigraphy? How far back are biostratigraphic methods applicable? What

recent literature exists on the subject? How many taxa are known from the Precambrian? These are some of the questions to be addressed in this review.

Precambrian Fossil Groups

The wide variety of life-forms that evolved between the early Archean and the beginning of the Cambrian is attested by the more than 1250 genus-level and an estimated 1700 species-level taxa that have now been reported, most of them since 1960 (Figure 1). Although many of these names are synonyms, or refer to structures ultimately shown to be inorganic, to be younger, or to be contaminants in preparations, there remain between 500 and 900 probably valid genus-level taxa. The remains can be grouped into the following broad categories (Figure 2):

Microfossils (acritarchs, cryptarchs, vase-form microfossils [melanocynillids], "calcareous algae"); **Megafofossils** (body fossils): soft-bodied Metazoa, carbonaceous films, including Metaphyta and microbial colonies; small shelly Metazoa (not here considered Precambrian); **Ichnofossils** (trace fossils); **Stromatolites** (spongiosomes); **Oncolites and catagraphs** (micro-phytolites); **Chemofossils** (elemental, isotopic, and molecular indices of the biosphere); **Dubiofossils** (questionably biogenic remains); **Pseudofossils** (structures resembling fossil organisms, but abiogenic); **Nonfossils** (contaminants and artifacts of preparation).

The stratigraphic distribution of the groups is plotted in Figure 3, indicating the approximate limits between which each is of potential biostratigraphic use. The frequencies shown are estimates of diversity values, reflecting not only numbers of taxa, but also, in part, the number of specialist workers studying particular intervals (e.g., compare Table 3 in Walter and Heys (1985), which can be read as a histogram, with their figs. 1 and 5).

Remains from all categories, excluding the last 3, have been utilized to prepare various "biostratigraphic" schemes. These schemes were generally developed over the past 25 years by specialists working with one group in particular sedimentary lithofacies, often independently from specialists studying a different facies. Most of the major Proterozoic sequences in the Soviet Union, China, and Australia have now been studied in detail sufficient to show successions of biozones and the utility of paleontologic analysis. Figure 4 presents a geographic overview of the location of the paleontologically and biostratigraphically most significant areas. To illustrate the biotic diversity as well as the stratigraphic ranges of particular taxa of the most widely used groups of remains, data are chosen from two well studied and stratigraphically long-ranging sections, namely the stratotype of the Riphean, and the Vendian in the Ukraine (Figures 5 and 6); the data are compiled from recent publications on the subject.

PRECAMBRIAN GENERA

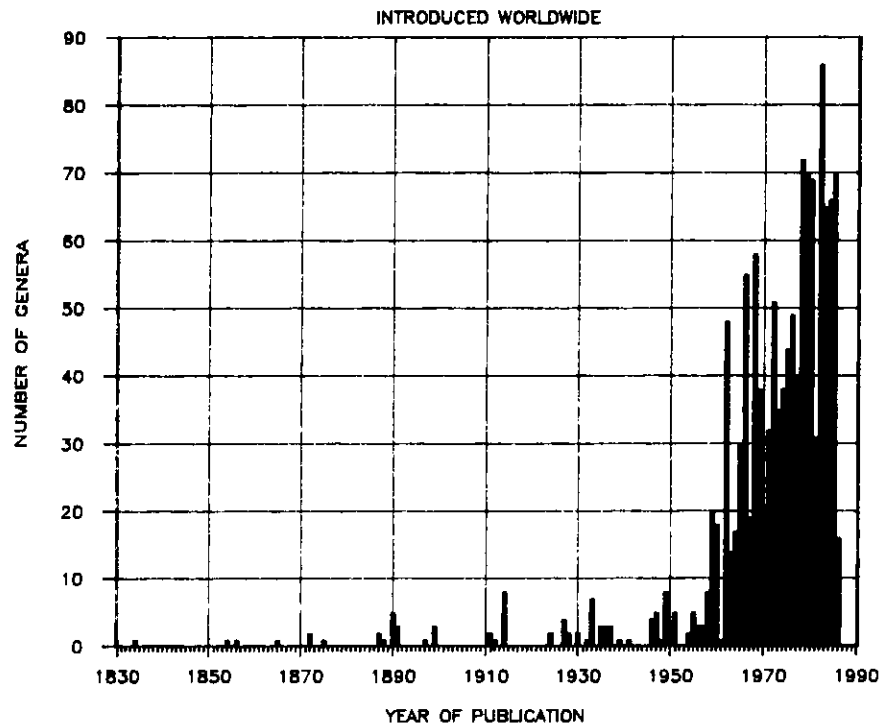


Figure 1 Histogram showing number of genera newly reported from Precambrian rocks each year.

PRECAMBRIAN REMAINS

Code	Type	Size	Form	Significance		
				biologic	geologic sedim.	chronologic
B	MEGAFOSSILS	cm		•••	•	•••
M	MICROFOSSILS	µm		•••	•	••
C	CHEMOFOSSILS	nm		••	•	?
I	ICHNOFOSSILS	cm		••	••	••
S	STROMATOLITES	dm		••	••	••
O	ONCOLITES	mm		•	••	?
K	CATAGRAPHs	mm		?	•	?
D	DUBIOFOSSILS			?	?	?
P	PSEUDOFOSsILS			-	•••	-

Figure 2 Classification and attributes of Precambrian remains. The frequency of dots in the last three columns indicates the relative quality of information provided by the remains. (From Hofmann, 1981, fig. 23.1).

Microfossils (acritarchs, cryptarchs, melanocyrillids, "calcareous algae")
Precambrian microfossils comprise structurally preserved remains of organisms visible only with the aid of optical or electronic microscopes. They range in size from sub-micrometric to the limits of resolution by the eye, and are found in rocks as old as 3.5 Ga, making them, together with the stromatolites, the oldest direct evidence that life existed then.

Two quite different methods have been used to study these remains. The older one, until relatively recently favoured by paleontologists in North America, relies on petrographic thin sections, usually of early diagenetic black cherts from dolomites, or other rock types likely to contain microfossils, such as carbonaceous mudstones. The method was first used by Cayeux (in 1894) on Brioverian (Late Proterozoic) cherts from France, though the remains described were questionable Precambrian microfossils. Other doubtful remains were subsequently reported from various regions. It was not until the discovery of the 2.0 Ga old Gunflint Formation microbiota (Tyler and Barghoorn, 1954) that the existence of Precambrian microfossils became more firmly accepted.

The subsequent find of the Bitter Springs (Schopf, 1968) and other microbiotas removed any lingering doubts. The petrographic method has the advantage of allowing the study of the sedimentary context of individual microfossils within the rock matrix, unmodified by manipulation, and with their orientation and mutual spatial relationship to other individuals preserved, including microbial mat organization. A disadvantage is that many samples may have to be cut before one is found to contain microfossils.

The second method is maceration, by which 50-100 g samples (or larger, if necessary) of promising lithologies are placed in mineral-dissolving acids (e.g., HCl, HF). Essentially intact organic-walled microfossils, as well as other, amorphous organic matter, remain as an insoluble residue. The microfossils are washed, further treated, and then mounted on glass slides for observation under the microscope (metal stubs for the scanning electron microscope). This method has the advantage of concentrating microfossils from larger volumes of rock, and thus speeding up the prospecting for microfossils, and of liberating individuals from the matrix. Disadvantages are that the disaggregation

process destroys information on the orientation and spatial relations of cells, some modification of the morphology may occur, and contaminants and artifacts may be introduced. The method has been applied mainly to clastic sequences, and the biotas recovered have been planktonic as a rule; it was first extensively applied to Precambrian samples by Timofeev (1959), after having been pioneered for younger Paleozoic sequences by A. Eisenack about 1930.

Both methods require observation at high magnification, at least 250x for the larger, and at least 1000x for observation of the smaller types, which may be why geologists working with lower magnifications have not noticed them more often. Inasmuch as both methods evolved independently, and two distinct environmental settings are represented (benthic *versus* planktonic), two different taxonomies have arisen. Attempts have been made only relatively recently to integrate the two lines of research. Those studying microfossils in thin sections have tended to treat them taxonomically in a way analogous to that for modern cyanobacteria and bacteria because the observed microfossils often occur in fossilized mats, and exhibit size, and

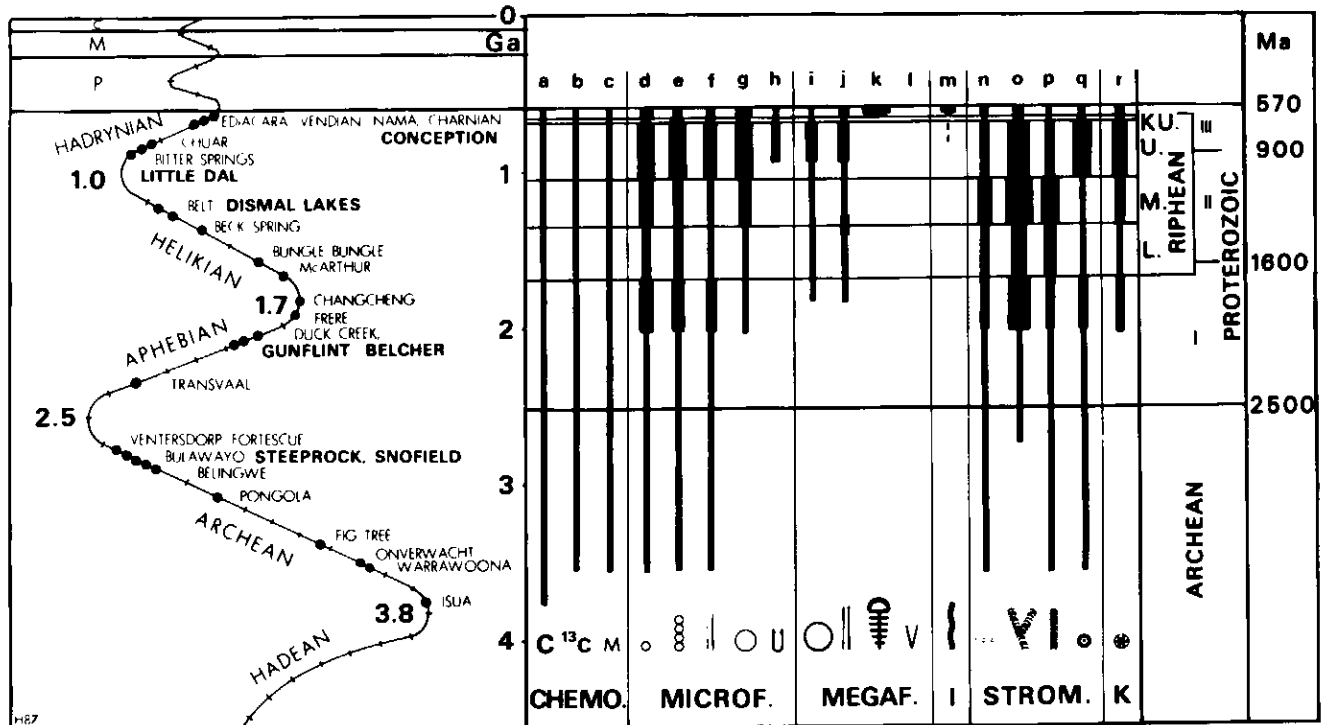


Figure 3 Stratigraphic distribution and importance of various categories of Precambrian remains (modified after Hofmann, 1981, fig. 23.10). Frequencies are estimates of diversity, but also reflect number of workers active in studying particular interval. Selected important fossiliferous stratigraphic units are placed in their geochronologic context in the left column; Canadian units are emphasized in boldface type. The attenuating curve schematically delineates major chapters in earth history and biological evolution. Numbers in left column represent 10⁹ years (= Ga).

