

## Geological Society of America Bulletin

### Integrated chemostratigraphy and biostratigraphy of the Windermere Supergroup, northwestern Canada: Implications for Neoproterozoic correlations and the early evolution of animals

GUY M. NARBONNE, ALAN J. KAUFMAN and ANDREW H. KNOLL

*Geological Society of America Bulletin* 1994;106, no. 10;1281-1292  
doi: 10.1130/0016-7606(1994)106<1281:ICABOT>2.3.CO;2

---

**Email alerting services**

click [www.gsapubs.org/cgi/alerts](http://www.gsapubs.org/cgi/alerts) to receive free e-mail alerts when new articles cite this article

**Subscribe**

click [www.gsapubs.org/subscriptions/](http://www.gsapubs.org/subscriptions/) to subscribe to Geological Society of America Bulletin

**Permission request**

click <http://www.geosociety.org/pubs/copyrt.htm#gsa> to contact GSA

Copyright not claimed on content prepared wholly by U.S. government employees within scope of their employment. Individual scientists are hereby granted permission, without fees or further requests to GSA, to use a single figure, a single table, and/or a brief paragraph of text in subsequent works and to make unlimited copies of items in GSA's journals for noncommercial use in classrooms to further education and science. This file may not be posted to any Web site, but authors may post the abstracts only of their articles on their own or their organization's Web site providing the posting includes a reference to the article's full citation. GSA provides this and other forums for the presentation of diverse opinions and positions by scientists worldwide, regardless of their race, citizenship, gender, religion, or political viewpoint. Opinions presented in this publication do not reflect official positions of the Society.

---

**Notes**

# Integrated chemostratigraphy and biostratigraphy of the Windermere Supergroup, northwestern Canada: Implications for Neoproterozoic correlations and the early evolution of animals

GUY M. NARBONNE *Department of Geological Sciences, Queen's University, Kingston, Ontario, Canada K7L 3N6*  
 ALAN J. KAUFMAN }  
 ANDREW H. KNOLL } *Botanical Museum, Harvard University, Cambridge, Massachusetts 02138*

## ABSTRACT

The thick, richly fossiliferous succession of the upper Windermere Supergroup, Mackenzie Mountains, northwestern Canada, provides a test of integrated biostratigraphic and chemostratigraphic frameworks in terminal Proterozoic correlation. The C- and Sr-isotopic abundances of lower Keele Formation carbonates approximate those for other pre-Varanger samples, confirming that the simple disc-like fossils of the underlying Twitya Formation predate all known diverse Ediacaran faunas. "Tepee" and Sheepbed carbonates record strong post-glacial isotopic excursions; in contrast,  $\delta^{13}\text{C}$  values for Gametrail through Risky carbonates vary only within the narrow range of about +1‰ to +2‰. A second negative excursion occurs in Ingta Formation carbonates that immediately underlie the paleontologically determined Precambrian-Cambrian boundary. The upper Windermere profile as a whole compares closely with curves determined for other terminal Proterozoic successions. The lowermost diverse Ediacaran assemblages in the Sheepbed Formation correlate chemostratigraphically with the oldest fauna in Namibia, but the two assemblages differ in taxonomic composition. Blueflower assemblages correlate both chemostratigraphically and taxonomically with faunas from Australia, China, Siberia, and elsewhere. Increasing data support the hypothesis that paleontological and geochemical data together provide a reliable means of correlating terminal Proterozoic sedimentary rocks throughout the world.

## INTRODUCTION

In studies of Phanerozoic rocks, biostratigraphy is the cornerstone of correla-

tion. Nonbiological correlation techniques such as magnetostratigraphy and chemostratigraphy play important roles, but both provide oscillating rather than vectorial signals, making them difficult to interpret in the absence of biostratigraphic constraints. Events are commonly discussed in terms of absolute time, although few sedimentary successions have been dated directly. Estimates of absolute age are possible because the chronostratigraphic scale can be calibrated radiometrically in a few key sections.

A similar approach is possible for Neoproterozoic (1000–545 Ma) stratigraphy, although the limited distribution and diversity of fossils requires a more integrative approach, with greater reliance on nonbiological techniques. Chemostratigraphy, particularly variations in the C- and Sr-isotopic compositions of carbonates, can provide sig-

nificant stratigraphic information (for example, Knoll and others, 1986; Kaufman and others, 1991; Kirschvink and others, 1991). The C isotopes show particular promise for the correlation of terminal Proterozoic (ca. 610–545 Ma) strata. The global composite curve illustrated in Figure 1, slightly modified from Knoll and Walter (1992), shows strong negative and positive excursions following the Varanger ice age and near the Proterozoic-Cambrian boundary, with smaller variation in the connecting interval. This suggests that C isotopes can be useful in subdividing and correlating terminal Proterozoic successions. However, because the curve is not monotonic, these data must be supplemented by Sr-isotopic data (which vary only within narrow limits during most of the post-Varanger Proterozoic; Kaufman and others, 1993) and biostratigraphy.

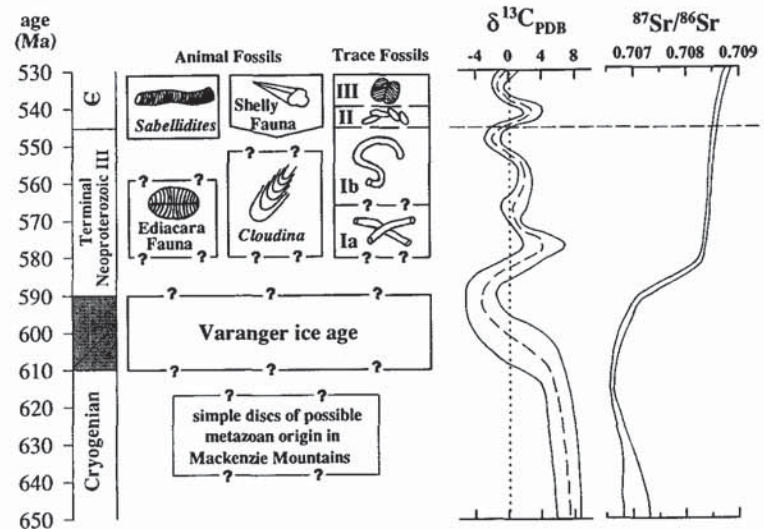


Figure 1. Global composite of Neoproterozoic-subtrilobite Cambrian stratigraphy (after Knoll and Walter, 1992, Fig. 3).

Data Repository item 9434 contains additional material related to this article.

Geological Society of America Bulletin, v. 106, p. 1281–1292, 5 figs., 2 tables, October 1994.

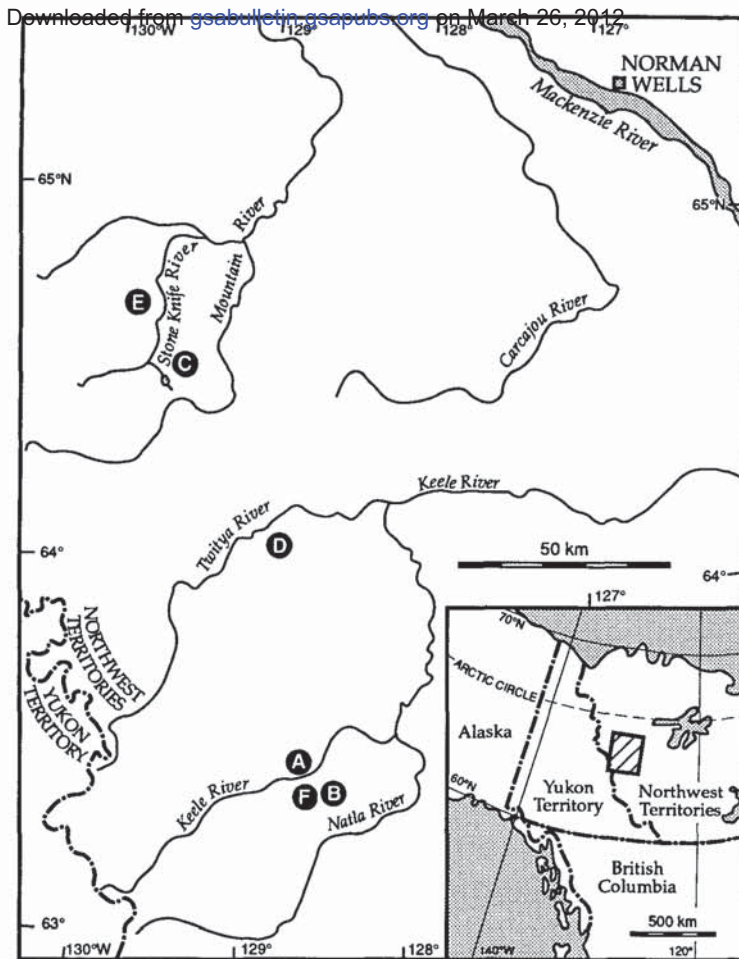


Figure 2. Location of sections studied.

Given the increasing resolution of stratigraphic ranges for terminal Proterozoic acritarchs (for example, Knoll, 1992b), trace fossils (Crimes, 1987; Narbonne and Myrow, 1988) and, to a lesser extent, metazoans (Sokolov and Fedonkin, 1984), an integrated bio- and chemostratigraphic framework offers the most promise for accurate correlation of both terminal Proterozoic (Knoll and Walter, 1992) and basal Cambrian (Kirschvink and others, 1991; Brasier and others, 1990) strata.

Thick, lithostratigraphically well-described sections containing both fossils and carbonates offer critical tests of proposed chronostratigraphic relationships (Knoll and Walter, 1992). The Mackenzie Mountains of northwestern Canada (Fig. 2) contain a thick succession of Neoproterozoic to Lower Cambrian strata that includes siliciclastic rocks with abundant Ediacara-type fossils and trace fossils (Hofmann and others, 1990; Narbonne and Aitken, 1990; Mac-

Naughton and Narbonne, 1992) interbedded with carbonate strata suitable for isotopic analysis. In this paper, we present new data on the C isotopic composition of upper Windermere Supergroup carbonates from the Mackenzie Mountains and evaluate these in light of fossil distributions in the same succession and chronostratigraphic data from other terminal Proterozoic sections.

**GEOLOGICAL SETTING**

The Neoproterozoic-Cambrian succession of the Mackenzie Mountains (Fig. 3) is thick and only moderately deformed. Acritarchs are dark, but with excellent preservation of spiny processes (Baudet and others, 1989), implying relatively minor metamorphism. Although the strata are predominantly siliciclastic, carbonates occur commonly as discrete formations and as interbeds within siliciclastic units. Most of

the carbonates are deep-water slope limestones that show no field or petrographic evidence of meteoric diagenesis. The Mackenzie Mountains exhibit an exceptionally complete record of early metazoan evolution, and the presence of diverse fossil assemblages—including Ediacaran megafossils, ichnofossils, and small shelly fossils—facilitates biostratigraphic correlation. These factors make the Mackenzie Mountains perhaps the best locality in North America for a chemostratigraphic study of the terminal Neoproterozoic.

**Lithostratigraphy**

Strata considered in this study consist of the upper part of the Neoproterozoic Windermere Supergroup and overlying Lower Cambrian deposits (Fig. 3). Placement of the lower and upper boundaries of the Windermere in northwestern Canada has varied somewhat with new stratigraphic and paleontologic discoveries; in this paper, the term

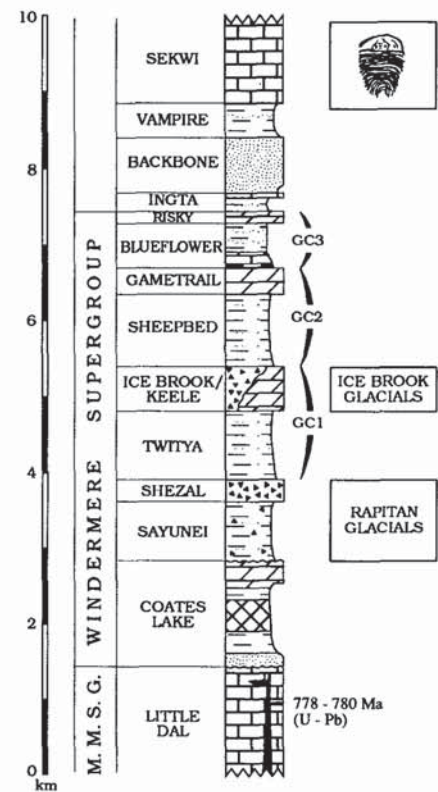


Figure 3. Neoproterozoic-Lower Cambrian stratigraphy in the Mackenzie Mountains. Brackets mark the three "grand cycles" (GC) described in the text. MMSG = Mackenzie Mountains Supergroup. The trilobite symbol denotes the presence of Lower Cambrian trilobites in the Sekwi Formation.

