

# THE LATE ORDOVICIAN MASS EXTINCTION

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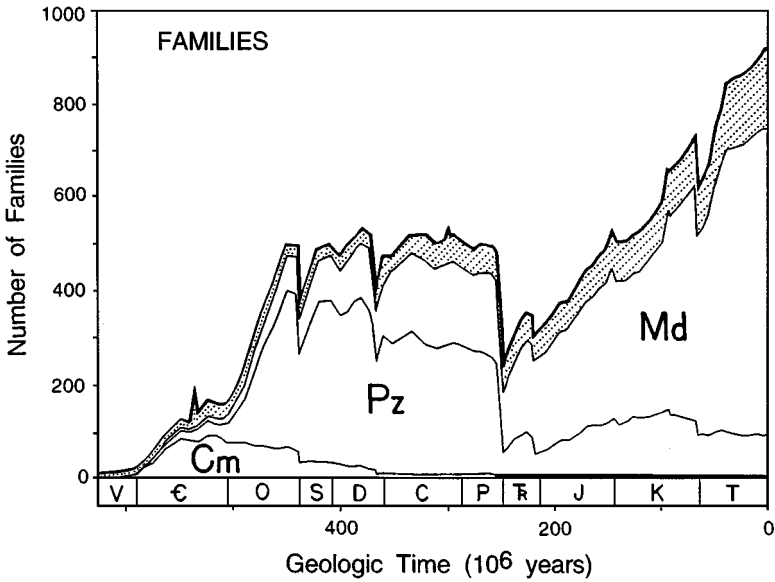
■ **Abstract** Near the end of the Late Ordovician, in the first of five mass extinctions in the Phanerozoic, about 85% of marine species died. The cause was a brief glacial interval that produced two pulses of extinction. The first pulse was at the beginning of the glaciation, when sea-level decline drained epicontinental seaways, produced a harsh climate in low and mid-latitudes, and initiated active, deep-oceanic currents that aerated the deep oceans and brought nutrients and possibly toxic material up from oceanic depths. Following that initial pulse of extinction, surviving faunas adapted to the new ecologic setting. The glaciation ended suddenly, and as sea level rose, the climate moderated, and oceanic circulation stagnated, another pulse of extinction occurred. The second extinction marked the end of a long interval of ecologic stasis (an Ecologic-Evolutionary Unit). Recovery from the event took several million years, but the resulting fauna had ecologic patterns similar to the fauna that had become extinct. Other extinction events that eliminated similar or even smaller percentages of species had greater long-term ecologic effects.

## INTRODUCTION

The Late Ordovician extinction was the first of five great extinction events of the Phanerozoic (Sepkoski 1996). In terms of the percentage of genera and families lost, it is the second largest (Figure 1). However, the ecologic changes accompanying the extinction were less severe than those of the other major extinctions (Copper 1994, Droser et al 2000, Bottjer et al 2001).

Estimates of taxonomic loss, based on literature reviews (Sepkoski 1996), suggest about 26% of families (Figure 1) and 49% of genera became extinct. Extrapolations from these higher taxonomic categories indicate about 85% of all species became extinct (Jablonski 1991).

High latitude Late Ordovician glaciation was initially recognized in north Africa (Beuf et al 1966, 1971; Dangeard & Dor 1971). Shortly thereafter the Late Ordovician extinction was attributed to effects of the glaciation (Sheehan 1973a, Berry & Boucot 1973). No other cause of the extinction has been suggested, and



**Figure 1** Family diversity of marine fossils. Cm, Cambrian evolutionary fauna (EF); Pz, Paleozoic EF; Md, Modern EF. (Stippled area) Poorly skeletonized fauna. (After Sepkoski 1991.)

no geochemical evidence of a Late Ordovician impact has been found in eastern Canada (Orth et al 1986), arctic Canada (Wang et al 1993b), the United Kingdom (Wilde et al 1986), or China (Wang et al 1993a).

The Ordovician world differed significantly from the recent. Several continental plates were dispersed along the equator, and the large Gondwana landmass approached the south pole in the Late Ordovician. The equatorial plates were covered by extensive epicontinental seas that have no counterpart today. Atmospheric CO<sub>2</sub> was many times higher than today, and greenhouse gases compensated for an approximately 5% dimmer sun. The oceans were inhabited by Paleozoic evolutionary fauna (EF), which was less diverse than is Modern EF. Communities were commonly epifaunal rather than infaunal, as in recent oceans. Community structures were simpler, with fewer predators than Modern EF. Cambrian EF had declined during the Ordovician radiation and existed primarily in offshore environments. Modern EF was just beginning to develop, primarily in near-shore settings.

In spite of being the oldest of the five extinctions, the underlying causes of the Ordovician extinction are better understood than all but the end-Cretaceous extinction, which was caused by an impact event. Ongoing research is focusing on (a) detailed studies of faunas on a bed-by-bed scale and (b) isotopic studies.

Currently the greatest uncertainty involves the interplay between atmospheric CO<sub>2</sub> levels and glaciation.

## Glaciers in a Greenhouse World

That a major glaciation developed in the Late Ordovician, when Earth was in an intense greenhouse interval, is a puzzle (Berner 1994, Brenchley et al 1994). Atmospheric  $p\text{CO}_2$  was about 16 times the present atmospheric level (PAL).

Interpreting changes in  $\delta^{18}\text{O}$  is problematic because it is easily affected by diagenesis and is sensitive to changes in sea-water temperature and to changes in the volume of water in glaciers; it is also sensitive to oceanographic changes. The best  $\delta^{18}\text{O}$  data is from brachiopod shells from tropical settings (Brenchley et al 1994, 1995). A temperature decline in the tropics of about 10°C would be needed to explain the entire  $\delta^{18}\text{O}$  excursion (Brenchley et al 1994). During other Phanerozoic glaciations, the tropics do not show major temperature changes. As a result, only part of the  $\delta^{18}\text{O}$  excursion can be explained by falling temperatures. Polar ice sheets store water with very negative  $\delta^{18}\text{O}$ , which would produce in the oceans a positive shift in  $\delta^{18}\text{O}$  of the magnitude needed to explain the brachiopod data.

The estimate of  $p\text{CO}_2$  at about 16 times PAL is based on a variety of independent lines of reasoning, including (a) computer models of the long-term carbon cycle, (b) measurement of  $^{13}\text{C}$  in limestone and soils containing goethite, and (c) the fractionation of  $^{13}\text{C}$  between carbonates and organic matter in marine sedimentary rocks (Berner 1994).

During the Ordovician, the sun's luminosity was about 95.5% of the current level (Kasting 1989). With the lower luminosity, a seven- to tenfold increase in  $p\text{CO}_2$  over the PAL was needed to maintain the current surface temperature of Earth (Berner 1994, Gibbs et al 1997). The higher  $p\text{CO}_2$  during the Ordovician can be explained by volcanic and metamorphic outgassing, approximately 2.2 times greater than recent levels (Berner 1994).

## THE LATE ORDOVICIAN GLACIATION

The glaciation began at about the beginning of the Hirnantian Stage, the last stage of the Ordovician. Glaciation ended in the latter part of the Hirnantian.

Late Ordovician glaciation is widely recognized in North Africa (Destombes et al 1985; Beuf et al 1971; Holland 1981, 1985; Deynoux 1985; Légrand 1985). Tillites, moraines, drumlins, and especially striated pavements are well preserved. The glacial features documented an ice sheet more than 6000 km in length, that extended across western and northern Africa (Guinea, Senegal, Mauritania, Mali, Algeria, and Libya) and into the Arabian Peninsula (McClure 1978, Hussein 1990).

North of the ice sheet, periglacial marine deposits are known from Morocco, Algeria, Tunisia, Mauritania, Libya, and possibly Turkey (Destombes et al 1985, Legrand 1985). Marine sediment with pebbles deposited by ice rafting are common in North Africa, Portugal, Spain, France, and Germany (Brenchley et al 1991, Legrand 1985, Robardet & Doré 1988). In southern Europe, drop stones are confined to the Hirnantian (Paris et al 1999).

Ordovician and Silurian strata are not preserved in central Africa. In South Africa, glacial and periglacial sediments have been found that correlate with the Late Ordovician glaciation (Cocks & Fortey 1986, Hiller 1992). Two glacial advances are recorded in the Pakhuis Tillite Formation. Each advance included grounded ice sheets and periglacial marine sediments. The overlying Cedarberg Formation is interpreted as glacial outwash. A Late Ordovician age is accepted for the Pakhuis Tillite, but the only faunas of Hirnantian age are from the Cedarberg Shale Formation (Cocks & Fortey 1986).

The Cedarberg faunas are anomalous, being found above the last evidence of a glacial advance. These Hirnantian age faunas could postdate the glaciation and represent a local high-latitude refuge, where cool water conditions persisted into postglacial times. Hirnantian faunas are present above glacial sediments in Argentina. However, isotopic evidence shows that in Argentina, the faunas are from the glacial interval. A refuge also may have existed in Norway, where postglacial faunas of Ordovician aspect survived into the earliest Silurian Period (Baarli & Harper 1986).