Abbreviations: C = Cenozoic; M = Mesozoic; P = Paleozoic; Ma = 10⁶ years; KU = Kudash unit.

- a = free carbon, kerogen
- b = fractionated isotopes of C and S
- c = molecular fossils
- d = coccooid microfossils < 30 μm
- e = filamentous microfossils
- f = tubular microfossils, sheaths
- g = coccooid microfossils > 30 μm
- h = vase-shaped microfossils
- i = megascopic carbonaceous disks
- j = megascopic carbonaceous ribbons
- k = soft-bodied metazoan fossils
- l = shelly fossils
- m = trace fossils (ichnofossils)
- n = stratiform stromatolites
- o = branching columnar stromatolites
- p = stromatolites with conical laminae
- q = oncolites
- r = catagraphs

Figure 4 (opposite page) Geographic perspective of selected paleontologically and biostratigraphically significant Precambrian sections. **A** = Archean (> 2500 Ma); **L** = 2500 - 1600 Ma; **M** = 1600 - 900 Ma; **U** = 900 - ~ 670 Ma; **V** = ~ 670 - "base of the Cambrian"; **C** = Cambrian. Larger dots are for important stratotype areas.

1	—	Tindir Gp.						V	C
2	—	Wernecke Mountains: Windermere (Ekwi) Supergroup.						V	C
3	—	Mackenzie Mountains: Little Dal Gp.; Windermere Supergroup					U	V	
4	—	Dismal Lakes Gp.			M				
5	—	Epworth Gp., Rocknest Fm.		L					
6	—	Snofield Lake carbonate	A						
7	—	Great Slave Supergroup		L					
8	—	Windermere Supergroup					U	V	
9	—	Belt (Purcell) Supergroup			M				
10	—	California: Pahrump Gp. and younger formations			M				
11	—	Grand Canyon: Nankoweap Fm.; Chuar Gp.			M		U		
12	—	Steepprock Gp.	A						
13	—	Animikie Gp., Gunflint Fm.		L					
14	—	Keweenawan, Nonesuch Fm.			M				
15	—	Belcher Supergroup		L					
16	—	Thule Gp.			M		U		
17	—	Eleonore Bay Gp.					U	V	
18	—	Isua Gp.	A						
19	—	Burin Peninsula: Chapel Island Fm.						V	C
20	—	Avalon Peninsula: Conception and St. John's Gps.						V	
21	—	Corumbá Gp.						V	
22	—	Bambuí Gp.					U		
23	—	Brioverian						V	
24	—	Charnian						V	
25	—	Visingsö Fm.					U	V	
26	—	Murchisonfjorden Supergp.					U	V	
27	—	Jatulian		L					
28	—	White Sea Coast: Valday "Ser."						V	
29	—	East European Platform: Vendian						V	
30	—	Podolia: VENDIAN						V	
31	—	Southern Urals: RIPHEAN			M		U		
32	—	Anabar Massif: Riphean, Yudomian, Nemakit-Daldyn Fm.			M		U	V	C
33	—	Olenek Uplift: Riphean, Yudomian			M		U	V	
34	—	Yudoma-Maya region: Riphean, Yudomian			M		U	V	
35	—	Aldan Shield: Riphean, Yudomian			M		U	V	
36	—	Lake Baikal region: Riphean, Yudomian			M		U	V	
37	—	Jixian region: CHANGCHENG, JIXIAN, and QINGBAIKOU "systems"		L	M		U		
38	—	Hutuo Gp.		L					
39	—	Huainan area: Feishui and Huainan Gps.					U		
40	—	Yangtze Gorge: SINIAN					U	V	
41	—	Meishucun area						V	C
42	—	Vindhyan Supergroup					U	V	
43	—	Anti-Atlas: Infracambrian; Adoudounian, Taliwinian					U	V	C
44	—	Hank Ser., Atar Gp.					U		
45	—	Nama Gp.						V	C
46	—	Transvaal Supergroup		L					
47	—	Ventersdorp Supergroup	A						
48	—	Bulawayo Gp.	A						
49	—	Belingwe Gp.	A						
50	—	Swaziland Supergroup, Onverwacht, Fig Tree Gps.	A						
51	—	Pongola Gp.	A						
52	—	Warrawoona Gp.	A						
53	—	Fortescue Gp.	A						
54	—	Duck Creek Gp.		L					
55	—	Earaheedy Gp., Frere Fm.		L					
56	—	Bungle Bungle Dol.		L	M				
57	—	Roper Gp.			M				
58	—	McArthur Gp.		L	M				
59	—	Bitter Springs Fm.					U		
60	—	Adelaidean, EDIACARAN			M		U	V	

cell and colony morphologies similar to those in equivalent modern microbial mats. The names of taxa thus frequently reflect their old age and presumed affinities with modern taxa, based on morphologic resemblance, even if their biochemical pathways are unknown (*viz.*, *Palaeolyngbya*, *Eoentophysalis*). Fossils in silicified benthic mat assemblages are relatively small, and are strongly facies-controlled; many exhibit extreme evolutionary conservatism, that is, their shape and that of their colonies have hardly evolved since at least 2 Ga ago, when some of the first diverse assemblages came to be preserved. It therefore is not surprising that these microfossils are compared with modern taxa on the basis of morphology. This comparison can be misleading, because identical shape and size can be seen in metabolically and biochemically completely distinct modern microbes. Such microfossils are thus not likely to be very helpful for biostratigraphy. (For a preliminary review of the biostratigraphic usefulness of stromatolitic microbiotas, see Schopf, 1977).

In contrast to the stromatolitic biotas, the microfossils in the fine-grained terrigenous clastics comprise mostly somewhat larger spheroidal to polyhedral vesicles. They are generally referred to the group ACRITARCHA (Evitt, 1963). The term acritarch is highly appropriate, meaning "of uncertain origin". The fossils are ornamented and unornamented vesicles and are presumably

planktonic. They are thought to represent algae or algal cysts, and have been divided into various subgroups, of which the sphaeromorph, acanthomorph, disphaeromorphs, and polygonomorphs are widely represented in the Precambrian.

Inasmuch as the acritarchs do not include filamentous forms, the general term Cryptarcha has been proposed by Diver and Peat (1979) to accommodate the filaments which, strictly speaking, are equally of uncertain affinities. Diver and Peat also included the sphaeromorph acritarchs in the Cryptarcha, and added a category for colonial or aggregated sphaeromorphs which they called synaplomorphs. Their proposal to transfer the sphaeromorphs from the acritarchs has not been unanimously accepted, and it might perhaps have been more useful to restrict the term cryptarch to the filamentous forms.

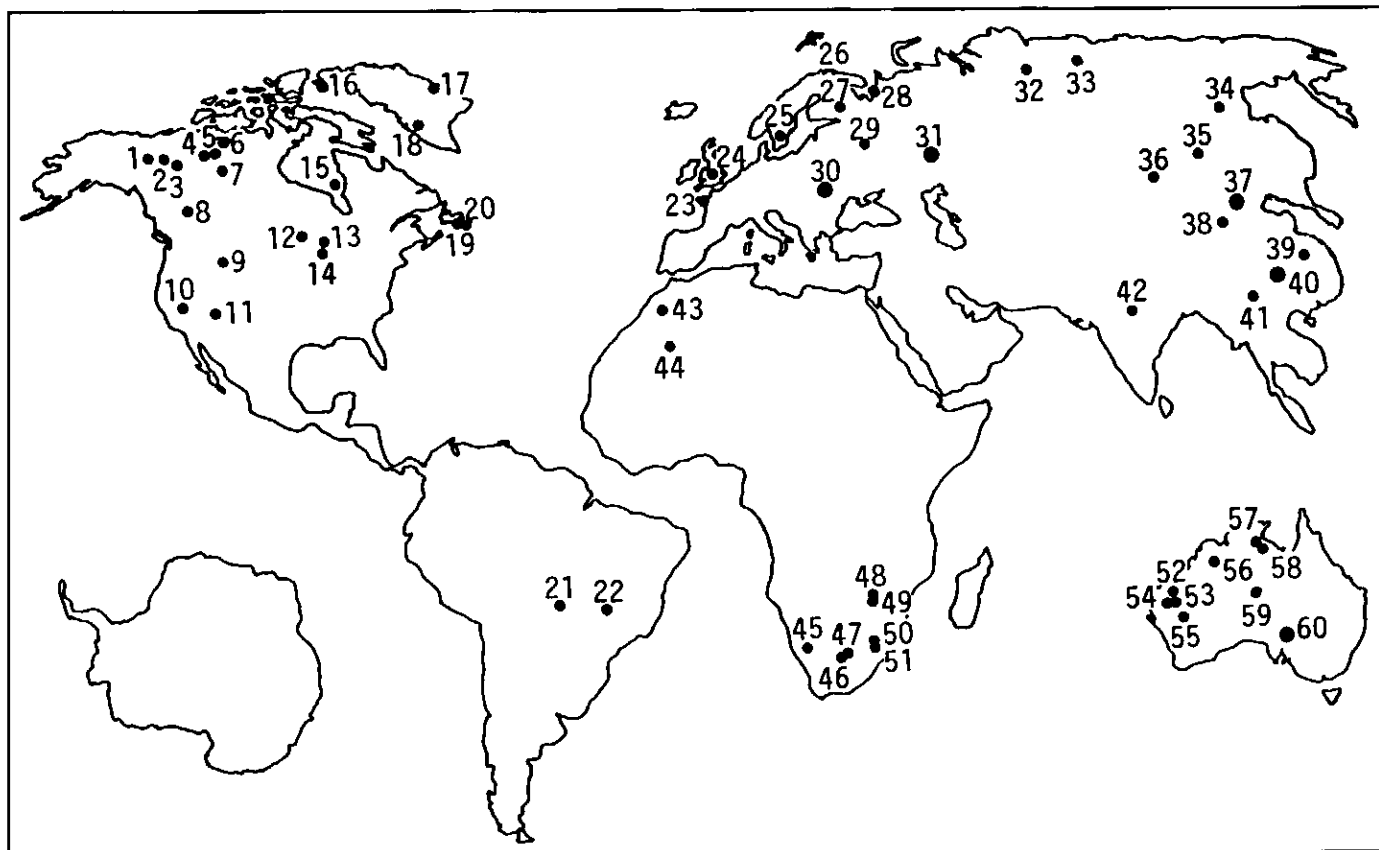
Whatever the merits of choice of assignment, these are the microfossils that have been found of most use in biostratigraphy. The stratigraphic ranges of scores of taxa have been determined in many Riphean and Vendian sections, which has permitted them to be correlated over long distances. It has also been possible to recognize low-diversity, stratigraphically long-ranging inshore, and more heterogeneous offshore associations (Vidal and Knoll, 1983). Published range charts for the acritarchs/cryptarchs can be found in Timofeev (1979) for the Archean to Cambrian in northern Eurasia, in Yankauskas (1982)