“Windermere” will be used to encompass all strata from the base of the Coates Lake Group to the top of the Risky Formation (Narbonne and Aitken, in press). A maximum age is provided by dikes, sills, and plugs dated at 778–780 Ma (U-Pb on zircons and baddeleyite) that cut the unconformably underlying Mackenzie Mountains Supergroup (Jefferson and Parrish, 1989; Heaman and others, 1992); the top of the Windermere is traditionally placed at the base of the lowermost formation containing Cambrian fossils (Eisbacher, 1981).

In the western part of the Mackenzie Mountains, the Windermere Supergroup is ~5–6 km thick (Fig. 3). It can be divided into two distinct successions (Ross, 1991; Aitken, 1991b). The lower succession, not sampled in this study, consists of nonmarine to shallow marine siliciclastics, carbonates, and evaporites of the Coates Lake Group (Jefferson and Ruelle, 1986; Jefferson and Parrish, 1989) overlain by the glaciogenic deposits of the Rapitan Group (Eisbacher, 1978; Yeo, 1981). These deposits accumulated in rift basins that may reflect the initial stage of plate separation along the western margin of Laurentia (Ross, 1991).

The upper succession of the Windermere Supergroup oversteps the grabens filled by the lower succession, and presumably represents post-rift regional subsidence on a passive margin (Ross, 1991). The upper succession consists of three, kilometer-scale, siliciclastic to carbonate “grand cycles” composed of, in ascending order, the Twitya-Keele, Sheepbed-Gametrail, and Blueflower-Risky Formations (Aitken, 1989, 1991b).

The lowermost “grand cycle” (GC1 on Fig. 3) is composed of intermediate- to deep-water siliciclastic rocks of the Twitya Formation that pass upward into carbonates of the Keele Formation (Aitken, 1991b). The Twitya Formation consists predominantly of siliciclastic mudstone with lesser amounts of turbiditic sandstone and channel-fills of granule conglomerate. In platform areas, the Keele Formation consists entirely of shallow-water limestone and dolostone interbedded with fine siliciclastic rocks on a meter to decameter scale. Near the shelf edge, these deposits are overlain by a lowstand deposit that consists predominantly of fluvial and shallow marine sandstone with thin packets of shallow marine carbonate.

The Ice Brook Formation (Aitken, 1991b) is composed of diamictites that were mainly deposited seaward of the Keele shelf edge. The Stelfox Member of

the Ice Brook Formation contains striated clasts, dropstones, till pellets, and other features typical of glaciomarine deposition; these represent deposits of a second Neoproterozoic glaciation in northwestern Canada (Aitken, 1991a, 1991b). Diamictites locally onlap platform carbonates of the Keele, but the temporal relationship between the Keele lowstand wedge and the Ice Brook diamictite remains uncertain.

The Keele and Ice Brook Formations are overlain by a thin but widespread unit informally known as the “Tepee dolostone” (Eisbacher, 1981; Aitken, 1991b), which is strikingly similar to the “cap dolomites” reported from Marinoan glacial deposits in West Africa (Deynoux and Trompette, 1976), South Australia (Williams, 1979; Lemon and Gostin, 1990), and East Greenland and Spitsbergen (Fairchild and Hambrey, 1984). The “Tepee dolostone” is predominantly a very finely crystalline buff dolostone, but at several localities preserves original limestone, including neomorphosed aragonite fans and rosettes.

The middle “grand cycle” (GC2) is entirely of deep-slope origin, and it consists of siliciclastic mudstone, turbiditic sandstone, and minor carbonate of the Sheepbed Formation that pass upward into ribbon-bedded dolostone of the Gametrail Formation (Aitken, 1989; Narbonne and Aitken, 1990). Carbonates in the Sheepbed Formation are almost entirely limestone and are composed of beds of ribbon-bedded lime mudstone, boulders and slide blocks of slope and shelf-edge limestone, and beds of resedimented ooids. Sheepbed carbonates show little evidence of alteration during burial diagenesis, but the Gametrail Formation has been completely dolomitized and contains gash-fills of saddle dolomite suggestive of hydrothermal activity (compare with Radke and Mathis, 1980).

The uppermost “grand cycle” (GC3) consists of the upper-slope Blueflower Formation and the overlying shallow-shelf Risky Formation (Aitken, 1989; Narbonne and Aitken, 1990). The Blueflower Formation is composed mainly of siliciclastic mudstone and turbiditic sandstone. Thick units of ribbon-bedded lime mudstone are common in the lower half of the formation; carbonates are rare in the upper half of the formation and are restricted to boulders and slide blocks of shelf-edge limestone. The Risky Formation is predominantly finely to medium-crystalline dolostone with a few patches of relict limestone. The top of the Risky Formation is a karstic disconformity that marks

the top of the Windermere Supergroup (Narbonne and Aitken, in press).

The overlying Ingta Formation consists predominantly of fine siliciclastic rocks of shallow-shelf origin (Aitken, 1989). Thin beds of lime mudstone, commonly intraclastic, occur sporadically near the base of the formation. The uppermost unit of the formation is a 25-m-thick complex of stromatolitic and oolitic limestones that have been variably dolomitized along strike. The top of the Ingta Formation is locally cut by small channels.

Overlying the Ingta Formation is the Backbone Ranges Formation, which consists of nonmarine and shallow marine quartz sandstone and siltstone (Fritz and others, 1983; Aitken, 1989). A single meter-thick bed of marine dolostone (locally limestone) occurs low in the formation. The Backbone Ranges Formation and the overlying Vampire Formation are ~1 km thick and pass gradationally upward into the trilobite-bearing carbonates of the Sekwi Formation (Fig. 3).

#### Lithostratigraphic and Sequence Correlation

Eisbacher (1985) and Young (1992) correlated the Rapitan glacial deposits of the Mackenzie Mountains with the Sturtian glaciation of Australia, based largely on general lithologic and stratigraphic similarity and the presence of thick, Fe-formation deposits in both regions. Both authors also suggested that the level of the Ice Brook diamictite is equivalent to the Marinoan glacial deposits in Australia. These correlations are supported by the biostratigraphic and chemostratigraphic evidence presented below; however, correlation of glacial levels is only useful in the lower part of the Windermere Supergroup, and attempted intercontinental lithologic and sequence correlations of higher Windermere strata by Eisbacher (1985) and Young (1992) reached conclusions quite different from those of the present study.

The other significant lithostratigraphic correlation is Young’s (1982) correlation of the Keele Formation with Unit 5 of the upper Tindir Group near the Yukon-Alaska border. Carbonates in upper Tindir Unit 5 were subsequently shown by Kaufman and others (1992) to exhibit C and Sr isotopes typical of the late Riphean (sub-Varanger); as shown below, Keele carbonates are isotopically similar to samples from Tindir Unit 5, consistent with Young’s (1982) correlation.

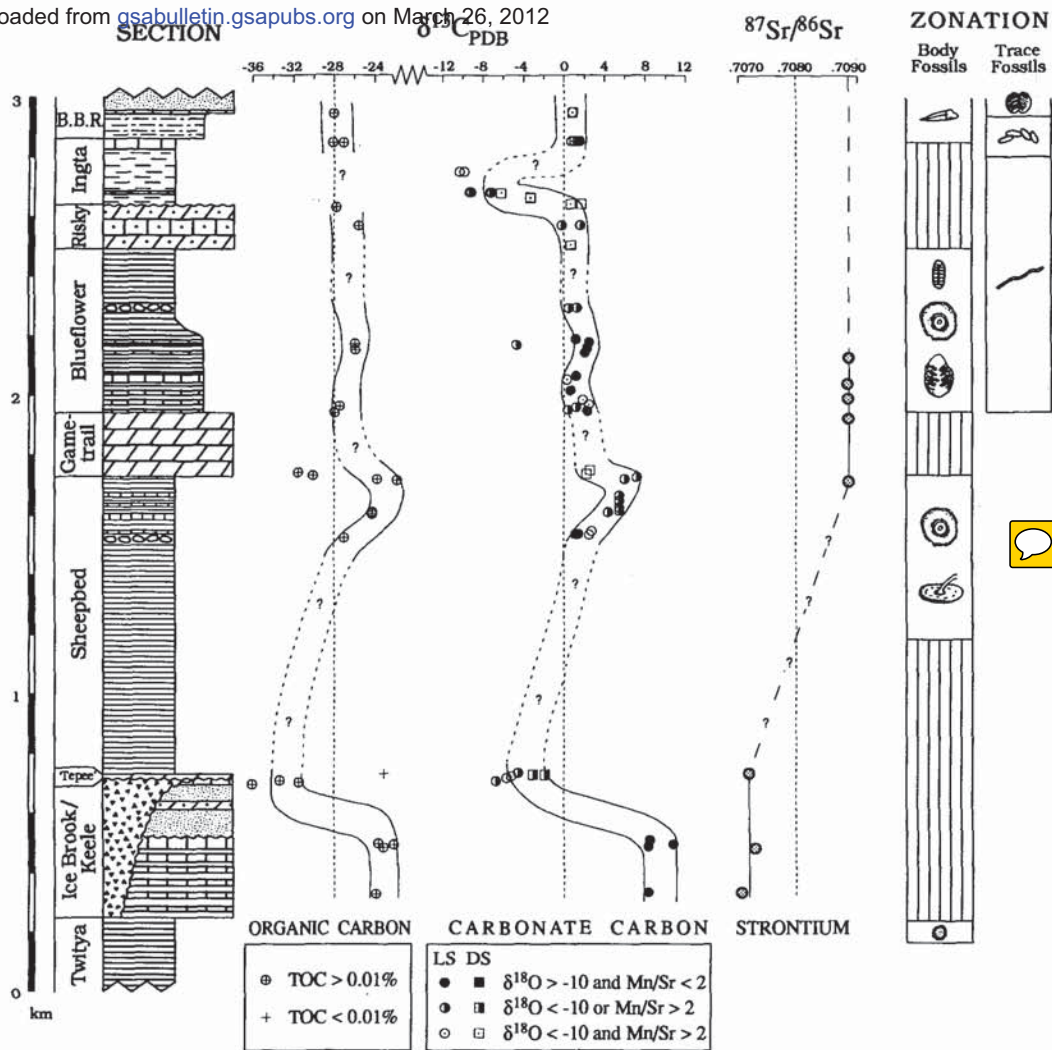


Figure 4. Integrated chemostratigraphy and biostratigraphy of Neoproterozoic (upper Windermere Supergroup) and subtrilobite Lower Cambrian strata in northwestern Canada. See the text for explanation of the fossil zones.

**Biostratigraphy**

Acritarchs occur throughout this succession but have thus far been studied only at a reconnaissance level. The Sheepbed and Blueflower Formations have yielded low-diversity assemblages of simple sphaeromorphs consistent with a terminal Proterozoic age, whereas the Vampire Formation contains a diverse assemblage of typical Early Cambrian acritarchs (Baudet and others, 1989).

Ediacara-type megafossils and ichnofossils are abundant and well described, and several distinct assemblages can be recognized (Fig. 4). The lowest Ediacara-type remains consist of a low-diversity assemblage of centimeter-scale discs and rings that occurs in the upper part of the Twitya Forma-

tion (Hofmann and others, 1990). Three taxa have been described: *Nimbia oclusa*, *Vendella?* sp., and *Iridinitus?* sp. These appear to be similar to the simplest (most primitive?) elements of the Ediacara fauna in the Russian Platform but lack the larger and more complex forms typical of the Ediacara fauna worldwide. The Twitya assemblage is significant in being the only known occurrence of even simple Ediacara-type remains below Proterozoic glacial deposits (Hofmann and others, 1990).