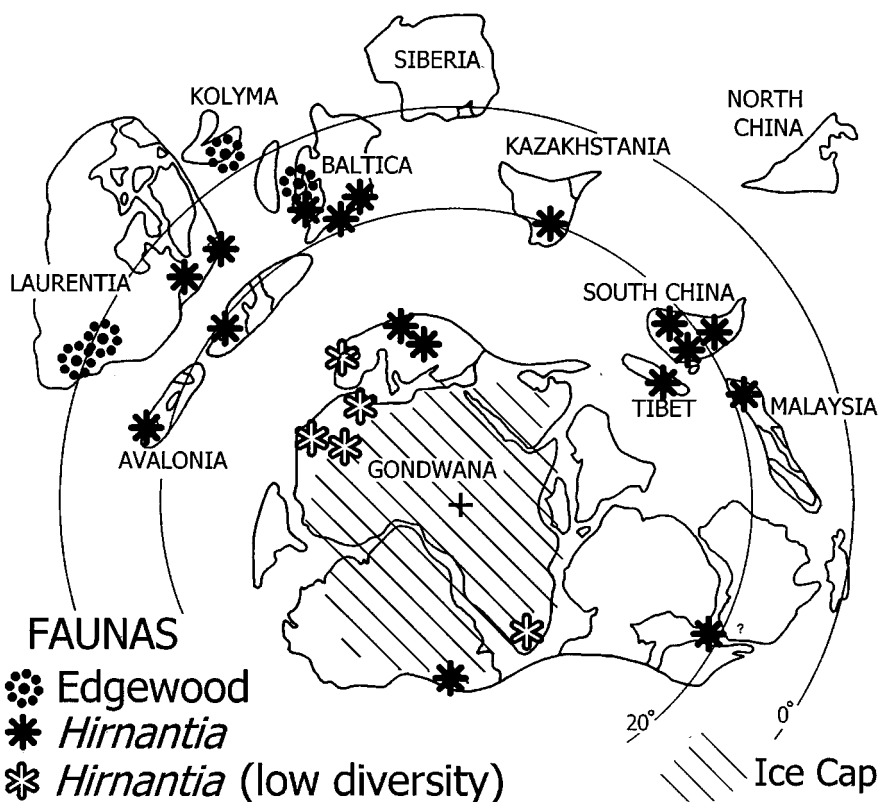
Correlations based on shelly fossils from this interval are difficult because faunas may have been tracking cool or warm water masses, making their presence diachronous from region to region. This problem is clearly shown in China, where the *Hirnantia-Dalmanitina* fauna locally ranges into the upper *Normalograptus persculptus* Zone (after the eustatic sea level rise), and elements of the fauna range into the Silurian Period (Rong et al 1999).

Evidence for glaciation in South America is less extensive than in Africa. A well-preserved record and good faunas are present only along the east side of the Andes in western Argentina and Bolivia. In the Argentine Precordillera, features of the widespread Don Braulio Formation strongly suggest terrestrial glaciation (Astini 1999, Peralta & Carter 1999). Three separate glacial advances were followed by the appearance of the *Hirnantia* fauna in near-shore sediments with ice-rafted clasts. Isotopic evidence of a positive  $\delta^{13}\text{C}$  from the *Hirnantia* fauna interval favor correlation with the main glacial drawdown interval elsewhere (see below). Striated glacial pavements are in the Late Ordovician Zapla Formation near the Argentina-Bolivia border (Martinez 1998). The Cancañiri Formation in southern Bolivia is a 175-m thick diamictite with marine deposits above and below. The Cancañiri Formation is a tillite deposited by a grounded glacier (Schönian et al 1999). In central Bolivia, marine periglacial deposits are present at the Ordovician-Silurian boundary interval (Díaz 1997).

The remainder of South America has a very poor Ordovician record. The only other area with reasonably certain latest Ordovician deposits is in northeastern

Brazil, where possible tillites are associated with stream deposits in the Amazonas and Parnaíba basins (Boucot 1988).

The extent of glaciers was reconstructed by Brenchley et al (1991), but at that time glaciers were not known in the Argentina-Bolivia region. Because there is strong evidence for glaciation in South Africa and South America, the ice cap may have covered much of Africa and eastern South America (Figure 2). The ice cap may have been on the order of 30,000,000 km<sup>2</sup> in size (Figure 2). This is considerably smaller than the Pleistocene ice caps, which covered more than 44,000,000 km<sup>2</sup> (Imbrie & Imbrie 1979). Comparisons of size are of little value because it is not possible to estimate the thickness of Ordovician glaciers. The sparse data over most of central Africa and eastern South America do not allow confidence that the ice cap was continuous over the region. Because the Pleistocene ice caps were discontinuous (for example, in Siberia), it is reasonable to expect that the Ordovician ice cap also was discontinuous over the region shown in Figure 2.



**Figure 2** Hirnantian faunas on map centered on south polar ice cap. [After Figure 1 of Harper & Rong (1995) and Figure 1 of Rong & Harper (1988).]

The Ordovician ice cap was mostly confined above 60° south latitude, with a possible small glacial lobe in South Africa to about 50° south. During the Pleistocene glaciation, the ice cap in North America moved to 50° north and in places extended to 40° north. Furthermore, because no continent was near the north pole, the glaciation was confined to the southern hemisphere, whereas Pleistocene ice caps were present at both poles.

The glacio-eustatic decline in sea level provides another way to compare ice volumes of the two glaciations. Estimates of maximum Pleistocene sea-level decline are about 100–150 m, whereas recent estimates suggest a decline during the Ordovician of less than ~100 m (Sheehan 1988, Brenchley et al 1994, Brenchley & Marshall 1999). However, large areas of the continents were covered by epicontinental seas during the Ordovician, whereas during the Pleistocene the extent of such seaways was near an all-time minimum for the Phanerozoic. Thus, in the Ordovician, more water needed to be sequestered in the glaciers to produce a sea-level decline equivalent to the Pleistocene.

The reconstruction of Figure 2 places the center of glacial ice in west Africa, as first suggested by Brenchley et al (1991). This position may approximate the Hirnantian pole. A pole location in North Africa, as shown in some prior reconstructions, would place the glaciers in Argentina, Bolivia, and South Africa, in much lower latitudes than would the position in Figure 2.

## ENVIRONMENTAL CHANGES DURING GLACIATION

Two environmental changes associated with the glaciation were responsible for much of the Late Ordovician extinction. First, the cooling global climate was probably especially detrimental because the biota was adapted to an intense greenhouse. Second, sealevel decline, caused by sequestering of water in the ice cap, drained the vast epicontinental seaways and eliminated the habitat of many endemic communities. Virtually all marine sections with sediments deposited above storm wave base record a regression near the end of the Ordovician (Cocks & Rickards 1988, Sheehan 1988).

Estimates of eustatic decline in the Late Ordovician are based on the displacement of various markers from preglacial to glacial times [e.g. marine communities (Landing & Johnson 1998)]. One of the better markers is erosion in midcontinent Laurentia, where underlying Late Ordovician marine sediments were incised about 48 m during maximum glacial drawdown (Kolata & Graese 1983). To produce a 48-m incision, eustatic decline had to lower sea level to expose the former sea bed, which had been several tens of meters below the storm wave base, then retreat enough to allow 48 m of erosion. A decline of more than 70 m is likely.

Brenchley & Marshall (1999) reviewed depositional patterns in Norway and England and found evidence that the drawdown was >100 m in this region. Harris & Sheehan (1997) found the Hirnantian stratigraphic sequence to involve considerably more than 50 m of glacioeustatic drawdown in Nevada and Utah.

## THE STABLE ISOTOPE RECORD

Stable isotopes provide an independent record of environmental changes across the Ordovician extinction. Studies of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  profiles across the extinction interval have been published for Anticosti Island, Québec (Orth et al 1986; Long 1993; Brenchley et al 1994, 1995); the Selwyn Basin, Northwest Territories, Canada (Wang et al 1993b); the Yukon Territory, Canada (Goodfellow et al 1992); Yichang, China (Wang et al 1993a); central Nevada (Kump et al 1999, Finney et al 1999); Baltica (Brenchley & Marshall 1999; Marshall et al 1997; Brenchley et al 1994, 1995; Kaljo et al 1999); Scotland (Underwood et al 1997); and western Argentina (Marshall et al 1997).