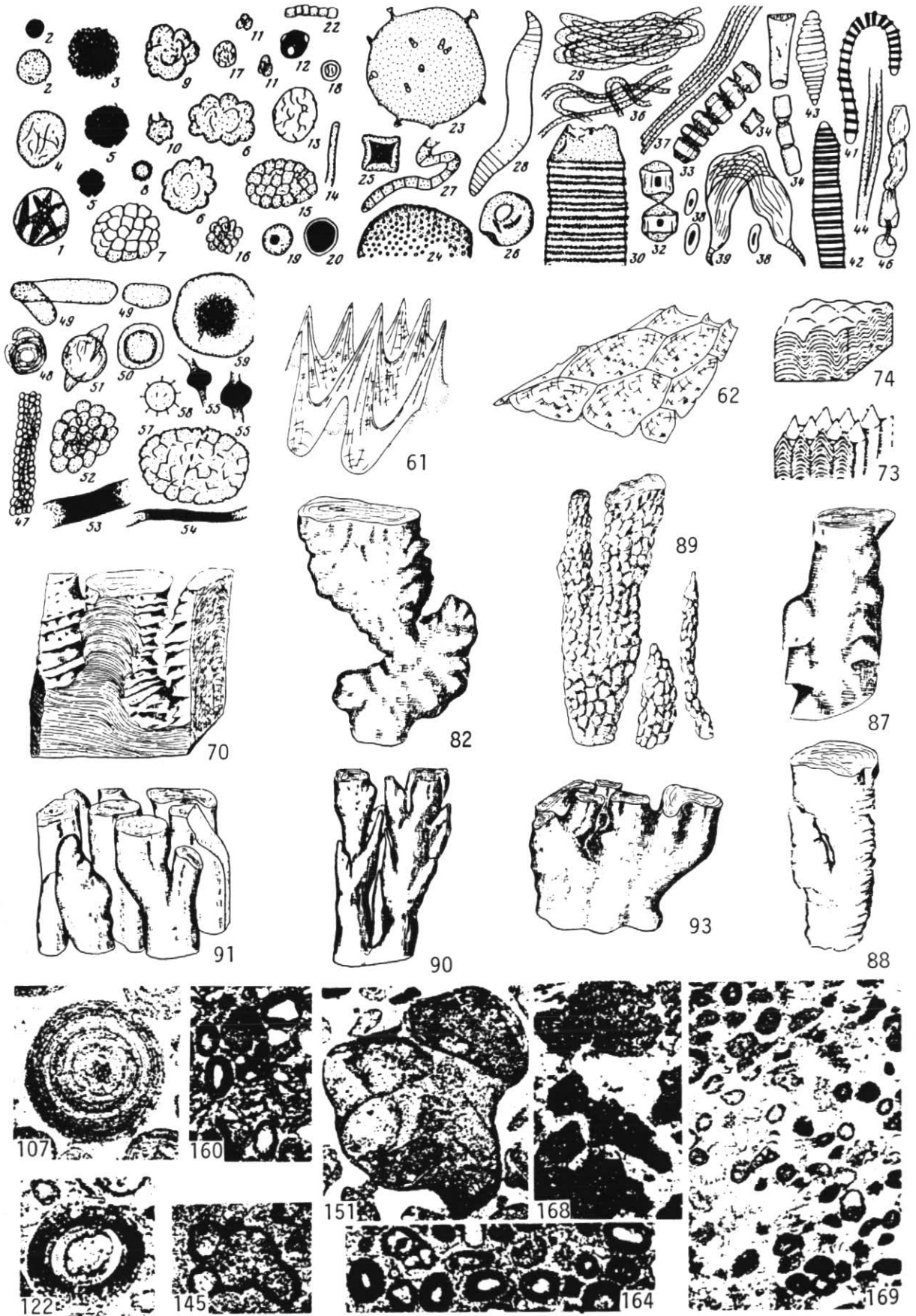
and Keller and Yankauskas (1982) for the Riphean stratotype of the southern Urals, in Aseeva (1983) for the Vendian of the Ukraine, in Vidal and Knoll (1983) for the Riphean and Vendian of Scandinavia, for the Mid- and Late Proterozoic of China in various papers in the book on the Sinian "Suberathem" (edited by Wang, 1980) and for the Sinian System stratotype in the Yangtze Gorges in Xing and Ding (1985).

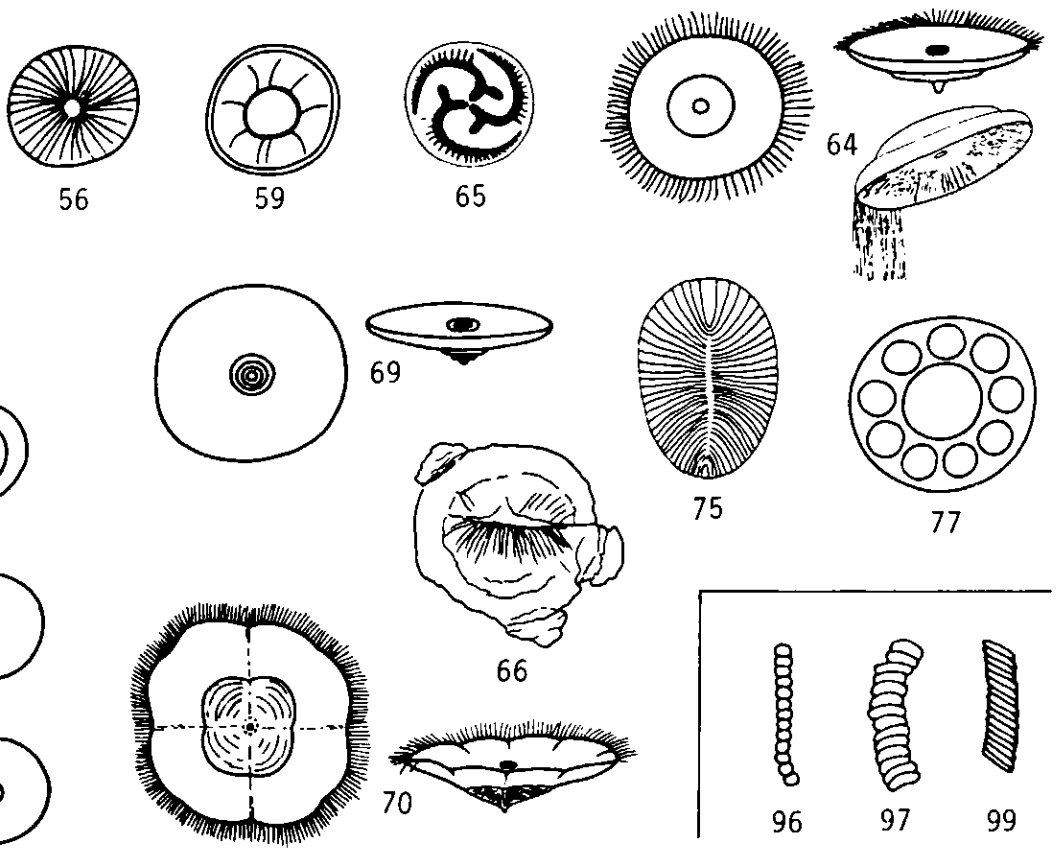
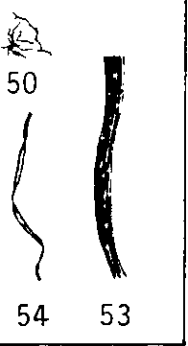
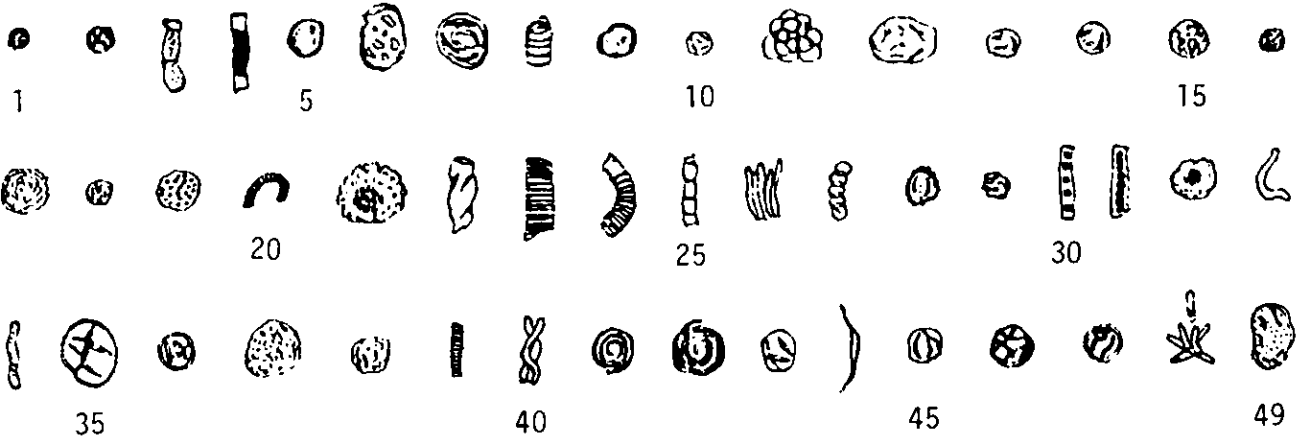
Reports of acritarchs/cryptarchs from pre-Riphean clastic sequences exist for some regions of the world, but they show neither the diversity nor the abundance seen in the younger Precambrian sections.

Given that the taxonomy of organic-walled microfossils is presently undergoing a review (*e.g.*, Yankauskas and Mikhailova, 1986), and that many synonymous taxa (particularly of smooth-walled spheroids such as *Leiosphaeridia* [Fig. 7]), and preparational artifacts are being eliminated, modifications in these range charts are inevitable. The charts, nevertheless, present interesting information for some generalizations.

There is a general trend with time, already observed by Timofeev and others long ago, of an increase in cell sizes, and progressively more ornamented vesicles. An apparent decline in diversity occurs around the time of the Vendian glaciations, followed by a radiation of acritarchs with new architecture in the Early Cambrian (Vidal and Knoll, 1983, fig. 4).