A more diverse assemblage of Ediacara-type fossils occurs in the Sheepbed Formation, where nine genera of centimeter- to decimeter-scale discoidal megafossils (for example, *Ediacaria*, *Medusinites*, and *Himalora*) are present (Narbonne and Aitken, 1990; Narbonne, 1994). The thick-bed-

ded dolostones of the Gametrail Formation apparently lack megafossils, but a diverse assemblage occurs in the overlying Blueflower Formation (Hofmann, 1981; Narbonne and Aitken, 1990; Narbonne, 1994). The Blueflower assemblage consists of nine genera of simple, subhorizontal trace fossils (for example, *Planolites* and *Helminthoidichnites*), along with discoidal fossils similar to those reported from the Sheepbed Formation, frond-like fossils, and a segmented fossil reminiscent of the dickinsoniids. Most of the taxa have an intercontinental distribution and thus have considerable potential for global biostratigraphy. The closest comparisons are with the Ediacara Member in the Adelaide “geosyncline” of (compare with Glaessner and Wade, 1966; Jenkins, 1992) and with the Redkino “series” of the Ven-

dian in the Russian Platform (Fedonkin, 1985a, 1985b, 1992). These assemblages contain virtually all of the Windermere taxa as well as forms not yet known from northwestern Canada.

The uppermost unit of the Windermere Supergroup, the Risky Formation, is composed mainly of thick-bedded dolostones that are not conducive to fossil preservation. Sandy interbeds contain simple burrows consistent with a terminal Neoproterozoic age.

The overlying Ingta Formation was formerly regarded as terminal Neoproterozoic in age (Aitken, 1989), but subsequent fossil discoveries indicate that it contains the Precambrian-Cambrian boundary (MacNaughton and Narbonne, 1992; Narbonne and Aitken, in press). The lower two-thirds of the formation contains abundant small, simple burrows (for example, *Helminthoidichnites* and *Planolites*) on virtually every bedding plane; a few centimeter-wide, unbranched feeding burrows occur near the base. Several ichnospecies of *Phycodes*, including *P. pedum*, and other branching feeding burrows occur ~80 m below the top of the formation and can be used to recognize the basal Cambrian *P. pedum* Zone (compare with Narbonne and others, 1987; Narbonne and Myrow, 1988). The lowermost definite shelly fossils in the Mackenzie Mountains, a single specimen of the protoconodont *Protoherztina* cf. *P. anabarica* along with several problematica (Conway Morris and Fritz, 1980), occur in carbonates now regarded as the top of the Ingta Formation (Aitken, 1989). More recent studies of this level by G. S. Nowlan (1993, personal commun.) have revealed additional taxa of simple, small shelly fossils of Nemakit-Daldyn aspect. The first appearance of the trilobite burrow *Rusophycus* low in the Backbone Ranges Formation marks the base of the *R. avalonensis* Zone, which constitutes the upper part of the subtrilobite Cambrian.

## GEOCHEMICAL PROCEDURES

Protocols followed in sample preparation and analysis are described in Appendix 1. More detailed discussion and justification for these protocols can be found in Derry and others (1992) and Kaufman and others (1991, 1993).

## RESULTS

### Evaluation of Signal Quality

All carbonates contain both  $^{13}\text{C}$  and  $^{12}\text{C}$ ; therefore, any carbonate sample fed into a

mass spectrometer will provide a  $\delta^{13}\text{C}$  value. The important question is whether the measured  $\delta^{13}\text{C}$  principally reflects the isotopic composition of the seawater from which the carbonate was precipitated, diagenetic inputs, or metamorphism. Several studies indicate that whole rock analyses of Proterozoic carbonates commonly approximate depositional compositions (Tucker, 1983; Knoll and others, 1986; Fairchild and Spiro, 1987; Burdett and others, 1990; Kaufman and others, 1991); however, post-depositional shifts in C isotopic composition have been documented often enough that all samples must be evaluated for possible alteration (for example, Fairchild and others, 1990; Kaufman and others, 1992).

Interestingly, some processes that Phanerozoic experience and intuition might flag as particularly troublesome appear to have had little effect on Proterozoic carbonates studied to date. In the absence of extremely high water/rock ratios or significant decarbonation, nearly primary  $\delta^{13}\text{C}$  values appear to be retained in Proterozoic marbles from high-grade metamorphic terrains in Scandinavia, Scotland, and North America (Valley and O'Neil, 1984; Ghent and O'Neil, 1985; Baker and Fallick, 1989a, 1989b; Wickham and Peters, 1993). Thus, the mild metamorphism experienced by Windermere carbonates does not necessarily invalidate the chemostratigraphic study of C isotopes.

Dolomitization is another potential agent of C isotopic alteration, but in Proterozoic successions analyzed to date, most dolomites are isotopically indistinguishable from associated limestones, presumably because in the Proterozoic, dolomitization commonly took place syndepositionally in the presence of fluids isotopically similar to seawater (Tucker, 1983; Fairchild and others, 1991). In general, the neomorphism of metastable  $\text{CaCO}_3$  at depth appears to have had a greater effect on C isotopic compositions (Fairchild and others, 1990).

Experience to date suggests that the processes most likely to have altered the C isotopic compositions of Proterozoic carbonates are biological. The microbial metabolism of sedimentary organic matter commonly produces products with a distinct isotopic composition. Photosynthetically derived organic C is strongly depleted in  $^{13}\text{C}$  relative to carbonate precipitated from the same water body. Respiration or fermentation of this organic matter yields isotopically light  $\text{CO}_2$ , which can be quantitatively important in diagenetic carbonate precipitation. Dissimilatory sulfate reduction and methanogenesis also produce isotopically

distinct products that can be incorporated into early diagenetic carbonate minerals (reviewed in Schidlowski and others, 1983). Abiological decomposition of volatile organic molecules at depth can mimic the isotopic effects of microorganisms, but the common occlusion of pore space by early diagenetic cements appears to have minimized this effect in Proterozoic rocks.

Diagenetic effects can be recognized in several ways. Knoll and others (1986) noted that in thick Neoproterozoic successions from Svalbard and East Greenland,  $\delta^{13}\text{C}_{\text{carb}}$  and  $\delta^{13}\text{C}_{\text{TOC}}$  (TOC = total organic C) covary smoothly throughout the sections, with a  $\Delta\delta$  of  $28 \pm 2\%$ . Diagenetic processes can alter the isotopic composition of either carbonate C or organic matter, but no process is currently known that could alter both signals by the same magnitude in the same direction. Thus, Knoll and others (1986) concluded that in the sections under study, neither phase was strongly affected by post-depositional processes. There is no reason to assume that  $\Delta\delta$  has been constant through time; to the contrary, there is evidence that isotopic fractionation has varied through time as a function of  $\text{pCO}_2$  and, perhaps, physiological evolution (Freeman and Hayes, 1992; Des Marais and others, 1992). Therefore, 28%–30% is not a magic number applicable to all carbonate–organic carbon pairs. However, there is no empirical evidence that photosynthetic fractionation varied strongly during the terminal Proterozoic interval. Metamorphism can drive isotopically light  $\text{CO}_2$  from organic matter, leaving residual organic C relatively enriched in  $^{13}\text{C}$  (Schidlowski, 1987). In cases where strong alteration is not evident in the low H/C of residual organic matter, marked deviations of  $\Delta\delta$  commonly coincide with other evidence for the post-depositional alteration of  $\delta^{13}\text{C}_{\text{carb}}$  (for example, Kaufman and others, 1992). Thus, unmetamorphosed Neoproterozoic samples in which  $\Delta\delta$  is significantly <28%–30% are best treated as suspect. Note that when samples contain very low concentrations of organic C (for example, the “Tepee dolostone” sample, which contains only 0.7 mg C/g), there is a high potential for contamination by recent organic matter. In such cases, measured  $\delta^{13}\text{C}$  commonly approximates  $-23\%$  to  $-25\%$ , the value of modern terrestrial organic C, and cannot be used to evaluate the carbonate  $\delta^{13}\text{C}$  signal.

Carbonates can also be screened petrographically and geochemically. Micrites, ooids, and early diagenetic cements are petrographic entities that are most likely to retain

primary C isotopic compositions. (In the absence of widespread skeleton formation, the "vital effects" that plague interpretation of Phanerozoic limestones are not at issue.) Further, phases that do not fluoresce under cathodoluminescence (CL) are likely to have escaped the obfuscating effects of diagenesis. Thus, preferential sampling of distinct petrographic and CL phases in thick sections further reduces the likelihood of analyzing isotopically altered carbonates (Fairchild and Spiro, 1987).

Oxygen isotopes are also sensitive indicators of diagenesis, with decrease in  $\delta^{18}\text{O}$  values often indicating increasing alteration. Within individual Proterozoic carbonate units, crossplots of  $\delta^{13}\text{C}$  versus  $\delta^{18}\text{O}$  commonly show no variation of  $\delta^{13}\text{C}$  with decreasing  $\delta^{18}\text{O}$ ; however, in cases where individual horizons show a wide variation in C-isotopic abundances,  $\delta^{13}\text{C}$  commonly plots against  $\delta^{18}\text{O}$  as a straight line of positive slope. In such cases, only samples with the most enriched  $^{13}\text{C}$  and  $^{18}\text{O}$  can be considered as potentially unaltered (see Fairchild and others [1990] for a Proterozoic example).

Veizer (1983) found that with increasing diagenetic alteration under the influence of meteoric fluids, Sr is expelled from carbonates while Mn is incorporated. Thus, Mn/Sr may be a useful tool in the screening of samples for subsequent isotopic analyses. Derry and others (1992) suggested that reliable Sr-isotopic values are likely to come only from carbonates having Mn/Sr < 2. In continuing work, Kaufman and others (1993) find that for C isotopes, samples with Mn/Sr as high as 10 commonly retain near-primary signatures.

The words "commonly" and "likely" occur frequently in the preceding paragraphs, because while screens based on TOC abundance,  $\Delta\delta$ ,  $\delta^{18}\text{O}$ , petrography, and elemental analysis can identify most isotopically altered carbonates, no known combination of screens is guaranteed to reveal all samples with altered  $\delta^{13}\text{C}$ . Stratigraphic context (what are the isotopic abundances of adjacent samples?) and sedimentological features (exposure surfaces, nodules, high organic C content) must additionally inform judgment. In the final analysis, the best way to be confident that stratigraphic variation seen in individual sections corresponds to secular changes in the world ocean is to demonstrate that the same stratigraphic variations occur in different sections that can be shown by independent means to be of comparable age.

In the present investigation, we have eval-

uated the reliability of our samples using the procedures discussed in the preceding paragraphs. One sample of concretionary limestone from the Ingta Formation (F2) and both samples from the Gametrail Formation (B12, B13) failed all field and geochemical tests; these data are included in Table 1 and Figure 4 for completeness, but were not used to construct the curve. All other samples passed the field tests and most passed one or more of the geochemical tests (as reflected in the density of the individual data points in Fig. 4). Very few "anomalous" values were obtained; nearly all samples yielded values consistent with trends shown by underlying and overlying samples. Significantly,  $\delta^{13}\text{C}_{\text{carb}}$  and  $\delta^{13}\text{C}_{\text{TOC}}$  covary smoothly throughout the sections with a  $\Delta\delta$  of 28‰–30‰ (Table 1 and Fig. 4), implying that diagenesis had at best a minor influence on the C-isotopic compositions. Indeed, smooth covariation of the two curves (Fig. 4) suggests that organic C could be analyzed for those intervals that lack carbonate beds, thereby increasing the resolution of the C-isotope curve for the Mackenzie Mountains.

Effects of diagenesis can also be evaluated by comparing strata with their less altered equivalents in conglomerates or breccias. Much of the Keele Formation has been affected by late diagenetic dolomitization and/or recrystallization to coarse spar. However, the Keele Formation was virtually the sole source of clasts in the Ice Brook (Aitken, 1991a, 1991b); clasts in this diamictite are unaltered limestone. Analysis of clasts from the diamictite yields isotopic values (mean  $\delta^{13}\text{C} = +8.6\text{‰}$ ) comparable to those in the lower and middle Keele succession (+8.2‰ to +10.6‰), indicating that late diagenesis had only minimal effects on the C isotopic signature of Keele carbonates.

Sedimentary facies also appear to have had only a minor influence on C-isotope ratios (see Appendixes 2 and 3). For example, shallow-water microbialite boulders in the Blueflower Formation (Sample B28) and slide blocks of hummocky cross-stratified limestone in the Sheepbed Formation (B1 and B2) exhibit C-isotope values that are consistent with those of periplatformal lime mudstones in the same formations. In contrast, shallow subtidal ooid-peloid grainstones in the Keele Formation (C1–C3) and in the Ingta Formation (F3, A6) are sedimentologically and petrographically similar, but differ in  $\delta^{13}\text{C}$  by 7‰–10‰.