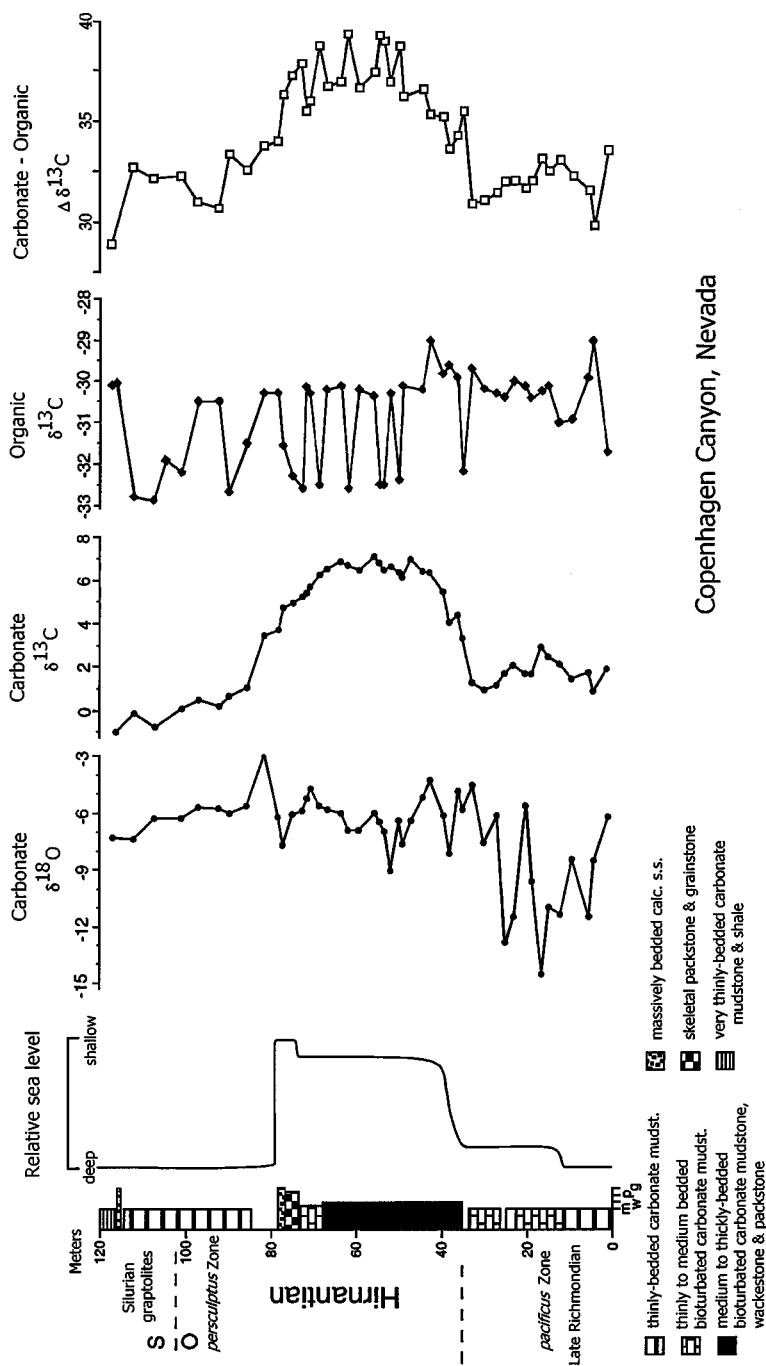
Although the analyses differed, with some based on brachiopod shells, whole-rock limestones and cements, and organic carbon from shales, the trends are remarkably similar. Furthermore, there is broad representation from low to high latitudes, and data is from both continental margins facing open oceans, oceanic regions, and epicontinental seas. A detailed profile with whole-rock and organic carbon analyses from central Nevada provides an example (Figure 3).

Copenhagen Canyon in central Nevada has one of the thickest and most continuous sections of limestone available (Kump et al 1999). The section was located on a western-facing, outer-carbonate ramp that was below the storm wave base prior to eustatic drawdown. The section shallowed to within wave base during the Hirnantian (Carpenter et al 1986, Kump et al 1999, Finney et al 1999). Whole rock or carbonate  $\delta^{13}\text{C}$  has a well-defined positive excursion of between 6% and 7%, between approximately 33 m and 82 m. The excursion of organic  $\delta^{13}\text{C}$  began earlier than the excursion of inorganic  $\delta^{13}\text{C}$  and had a positive shift of about 3% from the base of the section to about 42 m. Above 42 m, organic  $\delta^{13}\text{C}$  fluctuates between -30% and -33%.

The difference between carbonate  $\delta^{13}\text{C}$  and organic  $\delta^{13}\text{C}$ , termed  $\Delta\delta^{13}\text{C}$  in Figure 3, serves as a rough indicator of changes in atmospheric  $p\text{CO}_2$  (Kump et al 1999). In the case of the Copenhagen Canyon section changes in  $\Delta\delta^{13}\text{C}$  suggest that  $p\text{CO}_2$  may have fallen prior to the positive excursion of  $\delta^{13}\text{C}$ . However, during the excursion, which was probably tied to the main pulse of glaciation,  $p\text{CO}_2$  may have actually risen rather than declined.

Both the organic and carbonate  $\delta^{13}\text{C}$  excursions began in the *pacificus* zone (prior to the Hirnantian Stage) based on graptolites (Finney et al 1999). A similar pattern was found in Norway, where the  $\delta^{13}\text{C}$  excursion identified in bioclasts began prior to the Hirnantian, in rocks with Rawtheyan fauna below rocks with *Hirnantia* fauna. In both Norway and Nevada, the  $\delta^{13}\text{C}$  excursion is associated with the first indication of the glacio-eustatic regression.

Elsewhere, the initiation of glaciation, the beginning of the Hirnantian, and the isotopic excursion are usually interpreted to have begun simultaneously. Many of these sections were condensed and others included long intervals of nondeposition, which may not allow sufficient resolution to determine whether glaciation began in



**Figure 3** Stratigraphy and stable isotopic data from Copenhagen Canyon, Nevada. m, Mudstone; w, wackestone; p, packstone; g, grainstone. Carbonate  $\delta^{18}\text{O}$ : Whole-rock limestone expressed as per mil relative to the Late Cretaceous Pee Dee Formation belemnite standard (PDB) or the equivalent Vienna PDB (VPDB). Carbonate  $\delta^{13}\text{C}$ : Inorganic carbon from whole-rock limestones expressed as per mil relative to PDB (VPDB). Organic  $\delta^{13}\text{C}$ : Organic carbon from limestones, after removal of carbonate. Carbonate-organic  $\Delta\delta^{13}\text{C}$ : Isotopic difference between carbonate  $\delta^{13}\text{C}$  and organic  $\delta^{13}\text{C}$ , of individual samples expressed as  $\Delta\delta^{13}\text{C}$  in per mil units. [After Figure 1 of Kump et al (1999).]

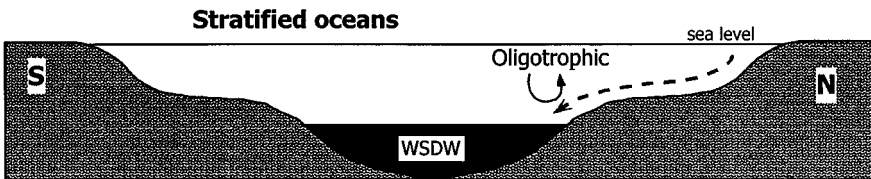


the Rawtheyan. However, because the Hirnantian faunas may have been tracking cool water and may have arrived in different places at different times, the extinction may not have taken place in any particular region until the sea level fell or cooler climates or cooler water arrived.

## PRODUCTIVITY HYPOTHESIS

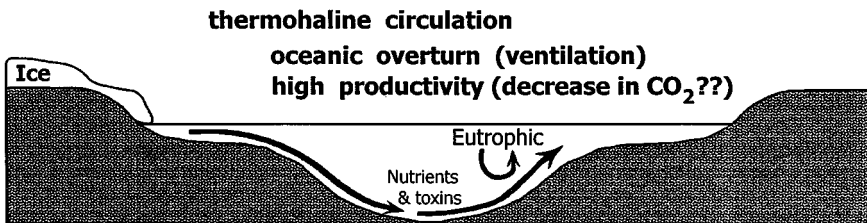
Brenchley et al (1994, 1995) provided the first explanation of how a continental glaciation could develop in the Ordovician (Figure 4). Increased primary marine productivity was stimulated by newly available nutrients brought to the surface by the initiation of thermal oceanic circulation. The oligotrophic oceans of the Ordovician became eutrophic. Increased primary productivity resulted in increased

### Pre-glaciation



### Hirnantian

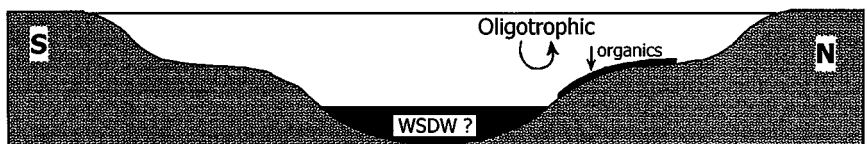
### Glaciation



### Post-glaciation

### Lower productivity

### BUT higher preservation of organics



**Figure 4** Depiction of differences in oceanic circulation and productivity between glacial and nonglacial time. Pre- and post-Hirnantian oceans shown with sluggish circulation and warm, saline deep waters derived from low-latitude evaporation. Hirnantian with strong thermohaline circulation that initiated change from oligotrophic to eutrophic ocean. [After Figure 3 of Brenchley et al (1995).]

burial of organic carbon in the oceans, which drew down atmospheric  $p\text{CO}_2$  to levels (7 to 10 times PAL), permitting full glaciation to develop.