		VENDIAN										ICAPERIAN	
		Drev.		Valday		Superseries		Ivanovo		Ivano		Ivano	
		Voln. Mogilev-Fodol.		Dan		Zna		Kru		Stu		Iha	
		Gru	Mog	Var	Nag	Dan	Zna	Kru	Stu	Iha			
1 Leiosphaeridia parva Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
2 Leiosphaeridia aenta (Schep.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
3 Trachythrichoides ovalis Herm.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
4 Rudjana Gol.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
5 Leiosphaeridia leccata (Tim.) Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
6 Stratiomorphus rubiginosus (Andr.) Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
7 Circuella mogilevica Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
8 Volyniella valdaica (Schep.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
9 Stratiomorphus plana Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
10 Leiosphaeridia minor (Schep.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
11 Polycavita bullata (Andr.) Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
12 Leiosphaeridia gigantea (Schep.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
13 Leiosphaeridia pelucida (Schep.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
14 Leiosphaeridia asapha (Tim.) Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
15 Stictosphaeridium sp.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
16 Orygatosphaeridium flexuosum (Tim.) Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
17 Polycavita concentrica Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
18 Trachysphaeridium partiale (Schep.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
19 Orygatosphaeridium induratum Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
20 Tubulosa tamopolica (Ass.) Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
21 Ljadovia perforata Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
22 Taenitrichoides jaroshevici Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
23 Spratella coruscata Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
24 Tubulosa corrugata Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
25 Decillatoropsis sp.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
26 Polytrichoides spp.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
27 Arctacellularia sp.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
28 Leiosphaeridia prunifera Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
29 Trematosphaeridium holtdahlia Tim.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
30 Halythrix sp.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
31 Palaeolynxys catenata Herm.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
32 Macillosphaeridium sp.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
33 Leiothrichoides typicus Herm.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
34 Leiothrichoides gracilis Piat.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
35 Leiosphaeridia jacutica (Tim.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
36 Leiosphaeridia effusa (Schep.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
37 Trachysphaeridium magna (Schep.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
38 Trachysphaeridium baviense (Schep.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
39 Decillatorites wernadskii Schep.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
40 Flagellus tenuis Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
41 Cochleatina canlovia (Ass.) Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
42 Cochleatina rara (Fask.)	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
43 Leiosphaeridia volynica Tim.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
44 Micropodaria fusiformis Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
45 Stictosphaeridium simplex Tim.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
46 Podoliteia irregularis Tim.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
47 Leiosphaeridia undulata Tim.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
48 Studencia bacolica Ass.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
49 Orygatosphaeridium sp.	Aseeva 1983	---	---	---	---	---	---	---	---	---	---	---	---
		2	18	31	15	18	19	18	17				
50 Eoholynia	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
51 Pilitella composita Ass.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
52 Fusostuamula vlasovi Ass.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
53 Vendotaenia antiqua Gril.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
54 Tyrasotaenia podolica Gril.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
		0	1	3	2	1	1	1	2				
55 Niobia dnjesteri Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
56 Irridinitus multiradiatus Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
57 Lomosoia melus Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
58 Cyclomedusa davidi Sprigg	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
59 Medusinites asteroides (Sprigg)	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
60 Vavelikisa velikanovi Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
61 Protodiploporosoma sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
62 Dickinsonia tenuis Glaess. & Mada	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
63 Neelana sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
64 Ediacaria flindersi Sprigg	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
65 Tribrachidium heraldicum Glaess.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
66 Protodiploporosoma rugulosum Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
67 Pseudorhizostomites sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
68 Niobia occlusa Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
69 Cyclomedusa plana Glaess. & Mada	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
70 Conodurites lobatus Glaess. & Mada	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
71 Valdania plumosa Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
72 Podoliserus micrus Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
73 Pteridinium sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
74 Paliella patelliformis Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
75 Dickinsonia costata Sprigg	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
76 Pinegia sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
77 Elasma aseevae Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
78 Pinegia stellaris Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
79 Neelana simplex Pali.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
80 Tyrasiana disciformis Pali.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
81 Cyclomedusa cf. plana	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
82 Bronzieella podolica Zaska-Nov.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
83 Tyrasiana coniformis Pali.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
84 Cyclomedusa serebrina Pali.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
85 Zimella sp.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
86 Atakia venisiformis Pal.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
87 Planolites grandis Sok.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
88 Medusinites petellaris Sok.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
89 Loevichnus surculatus Gur.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
90 Studencia galathea Gur.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
91 Sabellidites cambriensis Jan.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
92 Palaelina sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
93 Sabellidites ex gr. cambriensis Jan.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
94 Sokolovina costata Kirijanzov	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
		25	10	1	0	1	0	1	4				
95 Bergaueria sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
96 Neomerites sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
97 Palaeopascichnus delicatus Pali.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
98 Cochlichnus sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
99 Harlaniella podolica Sok.	Velikanov 1985	---	---	---	---	---	---	---	---	---	---	---	---
100 Gordia sp.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
101 Synalthis polonicus Fed.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
102 Traptichnus bifurcus Miller	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
103 Didymalichnus tirasensis Pali.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
104 Bergaueria major Pali.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
105 Traptichnus triplex Pali.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
106 Phycodes pedus Gell.	Fedonkin 1983	---	---	---	---	---	---	---	---	---	---	---	---
		4	1			1		3	7				
Total number of taxa in formation (n)		2	47	43	19	20	22	19	23	11			
Total number of taxa (N = 106)		2	44	41	18	19	21	18	22				
% Biotic diversity (100n/N)													

Figure 6. Compilation of stratigraphic ranges of fossils and taxonomic diversity, in the Vendian of Podolia (Ukraine), based on data for microfossils (1-49) in Aseeva (1983), for carbonaceous megafossils (50-54) from Velikanov (1985), and for metazoans (55-94) and trace fossils (95-106) from Fedonkin (1983, 1985) and Velikanov (1985). Numbering of illustrations identical to that in table; all microfossils are illustrated, but only every fifth microfossil is numbered. Note the two interpretations of Ediacaria (fossil 64): one as a sessile, the other as a mobile cnidarian.

Four distinct microfossil assemblage zones are recognized, coinciding with the four major divisions of the Riphean/Vendian in Eurasia (Yankauskas, 1982, p. 94-95; Keller and Yankauskas, 1982). The Lower Riphean assemblage is characterized by simple, long-ranging sphaeromorphs, and the Middle Riphean assemblage by essentially the same biota except for the addition of several new sphaeromorph taxa. The Late Riphean exhibits the most taxonomic diversity, and includes many filamentous forms, most of which carry over into the Kudash division (latest Riphean), but do not reach the Vendian. The Vendian has again a smaller taxonomic diversity, and saw the introduction of a few new, large filamentous forms, before the arrival of Early Cambrian ornate acritarchs (baltisphaerids).

In Scandinavia and East Greenland a four-fold division for the Upper Riphean and Vendian is recognized (Vidal and Knoll, 1983, p. 270). The stratigraphically lowest assemblage (Upper Riphean) consists almost exclusively of sphaeromorphs. A second assemblage (placed in the Lower Vendian by these authors, but questionably equivalent to the Kudash unit, and thus likely to be considered Riphean by others) contains some persistent Upper Riphean forms, as well as the first raspberry-like microfossils (*Bavlinella*; Figure 8, polyhedral acritarchs (*Octoedrixium*, *Podolina*), acritarchs with double walls (*Pterospersimorpha*), acritarchs with processes supporting an enveloping membrane (*Vandalosphaeridium*), and strongly ornamented large sphaeromorphs (*Favososphaeridium* [= *Dicytotidium*; see Yankauskas and Mikhailova, 1986]). The third assemblage is in the

Varangian glacial interval, and has a depauperate biota, dominated by *Bavlinella* and smooth sphaeromorphs. The fourth assemblage of Late Vendian age (Valday) is characterized by thin-walled sphaeromorphs and survivors from older strata such as *Bavlinella* and filamentous forms, some of which are megascopic. The first appearance of *Granomarginata squamosa* is thought to be a particularly good datum marking the lowermost Cambrian (Vidal and Knoll, 1983, p. 272).

In China, a series of distinctive assemblages also characterizes different stratigraphic levels, following trends observed in Europe.

Of unusual interest in Precambrian biostratigraphy are the thick-walled, vasiform microfossils (melanocyrrillids) in the size range of 30-200 μm (Figure 9). Although they are considered to be encystment stages of algae (Bloeser, 1985), they also resemble tintinnids and chitinozoans, and are therefore possible protozoans and early protistan heterotrophs. Their presence has been established in at least 13 formations on four continents in the interval of 950-700 Ma (Figure 10).

Another group of microfossils, reported from beds assigned to the latest Vendian, is usually referred to the "calcareous algae". Their affinities are not clear, and the taxa are more characteristic of Cambrian and younger rocks. They include *Renalcis*, *Girvanella*, *Obruchevella*, and similar structures, and they occur in beds that are close to the Cambrian.

An important recent discovery is a biota of scaly protistan microfossils resembling chrysophytes, diatoms, and rhizopods, found

in the Tindir Group of the Yukon, apparently just above the base of the Cambrian (Allison and Hilgert, 1986). This find makes it necessary to restudy comparable objects reported by Jost (1968) from the 1 Ga old Nonesuch Shale of northern Michigan, which are thought to be contaminants by some.

Megafossils (Body Fossils)

Megafossils are the macroscopic remains of organisms, those visible to the naked eye (generally > 0.2 or 0.3 mm). They include both animal and plant fossils, as well as macroscopic structures built by microbes. It is not always possible to make the distinction clearly. **Soft-bodied Metazoa.** Over the past 120 years, many supposed metazoan remains have been described, only to be later relegated to the inorganic realm, or found to be of younger age. However, many others have withstood criticism and are now accepted as *bona fide* body fossils. The best known examples of such metazoans are found in sequences immediately underlying the Cambrian (in the Ediacaran, Vendian, or Sinian interval). Over 100 species are now known worldwide.

Although simple metazoans may have been found early on in the Newfoundland succession (*Aspidella*, Billings, 1872), these have been regarded as doubtful by many workers, but they should be restudied to ascertain whether they are not, indeed, real fossils. Unquestionable elements of the Ediacaran fauna were first collected in the period between 1908 and 1914 by P. Range and H. Schneiderhöhn in the Nama Group, in what was then the former German colony of South-West Africa (now Namibia) (Richter, 1955, p. 244). The fossils, of undetermined

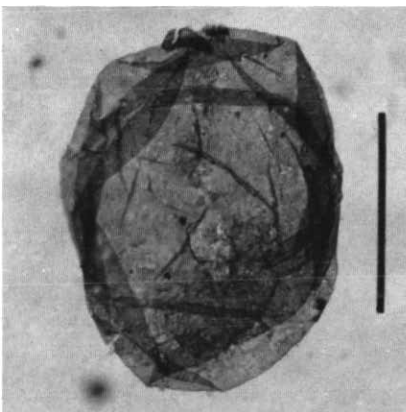


Figure 7 Leiosphaeridia, a sphaeromorph acritarch. Such vesicles are typical of Proterozoic planktonic assemblages, exhibiting a general increase in size with decreasing geologic age. This relatively large specimen is from the ~850 Ma old Red Pine Shale, Uinta Mountains, Utah, where it is found associated with *Chuarina*. Because of their size, such spheroids have also been assigned to *Chuarina*; they were previously referred to *Kildinella*. Bar scale = 100 μm .

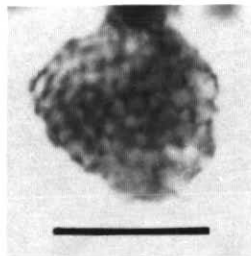


Figure 8 *Bavlinella*, a raspberry-like microfossil typical of the Early Vendian, but not restricted to this interval. Specimen from the Vampire Formation (Lower Cambrian) of the Wernecke Mountains, Yukon. Bar scale = 10 μm .

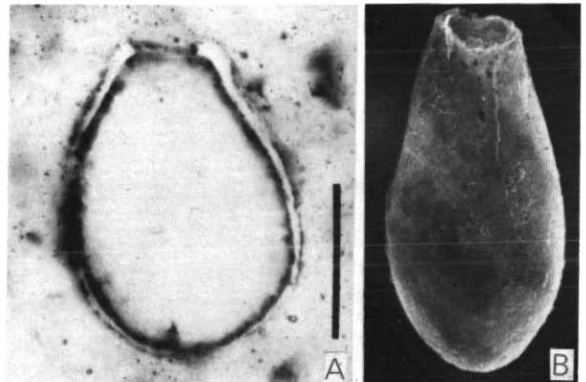
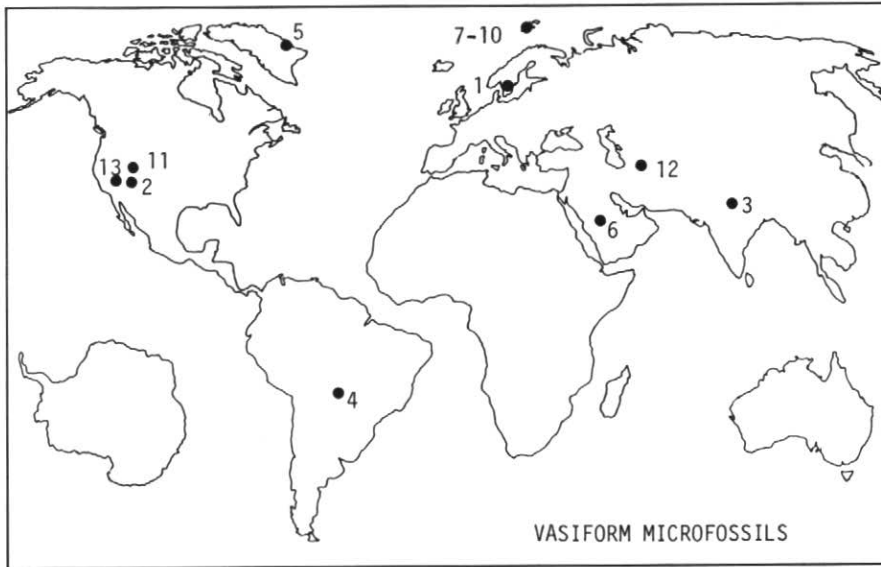


Figure 9 Vasiform Precambrian microfossils (*Melanocyrrillium*) from the Kwagunt Formation (Chuar Group), Grand Canyon, Arizona. **A:** Thin section view, courtesy of R.J. Horodyski. **B:** SEM view, courtesy of B. Bloeser. Bar scale = 50 μm .



affinities, were only later described by Gürich in the late 1920s and early 1930s (e.g., Gürich, 1930), presumably when geological attention was temporarily focussed on southern Africa because of the venue of the 12th International Geological Congress at Pretoria in 1929. At the time, the age of the Nama fossils was controversial, and both Cambrian and Precambrian assignments were considered, with a Cambrian age judged to be more likely.