Regional variation was evaluated by sampling the same bed in different localities up

to 60 km apart. Four stratigraphic levels were compared in this way (Table 1); the observed differences between mean values for the stratigraphically equivalent pairs ranges from 0.1‰ to 1.9‰, with an average difference of <0.8‰. This is comparable to the range of variation observed among microsamples within a single locality and provides strong support for the belief that the patterns determined in this study are representative of the entire region.

On the basis of all available evidence, we conclude that the major patterns exhibited in Figure 4 are primary features that reflect secular variations in the world oceans.

### C-Isotopic Data

As shown in Figure 4 and Table 1, the oldest samples analyzed in this study—limestones of the lower and middle Keele Formation—are strongly enriched in  $^{13}\text{C}_{\text{carb}}$  ( $\delta^{13}\text{C} = +8\text{‰}$  to +10.1‰). Carbonates of the Keele lowstand wedge and the "Tepee dolostone" are strongly depleted in  $^{13}\text{C}$  ( $\delta^{13}\text{C} = -2\text{‰}$  to -4.6‰). The lower Sheepbed Formation is essentially carbonate-free, but upper Sheepbed samples indicate a second interval of high  $\delta^{13}\text{C}$  values (+4.3‰ to +7‰). From the basal Gametrail through to the top of the Risky Formation, most carbonate samples lie within the narrow range of +0.5‰ to +2‰. Lower Ingta carbonates show a second, strong negative excursion (-3.5‰ to -9.3‰), above which scattered carbonate samples yield  $\delta^{13}\text{C}$  values ranging between 0 and +1‰.

The isotopic composition of TOC almost exactly mimics the isotopic variation recorded in carbonate C (Fig. 4). Lower and middle Keele TOCs are relatively enriched in  $^{13}\text{C}$  ( $\delta^{13}\text{C}_{\text{TOC}} = -22\text{‰}$  to -24‰; Table 1; see also Strauss and Moore, 1992), compared to upper Keele TOCs, which range from -31.4‰ to -36‰ (Table 2)—just like coexisting carbonate. As noted in the previous section, this relationship is to be expected if the stratigraphic variation within the Keele Formation is a primary feature. Probable correlates of the lower and middle Keele Formation in the upper Tindir Group, Yukon Territory (Young, 1982), also exhibit pronounced  $^{13}\text{C}$  enrichment in unaltered carbonate and organic C samples (Kaufman and others, 1992). Both lower and middle Keele and upper Tindir samples additionally have Sr-isotopic ratios and acritarchs that indicate pre-Varanger deposition (Fig. 4 and Table 2; see below). Examples from Svalbard and East Greenland (Knoll and others, 1986), Namibia (Kauf-

TABLE 1. ISOTOPIC AND ELEMENTAL COMPOSITIONS OF WINDERMERE SUPERGROUP CARBONATES

Number	Location*	Sample†	Formation	Height‡ (m)	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	$\delta^{13}\text{C}_{\text{TOC}}$	$\Delta\delta^{**}$	TOC (mgC/g)	Mn/ Sr††	Mg/ Ca††
					‰, PDB						
N88-59A	A9	ML/M	Sekwi	3745	-0.2	-7.0	-27.7	27.5	0.73	0.31	0.020
N88-59B	A9	ML/M	Sekwi	3745	0.1	-9.8	-27.8	27.9	0.60	0.43	0.025
		NL/DM	Sekwi	3745	1.0	-8.1	N.D. <sup>‡‡</sup>	N.D.	N.D.	2.86	0.542
JL-21.5	A8	NL/M	Sekwi	3646	0.2	-13.2	N.D.	N.D.	N.D.	1.48	0.022
JLB-141.4	A7	NL/DS	Backbone	2950	0.8	-12.1	N.D.	N.D.	N.D.	78.29	0.656
JLB-143.9	A7	NL/DS	Backbone	2950	0.6	-12.2	N.D.	N.D.	N.D.	28.39	0.569
I-5	F4	ML/M	Backbone	2950	0.7	-16.4	-23.7	24.4	0.21	1.47	0.017
N91-14A	A6	HL/S	Ingta	2855	0.9	-15.7	-24.7	25.6	0.26	4.21	0.024
N91-14B	A6	ML/M	Ingta	2855	0.8	-16.2	N.D.	N.D.	N.D.	7.54	0.017
I-4	F3	ML/M	Ingta	2855	1.2	-16.4	-24.3	25.5	0.28	3.61	0.024
		ML/M	Ingta	2855	1.4	-15.9	N.D.	N.D.	N.D.	3.20	0.015
I-3	F3	HL/S	Ingta	2855	0.6	-17.0	N.D.	N.D.	N.D.	3.90	0.023
I-2	F2	ML/M/S	Ingta	2750	10.4	-18.3	N.D.	N.D.	N.D.	13.31	0.026
		ML/M/S	Ingta	2750	-10.1	-19.2	N.D.	N.D.	N.D.	18.81	0.013
N91-13D1	A5	ML/M	Ingta	2680	-7.4	-16.7	N.D.	N.D.	N.D.	8.20	0.007
N91-13D2	A5	ML/M	Ingta	2680	-7.3	-16.4	N.D.	N.D.	N.D.	6.66	0.015
N91-13D3	A5	HL/M/DM	Ingta	2680	-6.4	-16.4	N.D.	N.D.	N.D.	21.89	0.196
		HL/S	Ingta	2680	-9.3	-11.7	N.D.	N.D.	N.D.	7.03	0.011
I-1A	F1	HL/M	Ingta	2680	-9.1	-15.7	N.D.	N.D.	N.D.	4.71	0.013
I-1B	F1	HL/M/DM	Ingta	2680	-9.5	-16.5	N.D.	N.D.	N.D.	7.83	0.009
N91-13C	A4	ML/DS	Ingta	2665	-3.5	-14.2	N.D.	N.D.	N.D.	46.00	0.607
N91-13B	A3	NL/DS	Ingta	2660	-3.5	-13.0	N.D.	N.D.	N.D.	25.94	0.206
N91-13A	A2	ML/DS	Risky	2639	1.5	-13.2	-27.7	29.3	0.25	26.40	0.533
		NL/DS	Risky	2639	0.5	-11.0	N.D.	N.D.	N.D.	56.45	0.625
N92-1A	A1	NL/M/S	Risky	2570	1.5	-16.1	N.D.	N.D.	N.D.	20.00	0.009
N92-1B	A1	ML/M/S	Risky	2570	1.5	-16.2	-25.5	27.0	0.28	0.32	0.001
		NL/S	Risky	2570	-0.4	-18.6	N.D.	N.D.	N.D.	0.92	0.001
		ML/M/S	Risky	2570	1.5	-16.1	N.D.	N.D.	N.D.	0.35	0.002
N91-R1	B29	ML/DS	Risky	2500	0.5	-8.7	N.D.	N.D.	N.D.	14.67	0.728
N91-R2	B29	HL/DS	Risky	2500	0.5	-8.0	N.D.	N.D.	N.D.	19.92	0.626
N91-23O	B28	ML/S	Blueflower	2290	1.1	-13.2	N.D.	N.D.	N.D.	41.29	0.029
		NL/S	Blueflower	2290	0.3	-10.4	N.D.	N.D.	N.D.	1.29	0.029
N91-23N	B27	NL/M	Blueflower	2185	1.1	-8.8	N.D.	N.D.	N.D.	0.05	0.008
N91-23M	B26	NL/M/S	Blueflower	2175	2.4	-7.1	-25.9	28.3	0.25	0.05	0.007
N91-23L	B25	NL/M/DM	Blueflower	2170	-4.8	-10.0	N.D.	N.D.	N.D.	0.09	0.012
N91-23K	B24	NL/M	Blueflower	2155	2.1	-7.6	-25.9	28.0	0.38	0.04	0.006
N91-23J	B23	NL/M	Blueflower	2145	1.9	-8.4	N.D.	N.D.	N.D.	0.21	0.017
N91-23I	B22	NL/M	Blueflower	2140	2.0	-7.5	N.D.	N.D.	N.D.	0.47	0.009
N91-23H	B21	NL/M	Blueflower	2060	1.0	-4.9	N.D.	N.D.	N.D.	0.06	0.017
N91-23G	B20	NL/M/DM	Blueflower	2050	0.1	-11.5	N.D.	N.D.	N.D.	0.21	0.011
N91-23F	B19	ML/M	Blueflower	2010	0.5	-7.7	N.D.	N.D.	N.D.	0.06	0.008
N91-23E	B18	NL/S	Blueflower	1979	1.8	-11.5	N.D.	N.D.	N.D.	10.83	0.667
N91-23D	B17	ML/S	Blueflower	1964	2.3	-11.2	-27.4	29.7	0.62	3.66	0.410
N91-23C	B16	NL/DS	Blueflower	1954	1.2	-11.0	N.D.	N.D.	N.D.	5.68	0.467
N91-23B	B15	ML/M	Blueflower	1946	0.3	-11.2	N.D.	N.D.	N.D.	0.14	0.006
N91-23A	B14	NL/M	Blueflower	1942	2.2	-7.5	-27.8	30.0	0.55	0.08	0.006
N91-21GT12	B13	ML/DS	Gametrail	1742	2.4	-10.7	-31.5	33.9	0.83	10.18	0.602
N91-21GT1	B12	ML/DS	Gametrail	1732	2.1	-12.2	-30.0	32.1	1.48	5.75	0.601
N91-21-26	B11	NL/M	Sheepbed	1720	7.1	-11.4	-23.6	30.7	1.19	0.44	0.012
N91-21-25	B10	NL/S	Sheepbed	1715	5.9	-11.0	-21.7	27.6	0.72	0.64	0.015
N91-21-23	B9	NL/S	Sheepbed	1660	5.3	-12.0	N.D.	N.D.	N.D.	0.35	0.012
N91-21-21	B8	NL/M	Sheepbed	1640	5.3	-12.9	N.D.	N.D.	N.D.	0.70	0.001
N91-21-19	B7	NL/DS	Sheepbed	1620	5.3	-12.0	N.D.	N.D.	N.D.	13.15	0.455
N91-21-17-5	B6	NL/M	Sheepbed	1609	5.3	-12.4	-24.2	29.5	1.84	0.27	0.010
N91-21-17-1	B5	NL/M	Sheepbed	1605	4.3	-12.6	-24.2	28.5	2.50	0.18	0.010
N91-22-33	B4	NL/M	Sheepbed	1540	2.6	-12.7	N.D.	N.D.	N.D.	0.04	0.006
N91-22-32B	B3	NL/M	Sheepbed	1530	1.3	-10.4	N.D.	N.D.	N.D.	0.05	0.014
N91-22-32A	B2	ML/M	Sheepbed	1529	1.3	-12.9	N.D.	N.D.	N.D.	0.11	0.008
		NL/DS	Sheepbed	1529	1.2	-11.2	N.D.	N.D.	N.D.	1.72	0.382
		ML/M	Sheepbed	1529	1.0	-12.9	N.D.	N.D.	N.D.	0.08	0.010
N91-22-31	B1	NL/M	Sheepbed	1528	2.4	-12.7	-24.2	26.6	0.74	0.07	0.011
N89-128A	C8	NL/M	Tepee	728	-4.6	-10.4	-27.0	22.4	0.07	0.07	0.007
N92-14A	C7	ML/DM	Tepee	722	-3.1	-6.7	N.D.	N.D.	N.D.	3.55	0.577
		ML/DM	Tepee	722	-3.1	-6.8	N.D.	N.D.	N.D.	2.78	0.669
N91-7	D2	ML/DM	Tepee	722	-2.1	-9.8	N.D.	N.D.	N.D.	7.14	0.599
N89-137	D1	NL/S	Ice Brook	N.D.	8.6	-11.1	-23.1	31.7	1.24	0.89	0.011
N92-14B	C6	NL/M	Keele	717	-5.4	-12.1	-33.3	27.9	0.43	0.06	0.003
N92-14C	C5	NL/M	Keele	712	-5.7	-11.1	-31.4	25.7	0.52	0.03	0.002
N92-14D	C4	NL/M/S	Keele	705	-6.9	-12.3	-36.0	29.1	0.87	0.35	0.009
N92-14G	C3	NL/S	Keele	500	8.3	-9.5	-23.6	31.9	0.53	0.13	0.015
N92-14H	C2	NL/M	Keele	495	8.2	-9.8	-22.1	30.3	0.64	0.17	0.009
N92-14I	C1	NL/M	Keele	493	10.6	-4.4	-23.2	33.8	0.34	0.27	0.022
N89-132	E1	NL/S	Keele	330	8.2	-7.3	-23.9	32.1	0.25	0.10	0.001

\*See location map in Figure 1

†NL = non-luminescent, ML = moderately-luminescent, HL = highly-luminescent, M = microspar, DM = dolomicrospar, S = sparite, DS = dolosparite

‡Height above middle of Twitya Formation

\*\* $\Delta\delta = \delta^{13}\text{C} - \delta^{13}\text{C}_{\text{TOC}}$ 

††Elemental ratios measured on a VG PQ2+ PlasmaQuad mass spectrometer

‡‡No data.

man and others, 1991), arctic Canada (Asmerom and others, 1991), the western United States (Zempolich and others, 1988; Wickham and Peters, 1993; Smith and others, 1994), and elsewhere (Strauss and Moore, 1992) indicate that strong  $^{13}\text{C}$  enrichment is broadly characteristic of carbon-

ates deposited between ca. 850 Ma and the Varanger ice age.