The glaciation ended when movement of Gondwana over the pole reduced snowfall, which reduced the size of the ice cap, which slowed oceanic circulation. As nutrients levels declined, productivity fell.

Prior to the approach of Gondwana to the south pole, mid-Ordovician oceans were stable with warm, saline deep water (Railsback et al 1990). Workers had long noticed that late in the Ordovician, many deeper-water deposits that had been oxygen poor during much of the Ordovician became aerated (Sheehan 1988, Armstrong & Coe 1997). Sequential changes from graptolite shales, to bioturbated muds, to the appearance of body fossils were apparent in many deeper-water regions.

Thus, in the Late Ordovician, the stable ocean appeared to change to an ocean with strong mixing caused by introduction of thermohaline, deep-water circulation similar to the recent ocean (Berry & Wilde 1978, Wilde et al 1990). Upwelling brought nutrients to the surface, stimulating primary production. Berry et al (1990) suggest that the graptolite extinction was caused by side effects of the increased circulation—oxygenation of the dysoxic environment graptolites preferred and of toxins in the upwelling areas. The positive shifts in  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  in brachiopod shells were consistent with this hypothesis.

Rapid onset of glaciation is indicated by rapid eustatic and isotope changes. The rapid changes help explain why the Ordovician glaciation produced a major extinction whereas the larger but slowly developing Pleistocene glaciation did not. Pleistocene biotas had time to adapt to the gradual changes but Ordovician biotas did not.

Brenchley et al (1994, 1995) pointed out that there is no evidence of widespread deposition of organic carbon at this time. In fact, because deep waters were oxygenated, deposition of organic carbon should have been inhibited. They suggested that organic carbon was sequestered where the oxygen minimum layer intersected the sea floor or in deep oceans.

The most important assumption of this hypothesis is that atmospheric  $p\text{CO}_2$  levels were reduced during the glacial interval to between 7 and 10 times PAL. The opposing hypothesis suggests that  $p\text{CO}_2$  levels increased to near 16 PAL, during the glaciation.

## WEATHERING HYPOTHESIS

Analysis of the Copenhagen Canyon section (Kump et al 1999) suggested that atmospheric  $p\text{CO}_2$  was high (~16 times PAL) during the glaciation. This is supported by data from soils that formed during the glacial interval in Wisconsin (Yapp & Poths 1992).

High  $p\text{CO}_2$  during the glaciation is incompatible with the productivity hypothesis, and Kump et al (1999) proposed a new explanation of the glaciation. In

the weathering hypothesis, Late Ordovician mountain building resulted in exposure and weathering of silicate terrains, which resulted in atmospheric  $\text{CO}_2$  consumption.

Falling  $p\text{CO}_2$  during the Late Ordovician initiated ice-sheet growth, which was further stimulated by albedo effects of the ice, and the glaciation began. As the size of the ice sheets grew, they began to cover high-latitude silicate terrains, which diminished silicate weathering (and reduced  $\text{CO}_2$  consumption). The  $p\text{CO}_2$  increased until it approached 16 times PAL during the glacial maximum. The greenhouse effect then overcame the albedo effect of the glaciers and the exposed sea floor, and the glaciation ended.

In Copenhagen Canyon, the inorganic  $\delta^{13}\text{C}$  excursion begins about 30 m above the base of the section (Figure 3). The positive excursion to about 6% and 7% is similar to other excursions reported from around the world. The decline in the upper part of the sections reaches levels slightly less positive than at the base of the section. This excursion is commonly assumed to track the Hirnantian glaciation.

The organic  $\delta^{13}\text{C}$  does not have a large excursion similar to that of the inorganic  $\delta^{13}\text{C}$ . There is a positive shift of about 3% low in the section and then an irregular increase to  $-29\%$  at 42 m. From 42 m to the top of the section, organic  $\delta^{13}\text{C}$  decreases slightly but is highly variable, fluctuating between  $-33\%$  and  $-30\%$ .

Two features of the organic  $\delta^{13}\text{C}$  record should be noted (Figure 3). A large, rapid fluctuation of organic  $\delta^{13}\text{C}$  begins at about 42 m. The fluctuations may not be a primary signal, but if the fluctuation is found in other sections it may indicate high-frequency  $p\text{CO}_2$  fluctuations.

Significantly, the positive excursion of the organic  $\delta^{13}\text{C}$  record begins lower in the section (near 10 m) than does the inorganic excursion. The organic excursion corresponds with the first sedimentological indication of shallowing.

The difference between inorganic and organic  $\delta^{13}\text{C}$ , or  $\Delta^{13}\text{C}$ , serves as a rough estimate of  $p\text{CO}_2$ . The  $\Delta^{13}\text{C}$  record in Copenhagen Canyon indicates that  $p\text{CO}_2$  began to fall near the time of the first indication of shallowing and well before the excursion of inorganic  $\delta^{13}\text{C}$ . Furthermore, during the height of glaciation,  $p\text{CO}_2$  rose to high levels. This is in agreement with the timing of the weathering hypothesis.

In the weathering hypothesis, Late Ordovician mountain building in the Appalachians and Caledonides served as the trigger for declining  $p\text{CO}_2$ . The marine record of Sr isotopic trends supports this contention. The Sr isotopic trend changed direction toward increasingly more radiogenic values in the Late Ordovician (Burke et al 1982). This presumably reflects the exposure and weathering of radiogenic rocks during Late Ordovician orogenies. A similar decline in  $p\text{CO}_2$  during the Cenozoic is thought to have been caused by the Himalayan orogeny (Kump & Arthur 1997).

Declining  $p\text{CO}_2$  in the Late Ordovician may have reached a critical threshold, estimated to be 10–12 times PAL (Gibbs et al 1997), below which the greenhouse ended and the rapid growth of ice sheets began. A positive feedback was produced by high albedo of (a) the ice sheets and (b) the change from water-covered platforms

to exposed carbonate rocks (Kump et al 1999). Erosion of the exposed carbonates produced the inorganic  $\delta^{13}\text{C}$  excursion.

As the ice sheets advanced, they covered areas of exposed silicate rock in Africa and South America that had been present through the Ordovician. This overwhelmed the effects of orogeny, and  $p\text{CO}_2$  rose. Greenhouse conditions then melted the glaciers, and silicate terrains were reexposed. Atmospheric  $p\text{CO}_2$  then fell toward preglacial levels.

An implication of the weathering hypothesis is that orogenically exposed siliceous terrains reduced the greenhouse effect in the Silurian period, initiating other glaciations. Physical evidence for glaciations is limited, but isotopic studies suggest Silurian glaciations may have occurred (Azmy et al 1998). Sea-level fluctuation during the Silurian (Landing & Johnson 1998) could have been driven by advancing and retreating ice sheets. Sequence stratigraphic analyses in the Great Basin suggest that several eustatic sea-level declines in the Silurian exposed the carbonate platform and displaced facies patterns down a carbonate ramp to levels approaching the Hirnantian glacial drawdown of sea level. The most intense sea-level decline in the Llandovery produced karsts at least 50 m deep, which suggests the sea-level decline was  $>50$  m, which approaches the decline during the glaciation (Harris & Sheehan 1998).

The weathering hypothesis is based on limited results from a single section. Before the hypothesis can be accepted, the presence of high  $p\text{CO}_2$  during the glaciation must be confirmed.

Both hypotheses have a similar problem. Mountain-building episodes and carbon sequestering intervals are not always associated with glacial episodes.

The two hypotheses are not entirely incompatible. Regardless of what initiated glaciation, when glaciers reached the margins of Gondwana, thermal convection and upwelling of the previously anoxic oceans must have begun. The currents did oxygenate the ocean basins, and upwelling must have raised nutrient levels. Similarly, weathering of silicate rocks must have been a partial control of atmospheric  $p\text{CO}_2$ , and regardless of the primary cause of glaciation, advancing glaciers must have reduced silicate weathering.

## THE LATE ORDOVICIAN EXTINCTION

Four of the five Phanerozoic mass extinctions are of about the same size, but they are smaller than the massive end-Permian Extinction (Table 1). The Ordovician mass extinction took place after the Paleozoic EF radiated and established a remarkable plateau of diversity that lasted until the end-Permian Extinction (Figure 1).

There was a distinct pattern in the extinction of the three EFs during the Late Ordovician extinction. The Cambrian EF had a 44% loss of families, the Paleozoic EF a 30% loss, and the Modern EF only a 4% loss (Sepkoski 1991).

Even though the Late Ordovician extinction eliminated large numbers of species, it did not have a lasting effect on the nature of the Paleozoic EF. By the middle

**TABLE 1** Percentage decline of marine animal diversity in the five mass extinctions of the Phanerozoic<sup>a</sup>

Mass Extinction	Filtered Genera	Families
End-Ordovician (Ashgill to Llandovery)	–49%	–26%
Late Devonian (Givetian to Famennian)	–47%	–22%
End-Permian (Guadalupian to Induan)	–76%	–51%
End-Triassic (Norian to Hettangian)	–40%	–22%
End-Cretaceous (Maastrichtian to Danian)	–39%	–16%

<sup>a</sup>From Sepkoski (1996). Diversity decline calculated from the first listed stage to the beginning of the second stage. Filtered genera means single interval genera were eliminated from calculation.