The next major find of diverse soft-bodied megafossils of problematic affinities was made by R.C. Sprigg in 1946 in the Ediacara Hills in South Australia (Sprigg, 1947, 1949). Again, the initial tendency was to attribute the find questionably to the Cambrian; it also took another 10 years before its significance was accepted by others. The change of opinion appears to have been furthered by the discovery of a third significant occurrence of fossils of soft-bodied organisms, in England's Charnwood Forest region (Ford, 1958); it focussed interest on the oldest complex organisms, by this time known from three continents. Paleontologists began to restudy these poorly understood remains to ascertain their probable systematic affinities, and to determine their stratigraphic position with respect to unquestionable Cambrian sequences.

Subsequent discoveries in rocks of approximately equivalent age in Eurasia (Zaika-Novatskiy, 1965) and in Newfoundland (Figure 11; Anderson and Misra, 1968) in the 1960s, and later elsewhere (e.g., Figure 12), have resulted in a substantial accumulation of data on the morphology, and the stratigraphic and geographic distribution of more

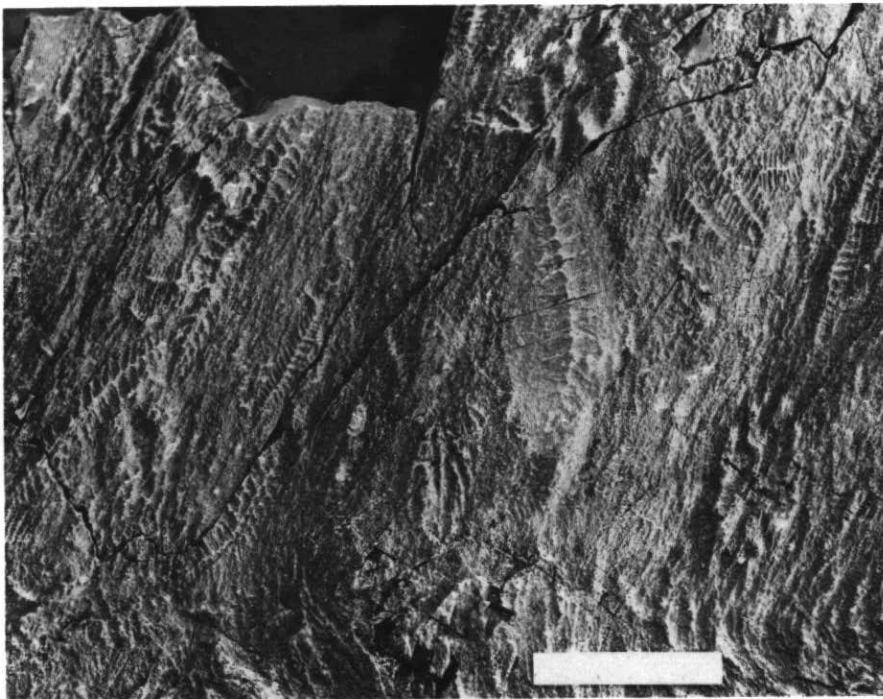


Figure 10 (upper) Known occurrences of vasiform microfossils (melanocyrrillids).

- 1 — Visingsö Fm.
- 2 — Kwagunt Fm.
- 3 — Satpuli Fm.
- 4 — Urucum Fm.
- 5 — Limestone-Dolomite Ser.
- 6 — Murdama Gp.
- 7 — Akademikerbreen Gp.
- 8 — Roaldtoppen Fm.
- 9 — Backlundtoppen Fm.
- 10 — Draken Cgl.
- 11 — Red Pine Sh.
- 12 — Taskazgan Fm.
- 13 — Beck Spring Dol.



Figure 11 (middle) Upper bedding surface view of soft-bodied metazoans from Mistaken Point, Conception Group, Avalon Peninsula, Newfoundland. Unnamed spindle-shaped forms predominate, but bushy and medusoid forms are also present. The fossils have been somewhat tectonized. Ruler is 15 cm long.

Figure 12 (lower) Ediacaran metazoans. View of lower bedding surface of low- and high-relief impressions of Beltanelliformis from the Windermere Supergroup of the Wernecke Mountains. (The high relief forms are referred to Nemiana by some authors, but complete intergradation of shapes can be observed.) (From Narbonne and Hofmann, 1987). Bar scale = 1 cm.

than two dozen localities of such fossils in the world (Figure 13), as well as speculation on the systematic relationships of the organisms. (For a recent book on the subject, see Glaessner, 1984.) The biota, best known from Australia and Europe, is still poorly understood regarding the affinities of many of its elements. It has, nevertheless, been used to correlate and date sedimentary sequences in widely separated parts of the world, much like other megafossils have served in the correlation of younger rocks. Moreover, proposals have been made to use the biota as a basis for the recognition of another Phanerozoic system/period below the Cambrian, although there is not yet any formal agreement as to its nomenclature and boundary (Jenkins, 1981; Cloud and Glaessner, 1982; Sokolov and Fedonkin, 1984; Xing, 1984). The distribution of the megafossils in the Vendian of the Ukraine is shown in Figure 6.

Carbonaceous films, including metaphytes and microbial colonies. Under this heading come ribbon-like films and regular and irregular carbonaceous compressions with round and angulate outlines. Because of a lack of distinctive characteristics other than gross shape, most of the forms are difficult to place, even at the highest hierarchical level (Kingdom). For example, a centimetre-sized oval carbon film on a bedding plane could equally well represent a compressed globular colony of a *Nostoc*-like cyanobacterium or an eucaryote. Without additional information, such as preserved microstructural details or chemical characterization, further assignment is not possible. Consequently, the broad category of carbonaceous films as used here thus includes both procaryotic and eucaryotic fossils. Until their affinities become better



Figure 14 Carbonaceous films. Association of *Chuarium* (disk) and *Tawuia* (ribbon), from Little Dal Group, Mackenzie Mountains. Bar scale = 5 mm. (From Hofmann, 1985b, p. 26).

established, the remains have been separated solely on the basis of morphology into informal categories, named after the dominant form-genus (Hofmann, 1985b):

Moranid remains: elliptical to irregularly round films without wrinkles;

Beltinid remains: irregular angulate films, broad fragments;

Vendotaenid remains: slender filamentous structures, generally unbranched, twisted or untwisted;

Eoholynid remains: aggregates of noticeably branched filaments;

Chuarid remains: thick-walled spheroids and compressed spheroids, with wrinkles more or less concentric;

Tawuid remains: compressed and uncompressed sausage-shaped forms, straight or bent, with rounded extremities and generally with marginal wrinkles;

Longfengshanid remains: oval to oblong structures with single stipe or appendage.

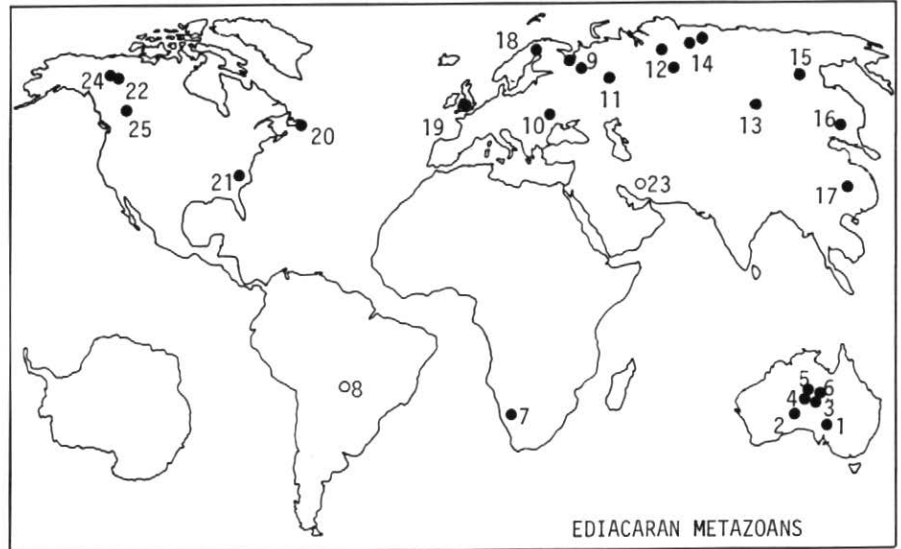


Figure 13 Known occurrences of Ediacaran fauna. Modified after Glaessner, (1984, fig. 1.8), with addition of localities 24 (Windermere Supergroup, Wernecke Mountains), and 25 (Miette Group, Rocky Mountains). Open circle where questionable.

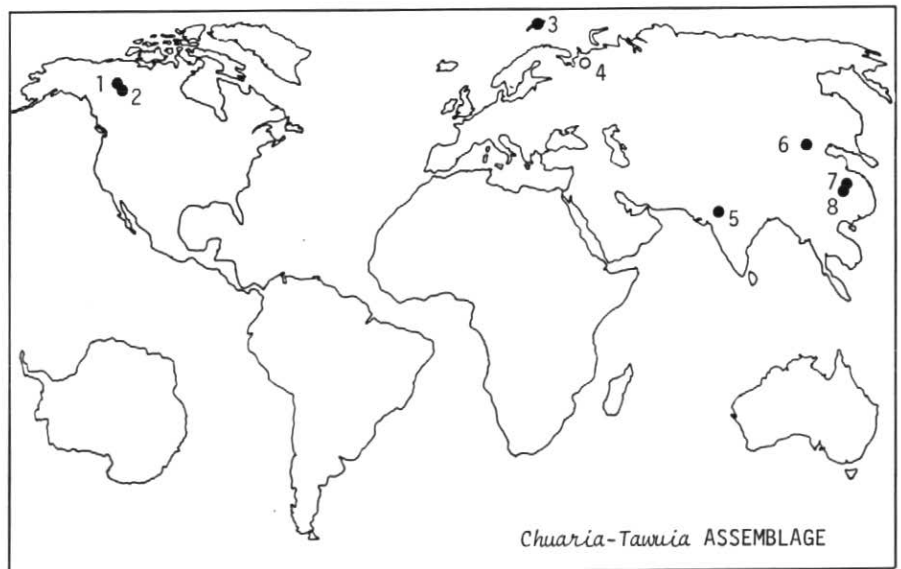


Figure 15 Known occurrences of *Chuarium-Tawuia* assemblage (after Hofmann, 1985b, fig. 2).

- 1 — Little Dal Gp., basal sequence
- 2 — Little Dal Gp., rusty shale unit
- 3 — Franklinsundet Gp., Kapp Lord Fm.
- 4 — Redkino Ser. (?)
- 5 — Semri Gp., Suket Sh.
- 6 — Qingbaikou System, Changlongshan Fm.
- 7 — Bagongshan Gp. (Huainan Gp.), Liulaobei Fm.
- 8 — Sidingshan Gp. (Feishui Gp.), Jiuliqiao Fm.