The marked  $^{13}\text{C}$  depletion of the "Tepee dolostone" matches  $\delta^{13}\text{C}$  values obtained for immediately post-Varanger (or interpreted post-Varanger) rocks in Svalbard and East Greenland (Knoll and others,

1986), Namibia (Kaufman and others, 1991), Australia (Jenkins and others, 1992; Calver, 1993), and elsewhere in western North America (Kaufman, unpublished data). In concert with the Keele data, Sheepbed analyses support the interpretation of the Ice Brook Formation as a



TABLE 2. ABUNDANCE AND ISOTOPIC COMPOSITION OF Sr IN WINDERMERE SUPERGROUP CARBONATES

Number	Sr* (ppm)	<sup>87</sup> Rb/ <sup>86</sup> Sr*	<sup>87</sup> Sr/ <sup>86</sup> Sr <sub>meas</sub> †
N91-23K	1467	0.0006	0.708616
N91-23H	1249	0.0010	0.708607
N91-23F	1410	0.0012	0.708416
N91-23A	791	0.0016	0.708551
N91-21-25	1306	0.0048	0.708892
N89-128A	1374	0.0004	0.707226
N92-14H	669	0.0015	0.707342
N89-132	904	0.0014	0.707124

\*Abundances and ratios determined on a Finnigan THO thermal ionization mass spectrometer

†Ratios determined on a Finnigan 262 thermal ionization mass spectrometer

Varanger glaciogenic deposit. Carbonates associated with Ediacaran faunas in the Sheepbed and Blueflower formations show similar values to those obtained by Kaufman and others (1991) from the two levels bearing Ediacaran faunas in Namibia. Risky through Sekwi samples have isotopic compositions that are consistent with a latest Proterozoic to Early Cambrian age, although only the negative values in the basal Ingta Formation suggest the marked stratigraphic variation seen in boundary sections in Siberia and Morocco. In both southern (Magaritz and others, 1986; Kirschvink and others, 1991) and northern (Knoll and others, in press) Siberia, as well as in Morocco (Magaritz and others, 1991), carbonates immediately beneath basal Cambrian (Nemakit-Daldyn) rocks are depleted in <sup>13</sup>C by up to 4‰. Most of the lower Ingta values are distinctly more negative than this. The Ingta beds in question contain minor amounts of phosphorite, a feature commonly associated with <sup>13</sup>C depletion in coexisting carbonate (Aharon and others, 1987; Brasier and others, 1990).

### Sr isotopes

The interpretation of <sup>87</sup>Sr/<sup>86</sup>Sr is compromised by diagenetic alteration and the presence in carbonates of clay minerals. Many of our upper Windermere samples are afflicted by one or both problems; thus, our samples yielded only a limited amount of useful data on the Sr isotopic composition of terminal Proterozoic seawater (Table 2). Empirically, it has been observed that samples with Mn/Sr > 2, δ<sup>18</sup>O < -10‰, and <sup>87</sup>Rb/<sup>86</sup>Sr > 0.001 have a low probability of yielding unaltered <sup>87</sup>Sr/<sup>86</sup>Sr values (Derry and others, 1989, 1992; Asmerom and others, 1991; Kaufman and others, 1993). Most Risky and younger samples are characterized by very high Mn/Sr and very low δ<sup>18</sup>O. Many (but not all) of the older samples have both low

δ<sup>18</sup>O and high <sup>87</sup>Rb/<sup>86</sup>Sr. What is left is a handful of analyses (Table 2 and Fig. 4) that corroborate previous analyses of terminal Proterozoic rocks.

Sample E1 from the lower Keele Formation yielded a <sup>87</sup>Sr/<sup>86</sup>Sr of 0.7071, consistent with other post-Sturtian but pre-Varanger carbonates from Svalbard (Derry and others, 1989) and Australia (Veizer and others, 1983), and slightly higher than correlative rocks from upper Tindir Unit 5 (Kaufman and others, 1992). Insofar as alteration is likely to increase <sup>87</sup>Sr/<sup>86</sup>Sr by the addition of radiogenic <sup>87</sup>Sr from clay minerals, the Keele sample extends the observation that pre-Varanger carbonates tend to have lower Sr isotopic ratios than post-Varanger samples. Samples from the Sheepbed, Blueflower, and Sekwi formations yielded values of 0.7084–0.7090, consistent with Ediacaran-aged and Cambrian carbonates from elsewhere (Kaufman and others, in press).

Perhaps the most interesting and reliable Sr determination is on a sample from the "Tepee dolostone." The sample is from a large rosette of originally aragonitic seafloor cement, now neomorphosed to calcite. It contains ~1350 ppm Sr and negligible Rb. Its <sup>87</sup>Sr/<sup>86</sup>Sr of 0.7072 is interesting because it indicates that the rapid Neoproterozoic increase in <sup>87</sup>Sr/<sup>86</sup>Sr of values near 0.7070 to 0.7085 did not begin until after the end of the Varanger glaciation in northwestern Canada (compare with Fig. 1).

## DISCUSSION

### Integrating Terminal Proterozoic Chemostratigraphy and Biostratigraphy

If the relationship between isotope values and biostratigraphy depicted in Figure 4 is appropriately correct, and if the isotopic compositions in Windermere carbonates reflect global ocean chemistry at their times of deposition, then Windermere fossil distributions should allow us to predict the stratigraphic pattern of isotopic variation within the succession. A comparison of Figure 4 and the global composite curve (Fig. 1; Knoll and Walter, 1992) shows that many features of the Windermere and global δ<sup>13</sup>C curves are congruent, thus fulfilling the prediction. For Keele through Risky carbonates, the stratigraphic relationships among C isotopes, fossils, and diamicite are just what would be predicted from global data. This reinforces the observation that C isotopes provide an important guide to terminal Proterozoic correlation.

A pronounced negative excursion occurs

in the lower part of the Ingta Formation, just below the faunally defined Precambrian-Cambrian boundary (Fig. 4). Similar excursions occur immediately beneath the base of the Cambrian (Nemakit-Daldyn) in Siberia (Knoll and others, in press) and Morocco (Tucker, 1986). Some caution in interpretation is warranted as the δ<sup>13</sup>C of the Ingta succession includes extremely negative values and low δ<sup>18</sup>O. On the other hand, equally low oxygen isotopic compositions in other parts of the section are not associated with low δ<sup>13</sup>C, and within the Ingta Formation the slope on a C/O plot is essentially zero.

The principal difference between the global composite (Fig. 1) and the Windermere curve (Fig. 4) is the lack of evidence for a basal Cambrian positive C isotope excursion that follows the negative excursion elsewhere. One potential explanation, that strata of appropriate age are not represented in the Mackenzie Mountains, is not supported by the biostratigraphic evidence presented above (Fig. 4). The scarcity of carbonates in the Backbone Ranges and Vampire Formations is a more likely factor in explaining the missing excursions. δ<sup>13</sup>C values for several samples of *Fallotaspis* and *Nevadella* zone limestone from the Sekwi Formation (Table 1) fall well within the range of previously measured Adtabanian carbonates.

### Correlation of Ediacara Faunas

Ediacara-type faunas are now known from more than 30 localities worldwide (Hofmann, 1987), and several distinctive assemblages have been documented (Glaessner, 1984; Jenkins, 1992). However, several factors have frustrated previous attempts to recognize stratigraphically restricted taxa suitable for zonal correlation. In many localities, including the classic section at Ediacara, preservational and environmental factors result in fossils being restricted to relatively thin portions of the terminal Proterozoic succession, making it impossible to observe directly any stratigraphic succession of faunas. Even where long, fossiliferous sections are available, marked discrepancies commonly exist in the order of first appearances of taxa in different sections. For example, the Mackenzie Mountains show stepped increases in the diversity, complexity, and size of Ediacara-type megafossils through the section, whereas in Podolia a high diversity fauna of large, complex forms (Mogilev Formation; Fedonkin, 1983) is overlain by a lower diversity fauna of mainly

ZONE	STRATIGRAPHIC UNIT	ISOTOPIC SIGNATURE		FAUNAL DISTRIBUTION								
				Simple discs and rings	Large or ornamented discs	Annulate discs	Tentaculate discs	Fronds	Shelly fossils	Simple trace fossils	Segmented fossils	
				$\delta^{13}\text{C}$	$^{87}\text{Sr}/^{86}\text{Sr}$	<i>Nimbia Nemiana</i>	<i>Ediacaria Cyclomedusa Medusinites</i>	<i>Kullingia</i>	<i>Hiemalora Eoporpita</i>	<i>Rangaea Pteridinium</i>	<i>Cloudina</i>	<i>Planolites</i>
III	BLUEFLOWER SCHWARZRAND EDIACARA DENGYING KHATYSPTYT	Constant, 0 to +2	Enriched	■	■	■	■	■	■	■	■	■
II	SHEEPBED KUIBIS	Rising sharply to +7	Enriched	■	■	■	■	■	■	■	■	?
I	TWITYA	Constant, > +8	Depleted	■								

▲ ▲ ▲ Level of Varanger/Marinoan Tillites    ■ Low diversity    ■ High diversity

Figure 5. Chemostratigraphic correlation of Ediacara-type faunas. Isotopic correlations are discussed in the text; faunal data are from the following sources, and references therein: Twitya Formation, N.W. Canada (Hofmann and others, 1990); Sheepbed Formation, N.W. Canada (Narbonne and Aitken, 1990; Narbonne, 1994); Kuibis Subgroup, Namibia (Germs, 1972, 1973; Crimes and Germs, 1982; Grant, 1990); Blueflower Formation, N.W. Canada (Hofmann, 1981; Narbonne and Aitken, 1990; Narbonne, 1994); Schwarzrand Subgroup, Namibia (Germs, 1972; Crimes and Germs, 1982; Grant, 1990); Khatyspyt Formation, Siberia (Fedonkin, 1985a, 1985b; Vodanjuk, 1989); Dengying Formation, China (Sun, 1986; Grant, 1990); and the Ediacara Member, Australia (Jenkins, 1992).

simple discs (Yaryshev Formation; Pali, 1976). In the past, the absence of independent criteria for testing correlations has also heightened the potential for circular reasoning in arguments based on "grade of evolution." C and/or Sr isotopes are now available for many of the key occurrences of Ediacara-type fossils, providing an independent means of assessing the stratigraphic significance of the taxa.

The Mackenzie Mountains exhibit three distinctive assemblages of predominantly cosmopolitan taxa, each characterized by a different isotopic signature (Figs. 4 and 5). The Twitya discs (Assemblage I) occur immediately below a zone of extremely enriched C ( $\delta^{13}\text{C}_{\text{carb}} > +8\text{‰}$ ) and relatively depleted Sr ( $^{87}\text{Sr}/^{86}\text{Sr} < 0.7072$ ); no other Ediacara-type assemblages are known to occur in successions that exhibit similar isotopic ratios. The Sheepbed fossils (Assemblage II) occur within an interval in which  $\delta^{13}\text{C}_{\text{carb}}$  rises sharply from near 0 to +7‰, and Sr ratios show strong enrichment ( $^{87}\text{Sr}/^{86}\text{Sr} = \sim 0.7085$ ); similar isotopic signatures are exhibited by the Kuibis Subgroup of Namibia (Kaufman and others, 1991; Derry and others, 1992). The Blueflower assemblage (Assemblage III) is characterized by relatively constant  $\delta^{13}\text{C}_{\text{carb}}$  that varies only

slightly within the range of +0.5‰ to +2‰ and enriched Sr ratios ( $^{87}\text{Sr}/^{86}\text{Sr} = \sim 0.7085$ ). Similar isotopic signatures have been described from the Schwarzrand Subgroup of Namibia (Kaufman and others, 1991; Derry and others, 1992), Rodda Group strata equivalent to the Ediacara Member in Australia (Jenkins and others, 1992; Calver, 1993), the Dengying Formation in China (Lambert and others, 1987), and the Khatyspyt Formation in Siberia (Knoll and others, in press).