Silurian, marine family diversity rebounded to the diversity plateau (Figure 1), and community complexity had recovered to preextinction levels.

Unlike the Paleozoic EF, the Cambrian EF did not recover the preextinction diversity (Figure 1). During the Ordovician radiation of the Paleozoic EF, the locus of the Cambrian EF moved progressively offshore (Sepkoski & Sheehan 1983, Sepkoski & Miller 1985). Part of the success of the Cambrian EF may have been an adaptation to dysoxic conditions of the deep oceans, which had little mixing. This environment was aerated by deep oceanic, density-driven currents during the glaciation (Berry & Wilde 1978, Wilde et al 1990).

The Modern EF appeared in the mid-Ordovician and continued to diversify through the Paleozoic. Located in near-shore environments, the Modern EF had just begun to radiate, but none of its components were permanently reduced or impeded for more than a few million years (Sepkoski & Sheehan 1983, Sepkoski & Miller 1985).

The extinction marked the end of an ecologic evolutionary unit (EEU), which was a period of stasis in evolution during which community compositions changed through in-place evolution of community members (Boucot 1983, Sheehan 1996). During an EEU, few lineages evolved new lifestyles that would allow them to move into new communities (Boucot 1983, Sheehan 1996). Morphologic evolution and speciation proceeded within communities, but the changes primarily were adaptations to life in the same niche.

Extinction events disrupted EEUs by eliminating many members of communities. Following extinction events, communities were restructured, with many surviving groups evolving new adaptations that allowed them to live in niches they had not occupied previously. The classic example of this process is the evolution

of mammals following the end-Cretaceous Extinction, when small insectivorous and omnivorous mammals evolved to become strict herbivores and carnivores and replaced dinosaurs in land communities.

The Ordovician extinction was severe in terms of the number of taxa lost but was less significant in terms of the ecologic consequences. Although the extinction marked the end of one EEU and was followed by reorganization of communities, there was relatively little evolutionary innovation during the recovery. Newly developing communities were largely drawn from surviving taxa that had previously lived in similar ecologic settings.

For example, new groups of brachiopods, especially among the spiriferids, atrypids, athyrids, stropheodontids, and pentamerids, increased in abundance in Silurian communities, whereas groups such as plectorthoids, orthoids, and plectambonitoids declined (Harper & Rong 1995, Harper et al 1999a). But the brachiopods remained community dominants, and although the new Silurian communities were restructured, their trophic organization was similar to that in the Ordovician (Droser et al 2000, Bottjer et al 2001).

Reef development was interrupted by the extinction, but the new Silurian reef communities were similar to preextinction communities (Copper 1994, Copper & Brunton 1991). Again, a modest change in trophic structure occurred.

Other extinction events produced more significant changes in the trophic structure. The mid-Devonian Extinction, although smaller in terms of taxonomic loss, had more severe changes in trophic structure of benthic communities (Droser et al 2000). Reef communities were also reorganized (Copper 1994).

## Two Pulses of Extinction

The extinction had two primary pulses (Brenchley et al 1994, 1995; Brenchley & Marshall 1999). The first pulse was at the initiation of the glaciation, when sea level declined, the global climate changed, and oceanic circulation increased. The second pulse of extinction occurred at the end of the glaciation, when sea level rose, the global climate returned to preglacial conditions, and oceanic circulation became sluggish. However, these pulses of extinction were probably caused by several different kinds of environmental disruption, and different environmental settings were affected by different disruptions.

Although some groups were more strongly affected by the extinction, every major group of organisms that has been studied during this event was effected by the extinction. In many groups, extinction was concentrated in only one of the two pulses. The various environmental changes affected each group in different ways.

The importance of particular environmental changes also depended on the environment in which organisms lived. For example, the biota in epicontinental seas was strongly affected by sea-level decline, whereas the biota in open marine settings was not. The tropical biota faced less-severe temperature changes than the biota in higher latitudes.

## Extinction in the Epicontinental Seas

The isolated epicontinental seas had strongly endemic provinces, whereas the open oceans and habitats along the margins of continents had more cosmopolitan faunas. This zoogeographic pattern has been described for brachiopods (Sheehan & Coorough 1990), corals (Elias & Young 1998), conodonts (Barnes & Bergström 1988), and bryozoans (Anstey 1986). Different physical changes associated with the glaciation played dominant roles in the two regions.

In the endemic epicontinental sea provinces, glacio-eustatic sea-level decline drained the seaways and eliminated habitat. Sea-level decline at the onset of glaciation was the single most important physical change. With the sea-level decline, epicontinental sea species may have attempted to migrate into marginal settings around the continent, but these habitats were already occupied by an incumbent fauna that had previously established its superiority in this habitat. Epicontinental sea endemics had been unable to establish themselves in these regions previously and were unable to do so during the fall in sea level.

## Shallow Benthos in the Open Oceans and Continental Margins

Sea-level decline in open marine and continental margin settings was of minor importance during any of the mass extinctions (Jablonski & Flessa 1986). Habitat may actually have increased in area because islands are essentially cone shaped and sea-level decline would increase the area of shallow water (Jablonski & Flessa 1986).

Climatic changes and changes in upwelling associated with increased oceanic circulation fueled the extinction. At the start of the glaciation, the harsher climate and increased oceanic circulation produced a pulse of extinction, after which survivors adapted to the new conditions.

The glaciation ended rapidly, and the climate returned to preglacial conditions. Sea level rose and oceanic circulation stagnated. In many regions, sediments with Hirnantian age faunas are overlain by deeper-water, anaerobic or dysaerobic sediments. These changes were associated with a second pulse of extinction, when organisms adapted to the glacial regime died.

During Phanerozoic glaciations, the band with tropical climates contracted, but the central tropics did not experience dramatic temperature changes. In the central tropics, open environments were probably primarily affected by changing oceanic circulation, whereas in progressively higher latitudes, temperature decline was progressively more important (Figure 4).

## Open Marine Extinction

Pelagic faunas in the open ocean contracted toward the equator as the glaciation intensified, probably as a result of cooling temperatures in mid-to-high latitudes.

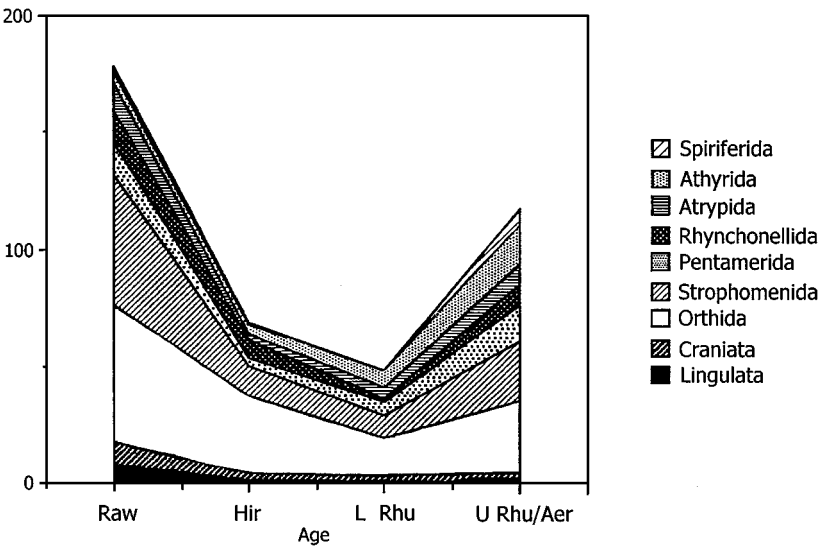
In addition, as oceanic circulation increased, changing nutrients and toxins from deep water entered the ecosystem (Berry & Wilde 1978, Wilde et al 1990). This caused an initial pulse of extinction. At the end of the glaciation, the preglacial temperature regime returned, and circulation stagnated, producing another pulse of extinction.

EXTINCTION IN THE PALEOZOIC EF BENTHOS

Brachiopods

Brachiopods were among the most common members of benthic communities during the Ordovician, and their history across the extinction event is well documented. Harper & Rong (1995) (see Figure 5) compiled standing diversity of genera in the main orders of brachiopods across the event. Brachiopods declined significantly in both pulses of the extinction. Many clades, such as Pentamerids, Athyrids and Spiriferids, expanded after the extinction (Figure 5), presumably filling vacated niches. Some groups, such as Orthids and Strophomenids, declined slightly. The inarticulates (Craniata and Lingulata) had the most significant lasting decline (Harper & Rong 1995, Holmer & Popov 1996). They were members of the Cambrian EF, which was particularly hard hit by the extinction.

The strongly endemic brachiopods of the epicontinental seas of the isolated plates of Laurentia, Siberia, and Baltic were nearly eliminated during the first



**Figure 5** Taxonomic changes of Brachiopods. Number of brachiopod genera in brachiopod orders through the Late Ordovician and early Silurian. [After Figure 4 of Harper & Rong (1995).]