Carbonaceous compressions are known from the Precambrian of most continents, and date back to about 2.0 Ga (for a recent review, see Hofmann, 1985b). The first ones to be reported (in 1854) were vendotaenids from the Vendian of the East European Platform, now referred to the genera *Vendotaenia* and *Tyrasotaenia* (Gnilovskaya, 1971).

When one examines the stratigraphic distribution of the films (Hofmann, 1985b), one can recognize the relatively early appearance of the moranid and beltinid remains, the slightly later introduction of the vendotaenids, and the much later introduction of the others. The distribution pattern suggests some fundamental differences between taxa in the two groupings: the older ones, which lack wrinkles, could be exclusively procaryotic colonies, whereas the churoids, tawuids, and longfengshanids, which are entities with relatively thick walls and exhibit wrinkling, are more likely to be eucaryotic organisms. Some *Chuar* and *Tawuia* fossils are said to be aggregates of filamentous algae [= *Nostoc*-like cyanobacterial colonies] (Sun *et al.*, 1986, p. 389; Sun, 1987). However, filaments have not been reported from typical *Chuar* and *Tawuia*.

Although an assemblage of large curved filaments (including vendotaenids, moranids, and possible tawuids) was discovered by Walcott in the 1890s in the ca. 1.4 Ga old Belt Supergroup (Walcott, 1899; Walter *et al.*, 1976), no further occurrences have been known from that time interval to provide a basis for comparison, until the recent discovery of similar spiraliform and sinuous megafossils (named *Sangshuania*) in the coeval Wumishan Formation in northern China (Du *et al.*, 1986). These biotas may become the basis for the oldest biozone based on carbonaceous fossils.

The next youngest carbonaceous fossils of potential biostratigraphic importance are in the Late Proterozoic (<900 Ma) *Chuar*-*Tawuia* assemblage (Hofmann, 1985a, 1985b; Sun, 1987), which has so far been identified in sections in northwestern Canada, India, Svalbard, and several areas in China, all from rocks approximately 900-700 Ma old (Figures 14 and 15). *Chuar* itself is reported from many more regions, and in rocks both older as well as younger than those yielding *Tawuia* (Hofmann, 1985b, fig. 3). While the true biologic affinities of these two genera and their stratigraphic ranges remain to be established, the presence of *Tawuia* and other associated large taxa is being used empirically to make broad correlations.

In the sequences younger than about 700 Ma, narrow ribbons referred to the vendotaenids (Gnilovskaya, 1971) become much more abundant, and their twisted remains profusely cover bedding surfaces at many localities. The *Vendotaenia* assemblage characterizes this biostratigraphic interval, which coincides in part with the biozone

of the Ediacaran metazoans. Three successive floras have been recognized on the basis of carbonaceous remains within the Vendian - Early Cambrian interval in the northern part of the East European Platform (Gnilovskaya, 1985, p. 56.): a lower flora with *Eoholynia*, *Orbisiana* and *Leiothricoides*, a middle one with *Vendotaenia*, *Aataenia* and *Leiothricoides*, and a latest Vendian - Early Cambrian one with *Tyrasotaenia* and *Dvinia*.

An important recent development has been the description of megascopic carbonaceous remains attributed to worms in the 900-700 Ma sequence in the Huainan district of Anhui Province, China (Zheng, 1980; Wang, 1982). These represent the first strong evidence of pre-Ediacaran (pre-Vendian) metazoans, according to Sun *et al.* (1986). The sausage-like fossils resemble, and are associated with, *Tawuia*, but are distinguished from it by uniform, closely spaced transverse structures, which suggest that their affinities may lie with primitive worm-like organisms. There may be merit in the suggestion that the *Chuar*-*Tawuia* assemblage represents a distinct biostratigraphic zone (Hofmann, 1985a, p. 331; 1985b, p. 29). With the addition of the Huainan biotas, this zone may eventually be split into an older sub-assemblage of *Sinosabellidites* and a younger one of *Pararenicola*-*Protoarenicola* (Sun *et al.*, 1986, p. 399).

Ichnofossils (trace fossils)

The term ichnofossil refers to tracks, trails, and burrows left by mobile animals. They are formed within the sedimentary environment soon after deposition, and thus reflect ambient physical and chemical conditions, as well as the gross morphology and behaviour patterns of their originators. They also indicate the state of biologic reworking of the sediment. The widespread preservation of well laminated sediments throughout most of the Precambrian is almost exclusively related to the nonexistence of burrowing organisms, though the absence of oxygenic waters in certain environments may also have contributed, particularly after burrowers had evolved by the Late Proterozoic. The introduction of bioturbation as a geologic process must have had wide-ranging mechanical and chemical effects upon the sediments and the preservation potential of primary sedimentary structures.

The literature on Precambrian trace fossils and supposed trace fossils, which can best be described as a "mixed bag", dates back to at least 1866 (Hofmann, 1982, Table 1). Many trace fossils were formerly assumed to be bodily preserved animals or plants. There are also numerous others reported as "worm burrows" *etc.* from the Precambrian which have subsequently been relegated to the pseudofossils as inorganic (*e.g.*, see Seilacher, 1956; Cloud, 1968). Nevertheless, during the past 30 years palichnology has developed remarkably as a subdiscipline, providing insight and significant information

on animal behaviour patterns, animal-sediment relationships, paleobiology, as well as some practical applications in correlation and biostratigraphy, particularly for the Ediacaran (Vendian) - Cambrian transitional interval. Important evolutionary changes in the burrowing capacity of organisms have been documented, particularly in areas indicated in Figure 16. For a recent summary on the biostratigraphic potential of trace fossils see Crimes (1987).

While the oldest structures reported as possible trace fossils are disputed (Early Proterozoic of Wyoming; Kauffman and Steidtmann, 1981), and also many younger ones, the abundance and diversity of trace fossils in the much younger Ediacaran/Vendian sequences makes their existence at that time indisputable. These traces are characterized by their generally small diameter, simple morphology, small species diversity, and their preferential development parallel to bedding planes (*e.g.* *Gordia*, *Planolites*; see Figure 17). Cambrian and younger ichnofaunas, in comparison are characteristically larger, more diverse, morphologically more complex, and include an abundance of vertically developed burrows (for graphic summaries see Fedonkin, 1981, figs. 5, 12; Crimes and Anderson, 1985, fig. 16; Paczeńska, 1986, fig. 3; or Crimes, 1987, figs. 1-3). In fact, in sections on several continents, there are such distinct breaks in the distribution of ichnotaxa around the Ediacaran-Cambrian transition, that these breaks have been considered as potentially useful in selecting the base of the Cambrian. However, as can be seen from several recent publications, while there may be more or less distinct breaks in the assemblages, particular taxa may occur on either side of the breaks, depending on the continent under consideration (*e.g.*, *Cochlichnus*, *Bergaueria*, *Neonereites*), and the date of publication of the information (*e.g.*, compare the Cambrian and younger range of *Cochlichnus* in fig. 5 of Fedonkin, 1981, with that on p. 116 of Fedonkin, 1985, which extends down into the Vendian). There is thus additional study required to resolve these discrepancies (which are probably due to taxonomy and incomplete collecting) before the proposed equivalence of the major breaks can be accepted.

On the other hand, there appear to be distinct ichnotaxa restricted to the Ediacaran/Vendian, such as *Bilinichnus*, *Intrites*, *Nenoxites*, *Palaeopascichnus* (Figure 17c), *Vendichnus*, *Vimenites*, and the rope-like *Harlanella podolica*, while others, more complex, are considered indicative of a younger age (*Phycodes pedum*, *Plagiogmus*, *Rusophycus*, *Cruziana*, *etc.*). The ichnofossils in the Rovno and Khmel'nitz Formations of eastern Europe have more affinity with those of younger rocks than with older ones, judging from Table 2 in Fedonkin (1985, p. 116). (It is therefore puzzling that this unit should be considered Vendian instead of Cambrian

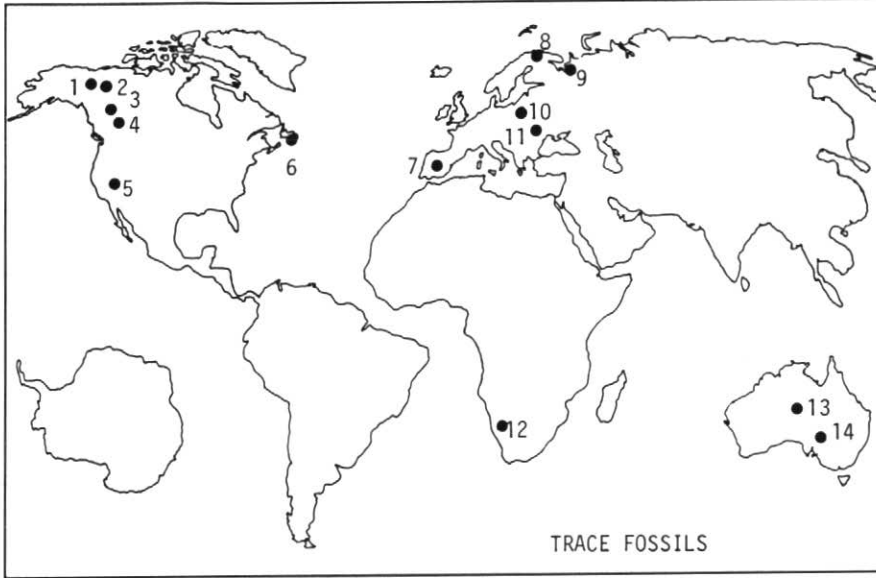


Figure 16 Occurrences of Proterozoic trace fossils in selected Ediacaran-Cambrian sections.

- 1 — Wernecke Mountains: Windermere (Ekw) Supergroup
- 2 — Mackenzie Mountains: Windermere (Ekw) Supergroup
- 3 — Cassiar Mountains: Stelkuz Fm.
- 4 — Rocky Mountains: Windermere Supergroup, Miette Gp.
- 5 — California: Wyman Fm.
- 6 — Burin Peninsula: Chapel Island Fm.
- 7 — Central and southern Spain: Pusa and San Jeronimo Fms.
- 8 — Tanafjord area: Innerelv and Mandraperelv Members
- 9 — White Sea coast: Valday "Series", Ust-Pinega Fm.
- 10 — Poland: Lublin Fm.
- 11 — Podolia: Valday "Series", Mogilev-Podolski and Kanilov Gps.
- 12 — Namibia: Nama Gp.
- 13 — Central Australia: Elkeru Fm.
- 14 — Southern Australia: Ediacaran

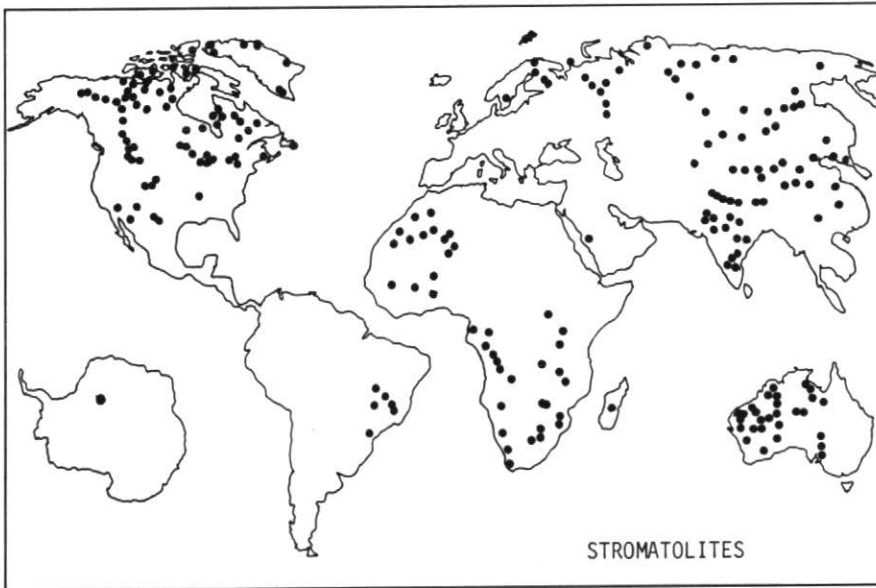


Figure 18 Reported occurrences of Precambrian stromatolites; the data are generalized, and not numbered, because the units are too numerous to list here; practically any carbonate sequence has stromatolites.