It has long been recognized that, despite the presence of some cosmopolitan forms, considerable differences exist among Ediacara-type faunas from different geographic localities (for example, see comparisons of the faunas from Newfoundland, Namibia, and Australia in Jenkins, 1992). Chemostratigraphic correlations (Fig. 5) indicate that these differences exist even among contemporaneous assemblages. For example, the Sheepbed Formation in the Mackenzie Mountains and the Kuibis Subgroup in Namibia both contain the oldest diverse assemblages of Ediacara-type fossils in their respective regions and exhibit strikingly similar C and Sr isotope values, yet they apparently have no megafossil taxa in common. Evidently, biogeographic, ecologic, and preserva-

tional factors can significantly influence the local composition of Ediacara-type fossil assemblages.

Nevertheless, when considered on a global basis, broad trends in the evolution of Ediacara-type organisms are evident (Fig. 5). Assemblage I (subtillite) contains a low diversity assemblage of centimeter-sized, predominantly unornamented discs and rings that represent the most primitive elements of the Ediacara fauna. Assemblage II (post-tillite) is considerably more diverse and contains most of the significant elements of Ediacaran fossil morphology, including discs (simple, ornamented, annulate, and tentaculate forms), fronds (holdfasts and actual fronds), lightly biomineralized organisms (*Cloudina*), and animal burrows (trace fossils such as *Planolites*). A "possible sprigginiid" described from this level (Germs, 1973) is incomplete and poorly preserved, and should be regarded as questionable. Assemblage III is the most diverse, and includes all morphotypes known from the underlying assemblage, plus segmented forms (dickinsoniids, sprigginiids) and problematic forms (for example, *Tribrachidium*).

When considered from a global standpoint, most of the truly cosmopolitan taxa of

Ediacara-type fossils (the genera specifically listed on the top of Fig. 5) have long time ranges, spanning at least two assemblage zones. Consequently, these taxa probably are suitable only for broad-scale correlations on a system scale, and their more restricted occurrences in individual sections probably reflect immigration, environment, and taphonomy rather than evolution. Some genera of discoid and frondose organisms, and some separate morphotypes such as segmented organisms (for example, dickinsoniids, sprigginids, and vendomiids) may well be restricted to assemblage III, particularly if the diverse faunas of Podolia and the White Sea (Fedonkin, 1985a, 1985b, 1992) are equivalent to those of the Ediacara Member as is generally believed. Carbonates are virtually absent from the Neoproterozoic of the Russian Platform, and chemostratigraphic confirmation of this relationship will require establishment of C-isotopic trends from organic matter alone.

### Paleobiological Implications

The idea that a Neoproterozoic rise in atmospheric oxygen levels made possible the Ediacaran radiation is >30 yr old (Nursall, 1959). More recently, geochemical data and models have been marshaled in support of the more specific hypothesis that  $pO_2$  rose significantly just prior to the appearance of diverse Ediacaran animals (Knoll, 1991, 1992a; Derry and others, 1992). As noted above, the earliest diverse animal fossils occur in association with the post-Varanger positive excursion in  $\delta^{13}C$ , as would be predicted from biogeochemical models (Derry and others, 1992). The Sheepbed and lower Nama assemblages (Zone II) indicate that the principal components of the Ediacaran fauna—cnidarians, “vendozoans” (“quilted” organisms of disputed affinities; Seilacher, 1989), and ancestral bilaterians (documented by trace fossils)—were all present at this early stage. The fauna included animals with biomineralized skeletons (*Cloudina*). This evolutionary pattern is consistent with molecular phylogenies that imply the diversification of diploblastic metazoans and ancestral triploblasts well before the explosive radiation of eucoelomate animals near the Proterozoic-Cambrian boundary (Raff and others, 1989; Lake, 1990; Patterson, 1989; Ghiselin, 1989; Christen and others, 1991). The fossils further suggest that macroscopic size may have evolved polyphyletically in clades that differentiated earlier, also consistent with a post-Varanger rise in  $pO_2$ .

The congruence of data from comparative

biology, paleontology, and molecular phylogeny is pleasing, but is it correct? The Mackenzie Mountains succession forces a critical reevaluation because, as noted above, the Twitya Formation contains centimeter-scale discs *below* a tillite correlated chemostratigraphically with the Varanger ice age (Hofmann and others, 1990). The assemblage is simple; it does not contain any of the very large, morphologically complex, or skeletonized fossils that characterize younger Ediacaran assemblages. Nor is it associated with trace fossils. Yet, if the discs are correctly interpreted as metazoans of cnidarian grade, then macroscopic animals in the broadest sense must have evolved several tens of millions of years before the postulated rise in atmospheric oxygen.

There are several possible ways of accommodating the Twitya discs. Conceivably, their interpretation as metazoans is incorrect; however, their similarity to younger Ediacaran discs widely accepted as cnidarians, the difficulty of producing comparable structures abiologically, and the presence in some specimens of distinctive radially oriented septa discourages this view (Hofmann and others, 1990). It is also possible that the hypothesis of significant atmospheric change after the Varanger ice age is incorrect. Again, however, the magnitude of the relevant geochemical signals for S (Ross and others, 1991), as well as the more completely documented C and Sr, and the simplicity and robustness of published models discourage rejection of this hypothesis. Further, the close stratigraphic association between the postulated rise in  $pO_2$  and the widespread appearance of large, complex Ediacaran metazoans demands that this concept be taken seriously.

Fortunately, it is possible to accommodate *both* a metazoan interpretation of the Twitya structures and post-Varanger environmental change. In the absence of well-developed circulatory and respiratory systems, animal size is limited by oxygen diffusion into tissues (Runnegar, 1982, 1991). Cnidarians achieve macroscopic size by means of a complex topology of cavities and septa—they are essentially very thin organisms that are complexly folded into a three-dimensional structure (Brusca and Brusca, 1990). If the Twitya discs represent cnidarians with some level of internal complexity, then it is likely that they could have lived at a  $pO_2$  of 3%–6% of present atmospheric levels (PAL) (Runnegar, 1991). Geochemical data on paleosols developed on sideritic Fe formation suggest that this level of oxygen was first achieved as early as 2100 Ma (Holland and Beukes, 1990). The

subsequent Proterozoic history of oxygen is not well established, but the presence of multicellular red and green algae in rocks as old as 1000 Ma strongly suggests that  $pO_2$  never fell below ~10% PAL during the Neoproterozoic. This conclusion is prompted by the need for such algae to obtain fixed N from the water column and the low levels of abiological N fixation expected when  $pO_2$  falls much below this level (Knoll and Holland, in press).

Thus, cm-scale cnidarians could have evolved prior the Varanger ice age. If correctly interpreted, the Twitya discs indicate that initial evolution of tissue-grade organization in the metazoan clade and the initial diversification of this clade both occurred well before the post-Varanger Ediacaran explosion. Large animals without either a well-developed circulatory system or the complex topology of septate cnidarians—and especially macroscopically mobile and skeletonized animals of this grade—require oxygen levels comparable to present levels (Runnegar, 1982, 1991). Thus, the evolutionary implication of the Mackenzie Mountains fossils taken as a whole may be that the animal clade evolved tissue-grade multicellularity and a measure of phylogenetic diversity significantly before the Varanger glaciation, but that post-Varanger environmental change made possible the polyphyletic expansion of the large and mobile organisms documented by Ediacaran fossils and trace fossils. With the evolution of sophisticated circulatory and respiratory systems, the requirement for high oxygen tensions would have been relaxed, permitting animals to colonize oceanic regimes in which oxygen availability was limited.

### CONCLUSIONS

The Windermere Supergroup of northwestern Canada provides chronostratigraphic data of critical importance to terminal Proterozoic stratigraphy. It is thick and richly fossiliferous, and contains a well-preserved isotopic record. The stratigraphic relationships between fossils and isotopic variations corroborate and extend previous data, suggesting the utility of an integrated framework for terminal Proterozoic chronostratigraphy. In particular, Windermere isotopic data support the idea that C isotopes can be used to correlate terminal Proterozoic successions throughout the Cordillera, even though fossils are rare in many sections. It also provides a chemostratigraphic signature for the base of the *Phycodes pedum* Zone (= base of the Cambrian) in northwestern Canada. Equally

important, integrated chemo- and biostratigraphy permit correlations with successions in Namibia, the Russian Platform, and northeastern Siberia, where efforts are underway to calibrate chronostratigraphic events using zircons in ash beds.

Of paleontological interest, C and Sr isotopes can be used to characterize and correlate Ediacara faunas worldwide. Isotopic data support inferences based on lithostratigraphy (Hofmann and others, 1990) and the bio- and chemostratigraphy of presumed correlatives in the upper Tindir Group (Kaufman and others, 1992) that the discoid fossils in the Twitya Formation predate all known occurrences of diverse Ediacaran remains. These primitive elements of the Ediacara fauna appeared just before the inferred terminal Neoproterozoic rise in  $pO_2$  and the diversification of the Ediacara fauna. Isotopic data suggest that the diverse Ediacaran fossils in the Sheepbed Formation are approximately coeval with the oldest known assemblage in Namibia, while Blueflower metazoans correlate with the classic Ediacaran assemblages in Australia and less diverse faunas in China and northern Siberia.

Reliable stratigraphic correlation among terminal Proterozoic sections is no longer simply a hope or a promise. Rapidly accumulating paleontological and isotopic geochemical data provide the framework necessary to test ideas about evolution, extinction, eustasy, tectonics, and environmental change near the end of the Proterozoic Eon.

#### ACKNOWLEDGMENTS

Field work was supported by Natural Sciences and Engineering Research Council of Canada Grant A-2648 to Narbonne; laboratory research was funded by National Science Foundation Grant BSR 90-90-17747 to Knoll. The Sr-isotopic and elemental analyses were supported by NSF Grant EAR 91-18628 to S. Jacobsen, who also provided helpful discussion. We are grateful to R. B. Blodgett, J. G. Clough, N. P. James, and G. M. Ross for critical reviews of the manuscript. R. B. MacNaughton provided the samples from locality F, and R. W. Dalrymple assisted with collecting samples from localities A–C.

#### APPENDIX 1: GEOCHEMICAL PROCEDURES

Polished thin and thick sections were prepared for petrographic and cathodoluminescence (CL) examination, respectively. Where possible, non-luminescent (NLM) or moderately luminescent

microspar (MLM) was isolated (5–10 mg) by microdrilling techniques from thick sections (compare with Kaufman and others, 1991). For the determination of Mn and Sr concentrations as well as Mn/Sr in carbonate, aliquots of microdrilled powders were weighed and leached in ultraclean, weak (0.5 N) acetic acid to avoid the dissolution of siliciclastic components noted to occur with the use of even a dilute solution of HCl. After leaching, solutions were decanted and diluted to 100 ml in 2%  $HNO_3$ ; residues were dried and weighed to determine percent dissolution. Elemental analyses were performed on a VG PQ2+ plasma source mass spectrometer. Gravimetrically determined standards were analyzed to develop response calibration curves and a 100 parts per billion  $^{115}In$  spike was added for normalization. Accuracy of elemental abundances determined by this technique are better than  $\pm 5\%$  compared to isotope dilution techniques.

The  $CO_2$  was evolved from powders of carbonate for determination of  $\delta^{13}C$  and  $\delta^{18}O$  by reaction with concentrated  $H_3PO_4$  ( $p > 1.89$  g/ml) using offline techniques in evacuated tubes at 90 °C for 12 hr and subsequently isolated by cryogenic distillation. Fractionation factors used for the calculation of  $^{18}O$  abundances of calcites and dolomites based on analyses of  $CO_2$  prepared at 90 °C were 1.00798 and 1.00895, respectively. Accuracy of these isotopic techniques as determined by multiple determinations ( $n > 25$ ) of standard materials is  $\pm 0.1\%$  for C and  $\pm 0.3\%$  for O.