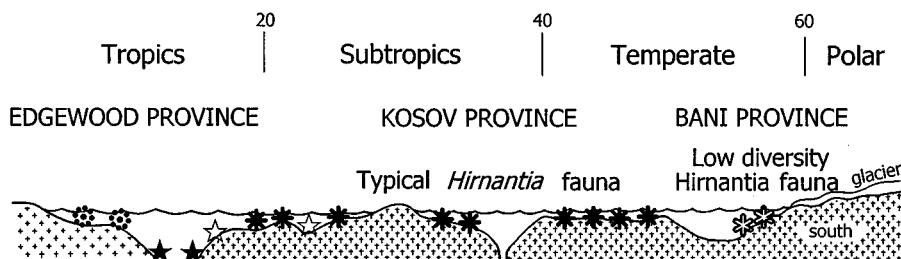
pulse of the extinction (Sheehan & Coorough 1990). Loss of habitat was the most likely cause of their extinction.

Brachiopods within the epicontinental seas were strongly endemic, but brachiopods from the margins of the same continents were cosmopolitan (Sheehan & Coorough 1990). After the extinction event, many taxa that during the Ordovician were living on the margins of the continent quickly invaded epicontinental seas.

The deepest-water Ashgill communities were in poorly oxygenated environments adjacent to graptolite shale facies and distal trilobite faunas. These communities, termed the *Foliomena* communities, are characterized by small size, thin shells, and adaptations for life on soft substrates (Sheehan 1973b, Cocks & Rong 1988, Harper & Rong 1995, Harper et al 1999b). The fauna first appeared in the mid-Caradoc and increased in diversity and geographic extent through the Ashgill. The fauna disappeared at the base of the Hirnantian, as did the facies in which it occurred. As with graptolites, ventilation of the ocean and other oceanographic changes may have disrupted the preferred habitat. In the Oslo region and in Bohemia, some elements did survive into the Silurian.

**The Hirnantia Fauna** At the beginning of the glaciation, a new set of brachiopod faunal provinces developed in temperate to subtropical regions (Figures 2 and 6). Typically, the new faunas suddenly replace a diverse set of Ashgillian open marine communities. The provinces include the tropical Edgewood Province, the temperate-to-subtropical Kosov Province, and the high-latitude Bani Province. The most common and widely distributed fossils at this time belong to the *Hirnantia* fauna sensu stricto, which was present in shallow-to-intermediate depths in the Kosov Province. However, many elements of the *Hirnantia* fauna are common in all the new provinces.

Epicontinental seas were drained, so the distribution is confined to the continental margins and open ocean environments. In areas that previously had carbonate deposition, the onset of siliceous deposition and incursion of the *Hirnantia* fauna probably records a cooling event associated with the glaciation. Although the



**Figure 6** Section across Hirnantian climatic belts showing depth distribution of brachiopod faunas in the three Provinces. [After Figure 7 of Rong & Harper (1988).]

*Hirnantia* fauna is commonly developed in noncarbonate sediments, it is found in carbonate settings in China, Estonia, and Austria.

Common brachiopods of the *Hirnantia* fauna include some that survived into the Silurian (*Hirnantia*, *Dalmanella*, *Leptaena*, *Hindella*) and others that became extinct at the end of the glaciation (*Kinnella*, *Draborthis*, *Paromalomena*, *Plectothyrella*).

The *Hirnantia* fauna is associated with the *Dalmanitina*/*Mucronaspis* trilobite fauna. The term *Hirnantia* fauna sensu stricto is best viewed as a group of communities from the Kosov faunal province, with related communities in other regions.

In high latitudes, especially near the margins of the ice sheets, an impoverished fauna with several members of the *Hirnantia* fauna is termed the Bani Province (Rong & Harper 1988). It must have been adapted to cold water environments.

The Edgewood Province is present in tropical regions of Laurentia and adjacent Kolya, with incursions into Baltica. It includes many genera common to the *Hirnantia* fauna sensu stricto. Carbonate deposition continued in these areas, and the Edgewood communities commonly overlie faunas with Laurentian affinities.

Hirnantian age brachiopods are unknown north of the paleoequator, with the exception of those from the Kolya in the Edgewood Province (Figure 2). They have not been recorded in Siberia, northern China, or the current western margin of Laurentia.

Deeper-water shelf assemblages are little known, partly because they were displaced during the decline in sea level. A few assemblages are known from the Kosov Province (Rong & Harper 1988). These deeper communities contain a few elements of the *Hirnantia* fauna (e.g. rare *Hirnantia*, *Kinnella*, *Hindella*, *Paromalomena*) but are dominated by brachiopods that are not common in the *Hirnantia* fauna. These include some genera that were common in this setting prior to the Hirnantian (e.g. *Dicoelosia*, *Skenidioides*, *Salopina*).

Once sea level rose at the end of the glaciation, the *Hirnantia* fauna and communities in the Edgewood Province disappeared as distinctive entities, although some genera survived and were present in the new Silurian communities. The deeper-water communities had many survivors that became important members of the Silurian fauna. The wide geographic distribution of these brachiopods contributed to the strong cosmopolitanism of Silurian faunas.

**Corals and Stromatoporoids** Rugose and tabulate corals originated independently during the Ordovician radiation. Generic abundance of tabulate corals exceeded that of the rugose corals in the Ordovician, but generic abundance of both were increasing into the Ashgill. The Ordovician extinction reversed the dominance, and rugose genera outnumbered tabulates for the rest of the Paleozoic (Scrutton 1988). However, both groups continued to increase in abundance until the Late Devonian extinction, which had a much greater effect on coral faunas than did the Ordovician event (Scrutton 1988, Droser et al 2000).

Two great coral realms were present (Webby 1992). A tropical realm in North America, Siberia, and tropical Gondwana was characterized by diverse solitary and

colonial rugose corals, and by tabulate corals associated with stromatoporoids. In a temperate realm, solitary rugosans dominated, tabulates were less diverse, and stromatoporoids were absent.

Changes in North American corals across the extinction have been extensively documented in a series of studies summarized by Elias & Young (1998). The endemic Richmondian corals of North America were common throughout the epicontinental seas. These faunas became extinct in the first pulse of extinction, when sea level fell. During the glacial interval, a narrow seaway, extending up a failed rift along the present southern margin of North America, was the site of the Edgewood Province, which in addition to corals includes well-described brachiopod, bryozoan, and crinoid assemblages.

Edgewood corals are unrelated to those of the endemic Richmondian faunas of North America. No solitary corals survived the extinction, and of the diverse Richmondian colonial corals, only *Calapoecia*, *Paleofavosites*, and *Palaeophyllium* survived into the Silurian. The Edgewood corals were derived from the marginal, more cosmopolitan, open-ocean environments that encircled North America. The postextinction coral fauna, which would become community dominants in the Silurian, is a mixture of the clades that had been common previously in the Ordovician and newly dominant clades (Elias & Young 1998, Young & Elias 1999).

As sea level rose after the glaciation, new solitary rugose genera were introduced, some new tabulate corals evolved from members of the Edgewood fauna, and some new tabulates immigrated into North American seaways (Elias & Young 1998, Young & Elias 1995).

The second pulse of the extinction had little affect. Apparently the rise of sea level renewed the epicontinental seas, and Edgewood Province corals simply took advantage of the newly available habitat.

Even though extinction levels were very high, standing diversity remained high. During the Richmondian Stage, the epicontinental seas of northern Manitoba had 30 species in 17 genera. During the glacial interval, 22 species in 15 genera of corals existed in the Edgewood Province. By the middle Llandovery in the Cincinnati Arch region, coral diversity increased to 54 species in 29 genera.

Because detailed studies of the marginal faunas and faunas from other regions need to be completed, it is difficult to look at global patterns in the same detail as the regional patterns that are so well documented in Laurentia.

In South China, a rugose coral-dominated assemblage with a few tabulate corals and no stromatoporoids is associated with the *Hirnantia* fauna (Rong & Chen 1987). This fauna resembles the cool-water coral realm and is in agreement with suggestions that the *Hirnantia* fauna is a cool-water fauna.

**Echinoderms** Although crinoids suffered considerable extinction, they were not displaced in importance after the event. In eastern North America, 13 families disappeared, a 45% decline. About 70% of genera were lost (Eckert 1988). Extinction was concentrated in the first pulse of extinction. In the Hirnantian Edgewood seaway, new groups of crinoids appeared, and of these 70% of the genera survived

into the Silurian (Ausich 1987, Eckert 1988). Generic diversity of crinoids quickly recovered, and morphologic disparity was essentially unaffected by the extinction (Foote 1999).

Several minor classes of echinoderms declined in diversity across the extinction event. These groups represent about half of the Paleozoic EF classes that declined (Sepkoski & Sheehan 1983). Cystoids were common in the Ordovician, but their post-Ordovician replacement by crinoids has been attributed to selective advantage of feeding structures in crinoids, rather than to the extinction event (Paul 1988). The poor fossil record of cystoids in the Llandovery makes the extinction difficult to interpret, but the poor Llandovery record probably reflects their demise in importance.