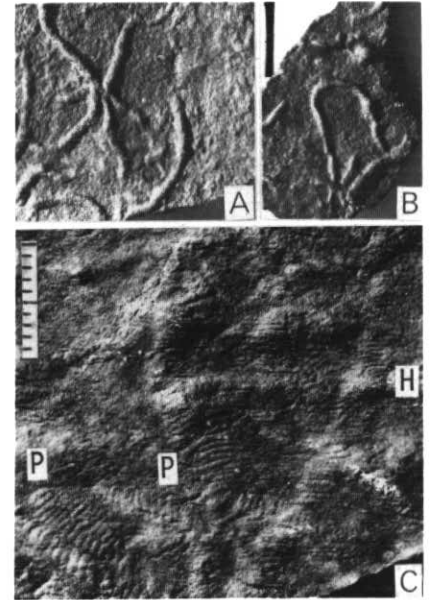


Figure 17 Simple horizontal trace fossils representative of the Ediacaran interval. A - Planolites and B - Gordia, Blueflower Fm., Wernecke Mountains, NW Canada. C - Palaeopascichnus (P) and Harlaniella (H), Chapel Island Fm., 2.2 m above base of Member 2, Fortune Head Section, Newfoundland (Narbonne et al., 1987). Scale for A and B shown in B, length = 1 cm; scale in C in mm.



Figure 19 Archaeozoon acadiense, the first Precambrian stromatolite to be treated taxonomically, from the Green Head Group, St. John, New Brunswick. This columnar branching stromatolite contains conical laminae, and strongly resembles stromatolites in Riphean Jacutophyton-Baicalia assemblages in Siberia and Mauritania. Bar scale = 5 cm.

(e.g., Sokolov and Fedonkin, 1984, figs. 1 and 4). It also seems odd and inconsistent with stratigraphic practice, that on the one hand the Rovno is assigned to the Baltic Series (a Cambrian unit), and at the same time it is placed in the Vendian System.)

Stromatolites

Stromatolites are fixed, laminated organosedimentary structures that represent the traces of integrated microbial communities. The sedimentary material accumulated by trapping or agglutination on organic mats, or by precipitation of mineral matter resulting from the metabolic activity of the microbes. The microbes are principally procaryotic (cells without membrane-bound nuclei: cyanobacteria and bacteria), although eucaryotic (nucleated cells) algae can participate in their construction.

Of all the fossils used in Precambrian biostratigraphy, they are the most widespread (Figure 18), and the most evident to field geologists; they have therefore received the greatest attention and contributed the greatest volume to the literature on this subject. They are also, together with primitive microbes, the group having the longest stratigraphic record, dating back from the present to 3.5 Ga.

The first mention of a structure of what would now be called a Precambrian stromatolite is seemingly a reference to "gryphite shell impressions", reported by Franklin in 1829 from Madhya Pradesh, India (Mathur, 1979). These, and similar structures subsequently found elsewhere, were regarded as curious and problematic fossils. It was not until 1890 that the first Precambrian stromatolite was treated taxonomically, with the erection of *Archaeozoon acadense* (Matthew, 1890) from the Proterozoic of New Brunswick (Figure 19). The word *stromatolite*

(*Stromatolith*) itself did not enter the literature until 1908 (Kalkowsky, 1908), following the earlier introduction of the spongiostrome (Spongiostromidae) concept for the microfabric of the same kinds of structures (Gürich, 1906). The number of workers studying stromatolites increased slowly over the next few decades, and some significant papers were published (see tabular summary in Hofmann, 1973, p. 343). Although attempts at determining evolutionary trends in stromatolites and their use in correlation were started by V.P. Maslov (1939, 1945), sustained biostratigraphic stromatolite only began in the late 1950s in the Soviet Union, where extensive stromatolitic Middle and Late Proterozoic sequences provided the challenge. This work eventually resulted in the recognition of four distinct stromatolite assemblages (e.g., Raaben, 1969), corresponding to a previously established lithostratigraphic scheme for the Riphean stratotype. The assemblages were subsequently recognized on other continents (e.g., Walter, 1972; Preiss, 1976). As many as eight assemblages are now identified in the Middle and Late Proterozoic of China (Liang *et al.*, 1985), and two in the Early Proterozoic (Zhu, 1982). In Karelia, the Early Proterozoic also displays multipartite subdivisions (Makarikhin and Kononova, 1983).

The standard method of studying stromatolites has been to observe and collect manageable samples, usually of branching centimetric columnar stromatolites; these are then sawn longitudinally to produce parallel, oriented serial sections of the columns. The outlines of individual columns are traced from each slab onto separate transparent sheets, which are then used to reconstruct the stromatolite graphically in an isometric projection. Shading is added according to individual

judgment. Attributes of the laminae are also determined. Large slides, somewhat thicker than normal petrographic thin sections and much larger, are prepared to permit analysis of the microstructure, as well as other features.

The standard taxonomic practice has been to erect form genera and species (respectively called *groups* and *forms*, following the suggestion of Maslov, 1953, p. 109), principally on the basis of the reconstructed shape of the columns, branching pattern, size, shape and thickness of the laminae, and microstructure; binomial Latin designations are given to different combinations of selected attributes. The method has often been used without obtaining adequate statistical data on the variability of the taxa proposed, making it difficult to differentiate between apparently overlapping ones. Also, effects of diagenesis and sedimentary environment have frequently been disregarded. Moreover, authors have been inconsistent in the use of combinations of attributes in diagnosing group-level and form-level taxa, making it difficult to decipher evolutionary trends. Endemism is a further problem (e.g., Golovenok, 1985). The result has been that, although we have a stromatolite biostratigraphy, we still have no stromatolite theory, no model that shows which attributes changed in what way through time. Stromatolite biostratigraphy remains strictly empirical, being based on the recognition of disjunct assemblages of variably defined taxa and their observed stratigraphic ranges.

However subjective the method, it seems to work, for specialists claim that broadly similar assemblages can be recognized on different continents at similar stratigraphic levels. Of most use are columnar stromatolites, which reach their greatest diversity in the Mid- and Late Riphean, while coniform stromatolites peak in the Middle Riphean (Walter and Heys, 1985). One particular group, with diameters usually less than one or two centimetres (Figure 20; ministromatolites; pseudogymnosolenids), are particularly characteristic of the Early and Middle Proterozoic (Grey, 1984). Nevertheless, despite the success of stromatolite biostratigraphy, discrepancies exist (e.g., Figure 21; see also Golovenok, 1985, p. 82). As another example, most of the Mackenzie Mountains Supergroup in northwestern Canada, which has earlier been regarded as predominantly Middle Riphean on the basis of stromatolites (Aitken *et al.*, 1978, p. 485), has more recently been dated as between 880 and 770 Ma old, based on radiometric and paleomagnetic evidence (Park and Aitken, 1986, p. 308, p. 319), which would put it well into the Upper Riphean. Stromatoliteology is in need of more objectivity in the presentation of the morphologic data, to allow trends in all morphologic, material, and dimensional attributes through time to be quantified, compared, and related (Hofmann, 1977; Zhang and Hofmann, 1982).

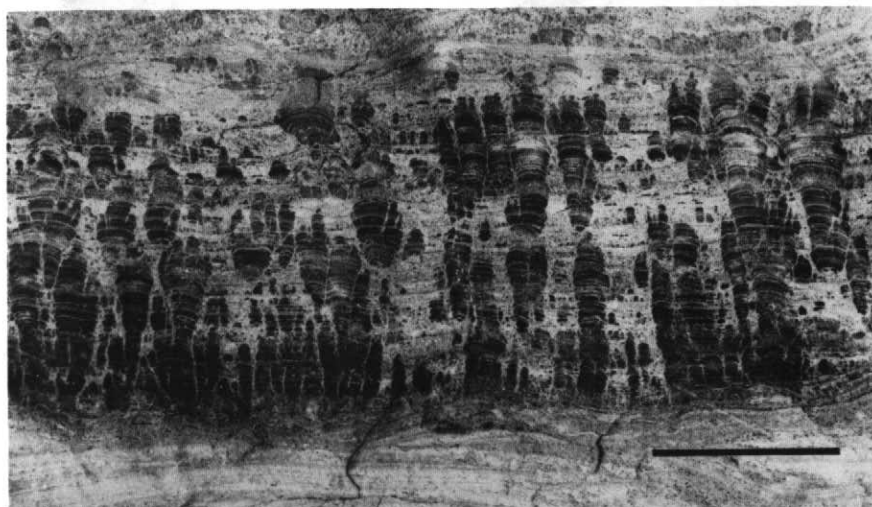


Figure 20 Ministromatolites typical of Early and Middle Proterozoic peritidal carbonate sequences, variously referred to as Pseudogymnosolen, Asperia, or calcareous tufa, from the McLeary Formation, Belcher Supergroup, Hudson Bay. Bar scale = 5 cm. (From Hofmann, 1977, p. 190)

Oncolites and catagraphs

These structures are commonly treated by Soviet specialists under the single heading "microphytolites", an unfortunate term, considering that eucaryotic photosynthesizers appear to have little if anything to do with their genesis; in hindsight, another term such as microbialite might have been a better designation. The structures are strongly facies-dependent, forming in shallow-water carbonate environments; they reflect energy conditions intermediate between those permitting microbial mat formation and those necessary for the accretion of ooids and pisoids (Swett and Knoll, 1985, p. 344).

Oncolites (oncoids) are sub-millimetric to centimetric, concentrically laminated grains, most commonly calcareous or dolomitic (Figure 22). They resemble ooids, but generally have more irregular lamination and shape. There is no unanimous opinion on the nature of these structures, whether they are biogenic or chemogenic. They are generally thought to be formed by surface accretion, by precipitation and binding of fine mineral matter, on cyanobacterial or bacterial layers that coat their surface. Oncoid growth is analogous to that of stromatolites, except that it proceeds centrifugally because of intermittent mobility of the grains in the agitated, carbonate-saturated shallow water settings where they are commonly found. The term was introduced as ONCOLITHI by Pia (1927,



Figure 21 Columnar branching stromatolite from the Lower Proterozoic Mavor Formation, Belcher Islands, Hudson Bay. These stromatolites have characteristics of some Upper Proterozoic groups such as *Gymnosolen*. Bar scale = 5 cm. (From Hofmann, 1977, p. 182).

p. 37) as a division of the SPONGIOSTROMIDAE to characterize structures that grew mobile on the substrate, in contrast to the STROMATOLITHI that grew in a fixed position.

Catagraphs are grains similar in size to oncoids, but are distinguished from them by being without concentric lamination, and having various characteristic internal fabrics that are thought to be due to microbial activity (Figures 23 and 24). Some of these grains would be called intraclasts by sedimentologists in North America; others appear to be recrystallized ooids. The grains, which can be round to angulate, often have a dark micritic boundary, suggesting that microbial boring contributed to the formation of this rind. The term was introduced by Maslov (1953, p. 111) as the "morphologic type" *Catagraphia*.