A third aliquot of micro-sample powder was leached in 0.5 M acetic acid for determination of Rb, Sr, and  $^{87}Sr/^{86}Sr$ . After centrifugation the supernate was decanted, dried and redissolved in 1.5 M HCl. A 1% aliquot of the solution was removed and spiked with isotope dilution techniques on a Finnigan THQ thermal ionization mass spectrometer. The Sr was isolated from the remaining solution by standard ion exchange techniques and isotopic compositions determined on a Finnigan MAT 262 thermal ionization mass spectrometer with dynamic double collection. Interference from  $^{87}Rb$  was controlled by measuring  $^{85}Rb$  with an SEM in ion counting mode (compare with Derry and others, 1992). Multiple NBS 987 standards analyzed during the course of this work yield an average value of  $0.710241 \pm 8$  (uncertainty given as  $2\sigma$  of the mean).

#### APPENDIX 2: PETROGRAPHIC DESCRIPTION AND SEDIMENTARY FACIES OF WINDERMERE SUPERGROUP AND LOWER CAMBRIAN CARBONATES<sup>1</sup>

#### APPENDIX 3: STRATIGRAPHIC LOCATION OF SAMPLES<sup>1</sup>

#### REFERENCES CITED

- Aharon, P., Schidlowski, M., and Singh, I. B., 1987, Chronostratigraphic markers in the end-Precambrian carbon isotope record of the Lesser Himalaya: *Nature*, v. 327, p. 699–702.  
Aitken, J. D., 1989, Uppermost Proterozoic formations in central Mackenzie Mountains, Northwest Territories: *Geological Survey of Canada Bulletin* 368, 26 p.

- Aitken, J. D., 1991a, Two Late Proterozoic glaciations, Mackenzie Mountains, northwestern Canada: *Geology*, v. 19, p. 445–448.  
Aitken, J. D., 1991b, The Ice Brook Formation and post-Rapitan, Late Proterozoic glaciation, Mackenzie Mountains, Northwest Territories: *Geological Survey of Canada Bulletin* 404, 43 p.  
Asmerom, Y., Jacobsen, S., Knoll, A. H., Butterfield, N. J., and Swett, K., 1991, Strontium isotopic variations of Neoproterozoic seawater: Implications for crustal evolution: *Geochimica et Cosmochimica Acta*, v. 55, p. 2883–2894.  
Baker, A. J., and Fallick, A. E., 1989a, Heavy carbon in two-billion-year-old marbles from Lofoten-Vesterdalen, Norway: Implications for the Precambrian carbon cycle: *Geochimica et Cosmochimica Acta*, v. 53, p. 2883–2894.  
Baker, A. J., and Fallick, A. E., 1989b, Evidence from Lewisian limestones for isotopically heavy carbon in two-thousand-million-year-old seawater: *Nature*, v. 337, p. 352–354.  
Baudet, D., Aitken, J. D., and Vestegain, M., 1989, Palynology of uppermost Proterozoic and lowermost Cambrian formations, central Mackenzie Mountains, northwestern Canada: *Canadian Journal of Earth Sciences*, v. 26, p. 129–148.  
Brasier, M. D., and nine others, 1990, The carbon- and oxygen-isotope record of the Precambrian-Cambrian boundary interval in China and Iran and their correlation: *Geological Magazine*, v. 127, p. 319–332.  
Brusca, R. C., and Brusca, G. A., 1990, Invertebrates: Sunderland, Massachusetts, Sinauer Associates, 922 p.  
Burdett, J. W., Grotzinger, J. P., and Arthur, M. A., 1990, Did major changes in the stable-isotope composition of Proterozoic seawater occur?: *Geology*, v. 18, p. 227–230.  
Calver, C. R., 1993, Chemostratigraphy of Ediacarian successions in the Adelaide Geosyncline and Officer Basin, in Jenkins, R. J. F., Lindsay, J. F., and Walter, M. R., eds., *Field guide to the Adelaide geosyncline and Amadeus basin, Australia: AGSO Record*, 1993/35, p. 82–84.  
Christen, R., Ratto, A., Baroin, A., Perasso, R., Grell, K. G., and Adoutte, A., 1991, An analysis of the origin of the metazoans, using comparisons of partial sequences of the 28S rRNA, reveals an early emergence of triploblasts: *EMBO Journal*, v. 10, p. 499–503.  
Conway Morris, S., and Fritz, W. H., 1980, Shelly microfossils near the Precambrian-Cambrian boundary, Mackenzie Mountains, northwestern Canada: *Nature*, v. 286, p. 381–384.  
Crimes, T. P., 1987, Trace fossils and correlation of late Precambrian and Early Cambrian strata: *Geological Magazine*, v. 124, p. 97–119.  
Crimes, T. P., and Germs, G. J. B., 1982, Trace fossils from the Nama Group (Precambrian-Cambrian) of South-West Africa (Namibia): *Journal of Paleontology*, v. 56, p. 890–907.  
Derry, L. A., Keto, L. S., Jacobsen, S. B., Knoll, A. H., and Swett, K., 1989, Sr isotopic variations in upper Proterozoic carbonates from Svalbard and East Greenland: *Geochimica et Cosmochimica Acta*, v. 53, p. 2331–2339.  
Derry, L. A., Kaufman, A. J., and Jacobsen, S. B., 1992, Sedimentary cycling and environmental change in the Late Proterozoic: Evidence from stable and radiogenic isotopes: *Geochimica et Cosmochimica Acta*, v. 56, p. 1317–1329.  
Des Marais, D. J., Strauss, H., Summons, R. E., and Hayes, J. M., 1992, Carbon isotope evidence for the stepwise oxidation of the Proterozoic environment: *Nature*, v. 359, p. 605–609.  
Deynoux, M., and Trompette, R., 1976, Late Precambrian mixtite: Glacial and/or non-glacial? Dealing especially with the mixtite of west Africa: *American Journal of Science*, 276, p. 117–125.  
Eisbacher, G. H., 1978, Re-definition and subdivision of the Rapitan Group, Mackenzie Mountains: *Geological Survey of Canada Paper* 77-35, 21 p.  
Eisbacher, G. H., 1981, Sedimentary tectonics and glacial record in the Windermere Supergroup, Mackenzie Mountains, northwestern Canada: *Geological Survey of Canada Paper* 80-27, 40 p.  
Eisbacher, G. H., 1985, Late Proterozoic rifting, glacial sedimentation and sedimentary cycles in the light of Windermere deposition, western Canada: *Palaogeography, Palaeoclimatology, Palaeoecology*, v. 51, p. 231–254.  
Fairchild, I. J., and Hambrey, M. J., 1984, The Vendian succession of northeastern Spitsbergen: Petrogenesis of a dolomite-tillite association: *Precambrian Research*, v. 26, p. 111–167.  
Fairchild, I. J., and Spiro, B., 1987, Petrological and isotopic implications of some contrasting late Precambrian carbonates, NE Spitsbergen: *Sedimentology*, v. 34, p. 973–989.  
Fairchild, I. J., Marshall, J. D., and Bertrand-Sarfati, J., 1990, Stratigraphic shifts in carbon isotopes from Proterozoic stromatolitic carbonates (Mauritania): Influences of primary mineralogy and diagenesis: *American Journal of Science*, v. 290A, p. 46–79.  
Fairchild, I. J., Knoll, A. H., and Swett, K., 1991, Coastal lithofacies and biofacies associated with syndepositional dolomitization and silicification (Draken Formation, upper Riphean, Svalbard): *Precambrian Research*, v. 53, p. 165–197.  
Fedonkin, M. A., 1983, Besskeletnaya fauna Podol'skogo Pridnestrov'ya [Nonskeletal fauna of the Podolian Pridnestrov'ya], in Velikanov, V. A., Aseeva, E. A., and Fedonkin, M. A., eds., *The Vendian of the Ukraine: Kiev, Akademiya Nauk Ukrainskoy SSSR, Naukova dumka*, p. 128–139 [in Russian].  
Fedonkin, M. A., 1985a, Sistematischeskoe opisanie vendikikh Metazoa [Systematic descriptions of Vendian Metazoa], in Sokolov, B. S., and Iwanowski, M. A., eds., *The Vendian system: Historic-geological and palaeontological basis: Moscow, Izdatel'stvo "Nauka"*, v. 1, p. 70–107 [in Russian]. English translation in Sokolov, B. S., and Iwanowski, M. A.,

<sup>1</sup>GSA Data Repository item 9434, Appendixes 2 and 3, is available on request from Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301.