**Bryozoa** Bryozoans families declined only about a 13% across the extinction (Taylor 1993). However, generic diversity declined substantially, and the two dominant Ordovician groups, the Cryptostomata and Trepostomata, declined and never attained their former diversity (McKinney & Jackson 1989).

Bryozoans were most common in tropical settings (Taylor & Allison 1998). The bryozoan record is well documented in Laurentia and Baltica (Tuckey & Anstey 1992). Epicontinental seas in North America had endemic faunas during the Ashgill (Anstey 1986). The extinction of endemic North American Bryozoa came in the first pulse of the extinction, with a loss of 86% of species and 21% of genera (Tuckey & Anstey 1992). During the Hirnantian, the Edgewood Province of North America had a low-diversity bryozoan fauna with Baltic affinities (Tuckey & Anstey 1992) that lost only 7% of its species and 5% of its genera by the end of the Hirnantian. Baltica had a different pattern of extinction, losing only 8% of its species and 5% of its genera in the first pulse, but 83% of its species and 22% of its genera at the end of the Hirnantian.

**Conodonts** As many as 80% of conodont species became extinct (Sweet 1990), and recent studies suggest even greater extinction (Barnes & Zhang 1999). In the Ashgill, a highly endemic, low-latitude, warm-water mid-continent realm was centered in Laurentia. A more cosmopolitan North Atlantic realm was present in open marine environments that are regarded by conodont workers as a cool realm. Low-latitude assemblages contain two to three times the number of species as high-latitude, peri-Gondwana settings (Barnes & Zhang 1999). Little change is present from the late Caradoc through the early and mid-Ashgill, and few new genera originated in this interval.

The extinction of conodonts is concentrated in the lower *N. persculptus* Zone. North Atlantic realm conodonts were nearly eliminated during the extinction, and most of the survivors were from the mid-continent realm (Barnes & Bergström 1988). Exact timing of the event is difficult because much of the data is from Anticosti Island, where the biostratigraphic correlations are at odds with the isotopic studies.

Conodont recovery from the extinction is very rapid on Anticosti Island. Just above the Ordovician-Silurian boundary (above the *N. persculptus* Zone),

21 species are present and of these 16 appear to have originated after the extinction (Barnes & Zhang 1999). Survival was high among conodonts with a simple cone morphology, which has been interpreted to be associated with a pelagic habitat (Sweet 1990).

**Ostracodes** A third of ostracode families disappeared across the extinction event. The most significant change was the replacement of hollinomorphs by beyrichians (Copeland 1981).

**Cephalopods** Nautiloids experienced severe extinction, with the most important orders declining to only a few genera (Crick 1990). Of eight Ordovician orders, (a) one became extinct, (b) three survived and by the Wenlock had regained or surpassed their Ordovician diversity, and (c) four survived but never regained their prior diversity (House 1988). Unlike most other groups, the postextinction faunas were highly endemic, which suggests that the extinction may have been concentrated in the more cosmopolitan taxa (Crick 1990).

## Biota in the Water Column

The history of graptolites is well known, but many other members of the plankton have been little studied (Rickards 1990). Some members of the plankton, such as larval stages of many organisms and possible soft-bodied organisms, must have been present but left a scant fossil record in the early Paleozoic.

The fossil record of primary producers is dominated by the Acritarchs, which were abundant from the Ordovician through the Devonian. Radiolarians were locally common, especially in offshore regions.

Chitinozoa, which are probably egg cases of undetermined small metazoans, are most abundant in the same sediments as graptolites (Paris & Nölvak 1999). Graptolites were the first abundant macrozooplankton in the fossil record, and they fed on minute phyto- and zooplankton.

The record of nektonic predators is dominated by cephalopods. Many trilobites had planktonic growth stages and some groups, especially the agnostids, probably lived in shallow water. Agnostids did not survive the extinction event. The extinction in the pelagic biota may have been more severe than in the benthos, but the poor fossil record makes generalizations difficult.

**Graptolites** The pelagic graptolites were expanding during the early Ashgill and the extinction event was sudden and devastating (Rickards 1977, Melchin & Mitchell 1991, Koren 1991). Graptolite distribution shrank from nearly global to being confined to the tropics (Skevington 1978). Diversity declined to about six species, and within the limits of stratigraphic resolution the extinction was very abrupt. Disparity declined also, and all the surviving species have a single astogenetic pattern (Melchin & Mitchell 1991).

The initial reduction of habitable area into the tropical belt was combined with the loss of the dysaeroic graptolite habitat and possible introduction of toxins

(Wilde et al 1990, Berry et al 1990). At the end of the glaciation, anoxia once again was common in the oceans, the temperature regime returned to preglacial levels, and graptolites radiated. Taxonomic diversity increased rapidly from a low of 6 to 20 species in the *N. persculptus* Zone and to 60 species by the *Normalograptus acuminatus* Zone. Disparity also rebounded rapidly, and all but two of the primary morphologic groups of the Silurian had evolved from a single group during postglacial Ordovician (Melchin & Mitchell 1991).

**Acritarchs** Acritarchs are organic walled microfossils that diversified in the Ordovician Period. They were significantly reduced at the end of the Ordovician but recovered and remained abundant through the Devonian Period. Many acritarchs were cysts or resting stages of planktonic algae. The four main morphologic groups in the Ordovician successfully survived the extinction event (Dorning 1993).

A global examination of the extinction of acritarchs is not yet possible. There was strong provinciality, with a strong latitudinal gradient (Dorning 1999, Wicander & Playford 1999, Servais 1997). Local studies of acritarchs show a rapid extinction event followed by rapid diversification during the Rhuddanian (Martin 1989, Duffield & Legault 1981).

**Radiolarians** No comprehensive study of radiolarians across the extinction event has been conducted. Local studies of faunas suggest there was only modest change across the boundary. For example, early Silurian radiolarian faunas from Nevada more strongly resemble Late Ordovician (Caradocian) faunas from localities in Nevada than any other described fauna (Noble & Aitchison 1995).

**Chitinozoans** A major reduction of chitinozoan species during the Ordovician extinction (Grahn 1988, Paris et al 1999, Paris & Nolvak 1999) was preceded by a gradual decline in species during the entire Ashgill. Whether the Ashgill decline was real or caused by the Signor-Lipps effect is unclear from the data presented. Local studies usually show nearly complete turnover of chitinozoan species across the extinction event, as for example, the Monitor Range of Nevada (Soufiane & Achab 1999).

Morphological innovations appeared continuously during the entire Ordovician, but following the Ordovician extinction no innovations appeared until almost the beginning of the Wenlock (Paris et al 1999). This trend is unusual because surviving groups commonly evolve numerous innovations following extinction events.

## THE CAMBRIAN EF

By the Late Ordovician, the Cambrian EF was offshore and isolated from the Paleozoic EF (Sepkoski & Sheehan 1983, Sepkoski & Miller 1985). The Cambrian EF was in decline, and the primary components were trilobites and inarticulate brachiopods.

## Trilobites

About 50%–60% of Rawtheyan genera survived into the Hirnantian. No genera appeared in the Hirnantian, and about half of the Hirnantian fauna became extinct by the end of the Hirnantian. Thus, about 70% of Rawtheyan genera were extinct by the Silurian (Lespérance 1988, Briggs et al 1988, Owen et al 1991, Adrain & Westrop 2000).

In the Rawtheyan, distinct genera of trilobites were present in different communities along environmental transects from shallow to deep water. In the Hirnantian, *Leonaspis*, *Brongniartella*, *Platycoryphe*, and *Dalmanitina* are widely distributed, eurytopic, and locally abundant, but other trilobites were uncommon. Most Hirnantian genera were endemic and were generally relicts of earlier faunas. The well-established biofacies of the Rawtheyan disintegrated (Owen et al 1991) during the first pulse of the extinction.

Trilobites are dominant members of the Cambrian EF, which declined during the Ordovician radiation of the Paleozoic EF (Figure 1). During the Ordovician radiation, new clades of trilobites, collectively referred to as the Whiterock fauna (Adrain et al 1998), appeared. During the Ordovician extinction, clades that originated during the Cambrian were entirely eliminated, and all survivors were members of the Whiterock fauna. Although the Whiterock fauna survived, it also underwent a 26% extinction of families.

Trilobite extinction was most severe in deep environments and eased into shallower depths (Owen et al 1991). This suggests that the surviving clades were primarily the newer clades, which had become integrated into shallower-water communities during the Ordovician. It appears that the Whiterock fauna trilobites evolved alongside and became part of the Paleozoic EF communities during the Ordovician radiation.

Asaphine trilobites, which had a planktic growth stage, had very high extinction, with only a single genus surviving into the Silurian (Chatterton & Speyer 1989). Similarly, unusually high extinction rates occurred among trilobites that were obligate planktic forms (Owen et al 1991), including the agnostids, which became extinct.