Oncolites and catagraphs were first used for regional stratigraphy in Siberia by Reitlinger (1959). She was able to distinguish a succession of three "complexes" or assemblages of taxa, which are apparently facies-controlled. These and other assemblages have subsequently been recognized elsewhere by specialists working

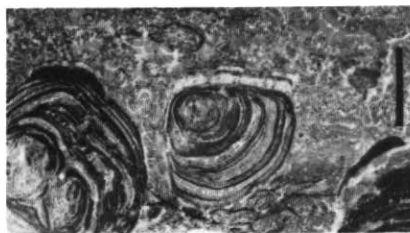


Figure 22 *Oncolites* (oncoids) referable to *Osagia*, from the Lower Proterozoic McLeary Fm., Belcher Islands. Bar scale = 1 cm. (From Hofmann, 1977, p. 192)



Figure 23 *Catagraphs* attributable to *Vesicularites*, from the Lower Proterozoic Kasegalik Formation, Belcher Islands. Bar scale = 1 mm. Such grains are intraclasts with micritic rims. (From Hofmann, 1977, p. 202)

with these remains, although carbonate petrologists outside the Soviet Union have not used them for biostratigraphic purposes because of their undetermined biogenicity. Certain groups (e.g., *Asterosphaeroides*, *Vesicularites*) originally thought to be restricted to the Late Proterozoic (Zhuravleva, 1964a, b), have since been noted in Early Proterozoic rocks. Recent tabular summaries of the stratigraphic ranges of oncolites and catagraphs are given by Zhuravleva (1982) for the Riphean of the southern Urals (Figure 4), by Golovenok (1985) for the Riphean and Vendian of Siberia, and Yakshin (1985, fig. 35) for the Riphean, Vendian, and Lower Cambrian of Siberia and eastern Europe.

As with the stromatolites, the taxonomy of oncoids and catagraphs is binomial. Morphological peculiarities and textural features are used to distinguish various taxa, likewise referred to as groups and forms. Diagenesis complicates taxonomy, and oncolite-catagraph biostratigraphy is also strictly empirical.

Chemofossils

This category comprises chemical evidence of the ancient biosphere, biogenic materials studied by chemical means. Long ago, the presence of elemental carbon (graphite) in sedimentary and metasedimentary rocks was taken as testimony of the existence of Precambrian life (e.g., Dawson, 1870). With the invention of the mass spectrometer by A.O. Nier in the 1930s, it became possible to analyze isotopic compositions of the elements, including those of importance in life cycles of organisms and their remains.

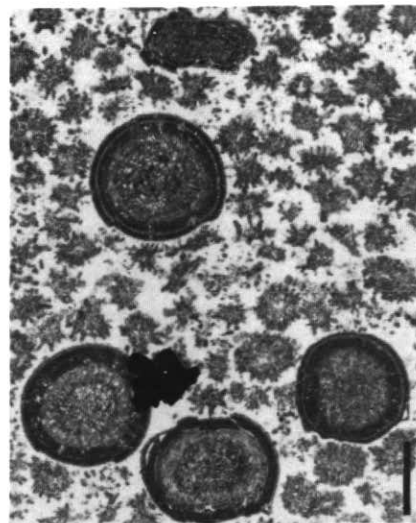


Figure 24 *Catagraphs* from the Lower Proterozoic Nastapoka Group, east coast of Hudson Bay. The larger structures, referred to *Radiosus* and the smaller ones, referred to the taxon *Asterosphaeroides* (*Nelcanella*), probably represent a bimodal assemblage of recrystallized ooids. Bar scale = 1 mm. (From Hofmann, 1977, p. 202)

Of particular interest here is carbon, whose light isotope, ^{12}C , is preferentially accumulated in organic matter during carbon fixation by autotrophs, chiefly by photosynthesis, leaving ^{13}C -enriched dissolved carbon in the ambient medium. As a result, carbonate minerals forming in the same environment as the coexisting organic matter are enriched in ^{13}C by an amount generally of the order of 20-30 per mil with respect to the organic carbon.

Curves showing the variation of the isotopic composition of organic matter, and of carbonate, over geologic time are most complete for the Phanerozoic, but have lately seen some significant input of data for the Precambrian (Schidlowski *et al.*, 1983). The values for the carbonate record exhibit little variation, whereas there is marked scatter for the kerogen, which reflects both primary and diagenetic and metamorphic effects. The difference between values for organic matter and carbonate ($\delta^{13}\text{C}_{\text{carbonate}} - \delta^{13}\text{C}_{\text{organic}}$) for each particular geologic epoch has consistently been about 25 per mil over the past 3.5 Ga, which has been interpreted as indicating the continuous existence of a biologically mediated fractionation processes (enzymatic carboxylation of CO_2 in the Calvin cycle) over this time interval.

The most recent application of C-isotope geochemistry to Precambrian stratigraphy is the study of closely spaced samples from stratigraphically continuous sequences (e.g., Tucker, 1986; Magaritz *et al.*, 1986; Knoll *et al.*, 1986; Aharon *et al.*, 1987). Because of the close spacing, and therefore great temporal resolution, it has been possible to determine short-range fluctuations in the isotope ratios, allowing comparisons to be made with other continuous sections.

This method is of interest not only for intra-basinal chemostratigraphic correlation, but also with respect to larger questions concerning events and processes in the global evolution of the biosphere and the atmosphere. Increases in primary organic productivity and burial rates of ^{12}C -enriched organic carbon both cause shifts towards a heavier isotopic composition of total dissolved carbon remaining in the water and of carbonate that precipitates from it; however, an enrichment in heavy carbon can also be caused by evaporitic conditions (e.g., Schidlowski *et al.*, 1984). Increases in burial rates of organic carbon would have been associated with significant positive shifts in the redox potential by a corresponding increase in O_2 in the environment, unless the excess reducing capacity was taken up by reductants such as iron or sulphur.

The curves presented by Knoll *et al.* (1986) show an enrichment of ^{13}C for most of the Late Riphean carbonates as well as kerogens, with brief periods of depletion, followed by an isotopically light Vendian interval, and a shift back to heavy composition near the base of the Cambrian. The data for the earlier geologic record are more scattered, but do show an

interval of isotopically abnormally light values for organic carbon in the Late Archean (Schidlowski *et al.*, 1983, p. 158).

It is too early yet to come to firm conclusions as to the significance of these isotopic variations and how they relate to data provided by paleontology. Further studies involving close sampling in additional continuous sequences, particularly of Early and Middle Proterozoic age is required. Similar high-resolution work on other biologically interesting isotopes, particularly of sulphur, and probably of nitrogen, would complement that on carbon. Combined, the data could provide a stronger support for particular hypotheses of the history of life and its environment.

The other major group of chemofossils includes organic compounds, fossils of molecular size. The abiogenic synthesis of amino acids in the early 1950s by S.A. Miller soon led to suggestions that organic geochemistry could play an important role in illuminating the evolution of the biosphere, and would supplement paleontological investigations. Many papers followed in the 1950s and 1960s, describing the organic constituents of the ancient rocks, and the concepts of molecular fossil, molecular paleontology, and biological marker compounds had become established. For a comprehensive review of organic geochemistry of the Precambrian for that period, see McKirdy (1974). The precise analytical techniques, developed in part for the lunar rock samples returned by the Apollo space program, have become so refined as to be capable of detecting and characterizing nanomole quantities of biochemical compounds. Some of these compounds can be attributed to specific taxonomic groups of organisms, such as the breakdown products of chlorophyll (pristane, phytane) to photosynthesizers, pentacyclic triterpanes derived from membranes of bacteria, and steranes indicative of eucaryotes. Complementary work in biochemical phylogeny, particularly the sequencing of DNA and RNA components of living organisms, has led to new perspectives on old lineages.

Trace quantities of carbonaceous material are not the only materials available for study. Seeping liquid hydrocarbons have long been known from the 1 Ga old Nonesuch Shale in Michigan. The recent discovery of oil in the 1.4 Ga old Valkerie Fm. of the Roper Group in Northern Australia (Anonymous, 1985) extends the observed geologic record of petroleum by 40%, to more than double the time interval of the Phanerozoic.

It has been found that the hydrocarbons analyzed from sediments older than about 1 Ga are less complex than younger ones, and are dominated by normal, methyl-branched alkanes and cyclohexylalkanes; steranes, which are generally markers for eucaryotic organisms, are either extremely low, or cannot be detected at all (Summons, 1986). This provides independent support of the inferred evolutionary trend in microbial

evolution based on morphological evidence gathered by paleontologists.

Biochemistry and biogeochemistry can be expected to play an increasingly important role in the study of ancient life.

Summary and Conclusion

Not only are fossils abundant in rocks predating the Cambrian, but they also exhibit great taxonomic diversity, though perhaps not quite as great as one may be led to conclude by scanning fossil lists, because of possible synonyms. The five most common groups (stromatolites, microfossils, oncolites/cata-graphs, megafossils, and trace fossils) have been used biostratigraphically. Precambrian biostratigraphy is still a very young sub-discipline of geology, and the schemes developed will no doubt undergo modifications as the ranges of taxa change with new observations, or as a result of taxonomic revisions. No universally accepted biozonation has yet emerged, and the divisions, as well as the names for them, are essentially regional in scope. There also is some rivalry between competing sections.

Thus far, the stromatolite category has shown the greatest morphologic diversity over the longest span of time, and it has therefore been the most widely applied. Much of the early work in Precambrian biostratigraphy was done in the Soviet Union, leading to the recognition of a four-fold division of the Riphean and the Vendian/Yudomian; stromatolite sequences elsewhere were subsequently compared with those in Eurasia, and corresponding ages were assigned to the correlated sequences.

Stromatolite biostratigraphy is nonetheless beset with difficulties in certain respects, such as taxonomy, and the fact that stromatolites are biosedimentary structures, rather than simply biologic structures. Much remains to be done to clarify the effects sedimentary processes and environmental conditions had on the attributes of the ancient stromatolites. The taxonomy is in need of revision. This is a daunting task that will require a knowledge of Russian and Chinese, because most of the taxa were described in these two languages. It will further require comparison of material from various institutes where type specimens are housed. It may also be useful to restudy material with the aim of quantifying the attributes, using modern equipment for morphometric analysis, in order to determine secular trends in morphology. While stromatolite biostratigraphy seems to work in general, it is still advisable to be cautious, as several anomalies attest.

Precambrian microfossils are relatively simple in morphology, but offer good potential, particularly for the Late Proterozoic. Here, too, taxonomic revision is now under way, and stratigraphic charts will change as a result. Data such as shown in Figures 3 and 5-6 can be expected to experience modification as a result.

Megafossils and trace fossils probably have the greatest biostratigraphic potential for the latest Precambrian (Sinian-Vendian-Ediacaran). In the last few years many new data have been published, and general patterns are emerging as these faunas become better known. Metaphytes in the Vendian also aid in the identification of biozones.

A pre-Ediacaran interval with carbonaceous compressions and vasiform microfossils is potentially recognizable, though much more work will be required before it is accepted.

Shelly fossils make their appearance near the base of the Cambrian, and are, of course, the chief biostratigraphic tools for the Paleozoic.

Oncolites and catagraphs, while widely used in the Soviet Union, have not yet been evaluated for biostratigraphy by similar studies on other continents. The reticence by geologists outside the Soviet Union appears to be related to the questionable biogenic nature of most of these structures.

Biogeochemistry is developing as a promising new area of research for Precambrian biostratigraphy.

Acknowledgements

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