- Downloaded from [pubs.geoscienceworld.org/gsa/gsabulletin](http://pubs.geoscienceworld.org/gsa/gsabulletin) on March 26, 2019
- Fedonkin, M. A., 1985b, Paleochronology vendskikh Metazoa [Paleochronology of Vendian Metazoa], in Sokolov, B. S., and Iwanowski, M. A., eds., The Vendian system: Historical and paleontological basis: Moscow, Izdatel'stvo "Nauka," v. 1, p. 112-116. [in Russian]. English translation in Sokolov, B. S., and Iwanowski, M. A., eds., 1990, The Vendian System, Volume 1, Paleontology: Berlin, Springer-Verlag, p. 132-137.
- Fedonkin, M. A., 1992, Vendian faunas and the early evolution of Metazoa, in Lipps, J. H., and Signor, P. W., eds., Origin and early evolution of the Metazoa: New York and London, Plenum Press, p. 87-129.
- Freeman, K. H., and Hayes, J. M., 1992, Fractionation of carbon isotopes by phytoplankton and estimates of ancient CO<sub>2</sub> levels: Global Biogeochemical Cycles, v. 6, p. 185-198.
- Fritz, W. H., Narbonne, G. M., and Gordy, S. P., 1983, Strata and trace fossils near the Precambrian-Cambrian boundary, Mackenzie, Selwyn and Wernecke Mountains, Yukon and Northwest Territories: Geological Survey of Canada Paper 83-1B, p. 365-375.
- Germis, G. J. B., 1972, The stratigraphy and paleontology of the lower Nama Group, South-West Africa: Chamber of Mines Precambrian Research Unit, University of Cape Town, Department of Geology Bulletin 12, 250 p.
- Germis, G. J. B., 1973, Possible springiid worm and a new trace fossil from the Nama Group, South West Africa: Geology, v. 1, p. 69-70.
- Ghent, E. D., and O'Neill, J. R., 1985, Late Precambrian marbles of unusual carbon isotopic composition, southeastern British Columbia: Canadian Journal of Earth Sciences, v. 22, p. 324-329.
- Ghiselin, M. T., 1989, Summary of our present knowledge of metazoan phylogeny, in Fernholm, F., Bremer, K., and Jönvall, H., eds., The hierarchy of life: Amsterdam, Elsevier, p. 261-272.
- Glaessner, M. F., 1984, Dawn of animal life: A biohistorical study: Cambridge, Cambridge University Press, 244 p.
- Glaessner, M. F., and Wade, M., 1966, The late Precambrian fossils from Ediacara, South Australia: Paleontology, v. 9, p. 97-103.
- Grant, S., 1990, Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic: American Journal of Science, v. 290-A, p. 261-294.
- Heaman, L. M., Lecheminant, A. N., and Rainbird, R. H., 1992, Nature and timing of Franklin igneous events, Canada: Implications for a Late Proterozoic mantle plume and the break-up of Laurentia: Earth and Planetary Science Letters, v. 109, p. 117-131.
- Hofmann, H. J., 1981, First record of a Late Proterozoic faunal assemblage in the North America Cordillera: Lethaia, v. 14, p. 303-310.
- Hofmann, H. J., 1987, Precambrian biostratigraphy: Geoscience Canada, v. 14, p. 135-154.
- Hofmann, H. J., Narbonne, G. M., and Aitken, J. D., 1990, Ediacaran remains from intertillite beds in northwestern Canada: Geology, v. 18, p. 1199-1202.
- Holland, H. D., and Beukes, N. J., 1990, A paleoweathering profile from Griqualand West, South Africa: Evidence for a dramatic rise in atmospheric oxygen between 2.2 and 1.9 BYBP: American Journal of Science, v. 290A, p. 1-34.
- Jefferson, C. W., and Parrish, R. R., 1989, Late Proterozoic stratigraphy, U/Pb zircon ages and rift tectonics, Mackenzie Mountains, northwestern Canada: Canadian Journal of Earth Sciences, v. 26, p. 1784-1801.
- Jefferson, C. W., and Ruelle, J. C. L., 1986, The Late Proterozoic Redstone copper belt, Mackenzie Mountains, N.W.T., in Morin, J. A., ed., Mineral deposits of the northern Cordillera: Canadian Institute of Mining and Metallurgy Special Volume 37, p. 154-168.
- Jenkins, R. J. F., 1992, Functional and ecological aspects of Ediacaran assemblages, in Lipps, J. H., and Signor, P. W., eds., Origin and early evolution of the Metazoa: New York and London, Plenum Press, p. 131-176.
- Jenkins, R. J. F., McKirdy, D. M., Foster, C. B., O'Leary, T., and Pell, S. D., 1992, The record and stratigraphic implications of organic-walled microfossils from the Ediacaran (terminal Proterozoic) of South Australia: Geological Magazine, v. 129, p. 401-410.
- Kaufman, A. J., Hayes, J. M., Knoll, A. H., and Germis, G. J. B., 1991, Isotopic compositions of carbonates and organic carbon from upper Proterozoic successions in Namibia: Stratigraphic variation and the effects of diagenesis and metamorphism: Precambrian Research, v. 49, p. 301-327.
- Kaufman, A. J., Knoll, A. H., and Awramik, S. M., 1992, Biostratigraphic and chemostratigraphic correlation of Neoproterozoic sedimentary successions: Upper Tindir Group, northwestern Canada, as a test case: Geology, v. 20, p. 181-185.
- Kaufman, A. J., Jacobsen, S. B., and Knoll, A. H., 1993, The Vendian record of Sr and C isotopic variation in seawater: Implications for tectonics and paleoclimate: Earth and Planetary Science Letters, v. 120, p. 409-430.
- Knoll, A. H., and Zharavlev, A. Yu., 1991, The Precambrian/Cambrian boundary: Magnetostratigraphy and carbon isotopes resolve correlation problems between Siberia, Morocco, and South China: GSA Today, v. 1, p. 69-71.
- Knoll, A. H., 1991, End of the Proterozoic Eon: Scientific American, v. 264, no. 10, p. 64-73.
- Knoll, A. H., 1992a, Biological and biogeochemical preludes to the Ediacaran radiation, in Lipps, J. H., and Signor, P. W., eds., Origin and early evolution of the Metazoa: New York and London, Plenum Press, p. 53-84.
- Knoll, A. H., 1992b, Vendian microfossils in metasedimentary cherts of the Scotia Group, Prins Karls Forland, Svalbard: Paleontology, v. 35, p. 751-774.
- Knoll, A. H., and Holland, H. D., 1994, Proterozoic oxygen and evolution: An update, in Stanley, S. M., ed., Biological responses to past global changes: Washington, D.C., National Academy Press (in press).
- Knoll, A. H., and Walter, M. R., 1992, Latest Proterozoic stratigraphy and Earth history: Nature, v. 356, p. 673-678.
- Knoll, A. H., Hayes, J. M., Kaufman, A. J., Sweet, K., and Lambert, I. B., 1986, Secular variation in carbon isotope ratios from upper Proterozoic successions of Svalbard and East Greenland: Nature, v. 321, p. 832-838.
- Knoll, A. H., Grotzinger, J. P., Kaufman, A. J., and Kolosov, P., 1994, Integrated approaches to terminal Proterozoic stratigraphy: An example from the Olenek Uplift, northeastern Siberia: Precambrian Research (in press).
- Lake, J. A., 1990, Origin of the Metazoa: Proceedings of the National Academy of Sciences, U.S.A., v. 87, p. 763-766.
- Lambert, I. B., Walter, M. R., Zang, W., Lu, S., and Ma, G., 1987, Paleoenvironment and carbon-isotope stratigraphy of upper Proterozoic carbonates of the Yangtze Platform: Nature, v. 325, p. 140-142.
- Lemon, N., and Gostin, V. A., 1990, Glaciogenic sediments of the Late Proterozoic Etatina Formation and equivalents, Adelaide geosyncline, South Australia, in Jago, J. B., and Moore, P. S., eds., The evolution of a late Precambrian-early Paleozoic rift complex: The Adelaide geosyncline: Geological Society of Australia Special Publication 16, p. 149-163.
- MacNaughton, R. B., and Narbonne, G. M., 1992, The Neoproterozoic-Cambrian boundary in the Mackenzie Mountains, northwestern Canada: Geological Society of America Abstracts with Programs, v. 24, no. 7, p. A113.
- Magaritz, M., Holzer, W. T., and Kirschvink, J. L., 1986, Carbon-isotope events across the Precambrian-Cambrian boundary on the Siberian Platform: Nature, v. 320, p. 258-259.
- Magaritz, M., Kirschvink, J. L., Latham, A. J., Zharavlev, A. Yu., and Rozanov, A. Yu., 1991, Precambrian/Cambrian boundary problem: Carbon isotope correlations for Vendian and Tommotian time between Siberia and Morocco: Geology, v. 19, p. 847-850.
- Narbonne, G. M., 1994, New Ediacaran fossils from the Mackenzie Mountains, northwestern Canada: Journal of Paleontology, v. 68, p. 411-416.
- Narbonne, G. M., and Aitken, J. D., 1990, Ediacaran fossils from the Sekwi Brook area, Mackenzie Mountains, northwestern Canada: Paleontology, v. 33, p. 945-980.
- Narbonne, G. M., and Aitken, J. D., 1994, Neoproterozoic of the Mackenzie Mountains, northwestern Canada: Precambrian Research (in press).
- Narbonne, G. M., and Myrow, P., 1988, Trace fossil biostratigraphy in the Precambrian-Cambrian boundary interval: New York State Museum Bulletin 463, p. 72-76.
- Narbonne, G. M., Landing, E., and Anderson, M. M., 1987, A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland: Canadian Journal of Earth Sciences, v. 24, p. 1277-1293.
- Nursall, J. R., 1959, Oxygen as a prerequisite to the origin of the Metazoa: Nature, v. 183, p. 1170-1172.
- Palij, V. M., 1976, Ostatki beskeletnoi fauny i sledy zhiznedejatelnosti iz otlozheniy verkhnego dokembriya i nizhnego kembriya Podolii [Remains of soft-bodied animals and trace fossils from the late Precambrian and Early Cambrian of Podolia]: Paleontologiya i Stratigrafiya Verkhnego Kembriya i Nezhnego Paleozoya Yugo-Zapada Vostochno-Evropeskoj Platformy, p. 63-77 [in Russian].
- Patterson, C., 1989, Phylogenetic relationships of major groups: Conclusions and prospects, in Fernholm, B., Bremer, K., and Jönvall, H., eds., The hierarchy of life: Amsterdam, Elsevier, p. 471-488.
- Radke, B. M., and Mathis, R. L., 1980, On the formation and occurrence of saddle dolomite: Journal of Sedimentary Petrology, v. 50, p. 1149-1168.
- Raff, R. A., Field, K. G., Olsen, G. J., Glavannoni, S. J., Lane, D. J., Ghiselin, M. T., Pace, N. R., and Raff, E. C., 1989, Metazoan phylogeny based on analysis of 18S ribosomal RNA, in Fernholm, B., Bremer, K., and Jönvall, H., eds., The hierarchy of life: Amsterdam, Elsevier, p. 247-260.
- Ross, G. M., 1991, Tectonic setting of the Windermere Supergroup revisited: Geology, v. 19, p. 1125-1128.
- Ross, G. M., Bloch, J. D., and Krouse, H. R., 1991, Sulphur isotope geochemistry of authigenic pyrite, Late Proterozoic Windermere Supergroup, Cariboo Mountains, British Columbia: Geological Association of Canada/Mineralogical Association of Canada Annual Meeting Abstracts, v. 16, p. 108.
- Runnegar, B., 1982, Oxygen requirements, biology, and phylogenetic significance of the late Precambrian worm *Dickinsonia* and the origin of the burrowing habit: *Alcheringa*, v. 6, p. 23-39.
- Runnegar, B., 1991, Precambrian oxygen levels estimated from the biochemistry and physiology of early eukaryotes: Paleogeography, Paleoclimatology, Paleocology (Global and Planetary Change Section), v. 97, p. 97-111.
- Schidlowski, M., 1987, Application of stable carbon isotopes to early biochemical evolution on Earth: Annual Review of Earth and Planetary Sciences, v. 15, p. 47-72.
- Schidlowski, M., Hayes, J. M., and Kaplan, I. R., 1983, Isotopic inferences of ancient biochemistries: Carbon, sulfur, hydrogen, and nitrogen, in Schopf, J. W., ed., Earth's earliest biosphere: Princeton, New Jersey, Princeton University Press, p. 149-187.
- Seilacher, A., 1989, Vendozoa: Organismic construction in the Proterozoic biosphere: Lethaia, v. 22, p. 229-239.
- Smith, L., Kaufman, A. J., Knoll, A. H., and Link, P., 1994, Chemostratigraphy in predominantly siliciclastic Neoproterozoic successions: A case study of the Pocatello Formation and lower Brigham Group, southeastern Idaho and northern Utah: Geological Magazine, v. 131, p. 301-314.
- Sokolov, B., and Fedonkin, M. A., 1984, The Vendian as the terminal system of the Precambrian: Episodes, v. 7, p. 12-19.
- Strauss, H., and Moore, T. B., 1992, Abundances and isotopic compositions of carbon and sulfur species in whole rock and kerogen samples, in Schopf, J. W., and Klein, C., eds., The Proterozoic biosphere: Cambridge, Cambridge University Press, p. 709-798.
- Sun, W. G., 1986, Late Precambrian pennatulids (sea pens) from the eastern Yangtze Gorges, China: *Parachania* gen. nov.: Precambrian Research, v. 31, p. 361-375.
- Tucker, M. E., 1983, Diagenesis, geochemistry, and origin of a Precambrian dolomite: The Beck Spring Dolomite, eastern California: Journal of Sedimentary Petrology, v. 53, p. 1097-1119.
- Tucker, M. E., 1986, Carbon isotope excursions in Precambrian/Cambrian boundary beds, Morocco: Nature, v. 319, p. 48-50.
- Valley, J. W., and O'Neill, J. R., 1984, Fluid heterogeneity during granulite facies metamorphism in the Adirondacks: Stable isotope evidence: Contributions to Mineralogy and Petrology, v. 69, p. 158-173.
- Veizer, J., 1983, Chemical diagenesis of carbonates: Theory and application, in Arthur, M., Veizer, J., and Land, L., eds., Stable isotopes in sedimentary geology: SEPM Short Course, v. 10, p. 3.1-3.100.
- Veizer, J., Compston, W., Calver, N., and Schidlowski, M., 1983, <sup>87</sup>Sr/<sup>86</sup>Sr in Late Proterozoic carbonates: Evidence for a "mantle event" at 900 Ma ago: *Geochimica et Cosmochimica Acta*, v. 47, p. 295-302.
- Vodanjk, S. A., 1989, Ostatki beskeletnaya Metazoa iz Khatapskoy sviiti Olenekskoga Podnyatiya [Remains of soft-bodied metazoans from the Khatapsky Suite of the Olenek Uplift], in Kholmontovskiy, V. V., and Sovetov, Yu. C., eds., The late Precambrian and early Paleozoic in Siberia: Novosibirsk, Akademiya Nauk SSSR, Sibirskoye Otdelnyye Institut Geologii i Geofiziki, p. 61-74 [in Russian].
- Wickham, S. M., and Peters, M. T., 1993, High  $\delta^{13}\text{C}$  Neoproterozoic carbonate rocks in western North America: Geology, v. 21, p. 165-168.
- Williams, G. E., 1979, Sedimentology, stable isotope geochemistry, and paleoenvironment of dolostones capping late Precambrian glacial sequences in Australia: Geological Society of Australia Journal, v. 26, p. 377-386.
- Yeo, G. M., 1981, The Late Proterozoic Rapitan glaciation in the northern Cordillera, in Campbell, F. H. A., ed., Proterozoic basins of Canada: Geological Survey of Canada Paper 81-10, p. 25-46.
- Young, G. M., 1982, The Late Proterozoic Tindir Group, east-central Alaska: Evolution of a continental margin: Geological Society of America Bulletin, v. 93, p. 759-783.
- Young, G. M., 1992, Late Proterozoic stratigraphy and the Canada-Australia connection: Geology, v. 20, p. 215-218.
- Zempolich, W. G., Wilkinson, B. H., and Lohmann, K. C., 1988, Diagenesis of Late Proterozoic carbonates: The Beck Springs Dolomite of eastern California: Journal of Sedimentary Petrology, v. 58, p. 656-672.

MANUSCRIPT RECEIVED BY THE SOCIETY APRIL 16, 1993  
 REVISED MANUSCRIPT RECEIVED DECEMBER 20, 1993  
 MANUSCRIPT ACCEPTED DECEMBER 22, 1993