## Inarticulate Brachiopods

Inarticulate brachiopods, also members of the Cambrian EF, were severely affected by the extinction (Holmer & Popov 1996). Six of 15 families disappeared, but unlike the pattern found on most members of the Paleozoic EF, diversity did not rebound in the Silurian (Holmer & Popov 1996, Harper et al 1993).

## THE MODERN EF

Molluscan-dominated near-shore communities included many elements of the Modern EF. Bivalves included infaunal nuculoids and epifaunal to semiinfaunal byssate mytiloids and pteriods (Pojeta 1985, Hallam & Miller 1988). Generic

extinctions were more than 60%. Greater extinction of epifaunal than infaunal bivalves has been attributed to a return of anoxia following the glaciation (Kriz 1984).

Gastropod generic diversity declined by only 31% across the extinction. The gradual radiation of gastropods during the early Paleozoic was not slowed by the extinction event (Erwin & Signor 1991).

## RECOVERY OF DIVERSITY

Diversity recovered during the first few million years of the Silurian Period. Groups such as graptolites, which speciated rapidly, recovered quickly, and were increasing by the end of the *N. persculptus* Zone at the end of the Ordovician Period (Melchin & Mitchell 1991, Koren 1991). In the earliest Silurian Period, normalograptids, dipograptids, monograptids, and coronograptids appeared sequentially by the end of the Rhuddanian Stage at the beginning of the Silurian (Rickards 1977, Berry 1996).

Most fossil groups regained prior levels of generic diversity by the middle-to-late Llandovery. In Baltica, Kaljo (1996) documented the relative pace of recovery of diversity by graptolites, corals, and chitinozoans. He also found that graptolites recovered most quickly, and corals increased in diversity through the Llandovery. Chitinozoans were unusually slow to radiate in the Baltic, a trend that Paris et al (1999) found to be true globally.

Family diversity rebounded to prior levels by the end of the Llandovery (Sepkoski 1991, 1996). The family record is particularly important because it provides insight into the recovery of morphologic diversity in the oceans. The loss of 26% of families during the event suggests that disparity declined significantly across the event. Recovery of family diversity suggests that disparity quickly returned to preextinction levels.

The pattern is consistent with the idea that extinctions remove constraints on evolution caused by the superior adaptations of incumbent species. Following the extinction, morphologic evolution progressed at a more rapid pace because there were fewer constraints, which allowed species to evolve, adapting to life in habitats they were previously unable to invade.

Taxonomic recovery of diversity took on the order of 5–7 million years (the first half of the Llandovery). The recovery may have been more rapid because the Lipps-Signor effect, which makes extinctions appear more gradual than they were (Sheehan & Watkins 1995), makes the record of recovery intervals longer than the actual recovery.

## RECOVERY OF ECOLOGIC STRUCTURE

Ecologic structures were eliminated by the extinction event. During the Ordovician, an array of communities were present in the epicontinental seas and on the shelf and slopes of all the continental plates. The first pulse of extinction eliminated the



epicontinental sea communities, and new Hirnantian age communities developed in shelf and slope settings.

The second pulse of extinction eliminated Hirnantian age communities, producing a sparse fauna in most regions. The low-diversity faunas then radiated and new communities formed.

Ecologic changes were most marked in the epicontinental seas. Marginal and open marine faunas, especially in deeper shelf and slope settings, had more survivors than the epicontinental seas. As a result, many new communities in the marginal regions had marked similarities with Ordovician communities.

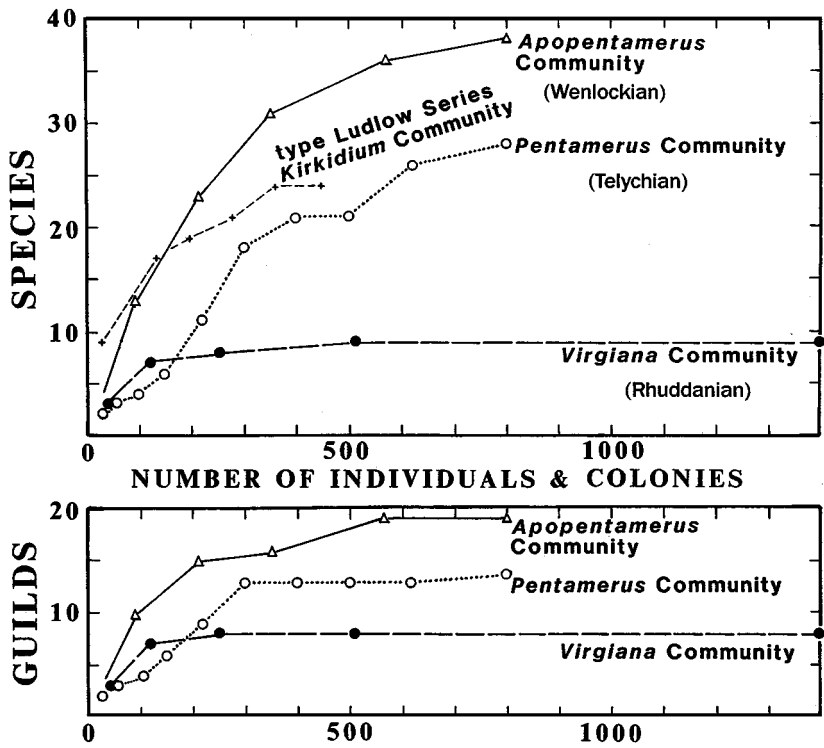
The disruption ended an ecologic evolutionary unit (EEU). EEUs were long periods of community stability during which organisms evolved but tended to stay within communities, rather than evolve features that would allow them to live in other communities (Boucot 1983). Paleozoic benthic communities were loose associations of species that repeatedly occur in similar habitats. The communities persisted for tens of millions of years (Boucot 1983). Jackson et al (1996) discuss examples of Pleistocene and recent communities that persist over geological intervals. Species evolved within these communities, and the communities changed, although communities themselves are not entities that could evolve (Bambach & Bennington 1996).

Extinction events terminated most EEUs (Sheehan 1996). Recovery intervals lasted several millions of years. During the recovery, many lineages evolved the ability to live in habitats they did not occupy prior to the extinction.

Prior to the extinction event, many of the groups that eventually moved into the renewed seaways had lived around the margins of the Ordovician seaways, but they had not been able to migrate into the seaways. A good example is the distinctive bilobed brachiopod *Dicoelosia*, which was common around the margin of Laurentia (e.g. in Gaspé, Québec, and Alaska) but never in the Ordovician epicontinental seas. After the extinction eliminated the incumbent fauna, *Dicoelosia* invaded the epicontinental seas of North America for the first time.

Incumbent species in the Ordovician epicontinental seas may have been better adapted to conditions in the epicontinental seas than were the marginal faunas. The extinction event removed incumbents and allowed other groups to move into the vacated habitats. This may be an example of competitive exclusion.

The first comminutes after the extinction commonly had low diversity (few taxa survived). During the early Silurian, more species evolved and alpha diversity of communities increased. Watkins (1994) has documented these changes in early Silurian communities in Wisconsin (Figure 7). He examined shallow-water communities (from environments ranging from near normal wave base down into the range of storm wave base). He found a recovery of both species diversity and the number of different guilds to which the species belonged through the early Silurian. Relatively few communities were present following the extinction, and individual communities occupied a wide range of physical habitats. Through time, the number of communities increased. As a result, individual communities developed narrower ecologic ranges (Sheehan 1980).



**Figure 7** Ecologic recovery of communities after the mass extinction. Diversity of species and guilds, exclusive of pelmatozoans, in Silurian collections from pentamerid-dominated communities in Wisconsin. The *Kirkidium* community is from the Ludlow of the Welsh borderland. [After Figure 5 of Watkins (1994).]

Another aspect of ecologic recovery is seen in the persistence of individual communities. During EEUs, many communities persisted for millions of years. However, during the recovery, early communities persisted for short periods and were then replaced by new communities composed of species that invaded from other regions (Sheehan 1996).

One example of this instability is in the shallow-water, pentamerid-dominated communities of North America. Sheehan (1980) documented the initial development of brachiopod-dominated *Virgiana* Community in western North America following the extinction. They disappeared abruptly at a sequence stratigraphic boundary in the Aeronian Stage (Harris & Sheehan 1997, 1998). The *Virgiana* community was replaced by a community dominated by *Pentamerus*, another pentamerid brachiopod, but not derived from *Virgiana*. The *Pentamerus* community persisted through another stratigraphic sequence and was replaced by the *Pentameroides* community in the Telychian Stage. In this instance, however, there was evolutionary continuity because *Pentameroides* evolved from *Pentamerus*.

The EEU was once more characterized by evolution of taxa persisting in particular habitats.

Similar ecologic patterns were found in conodont faunas from the Baltic. During the Llandovery, conodont faunas were first distributed broadly over the Baltic shelf and upper slope, but they gradually differentiated into two, and then three, distinct biofacies (P Männik, personal communication.)

Reefs declined in size, geographic distribution, and diversity during the extinction (Copper 1994). Reefs recovered quickly during the early Silurian and by the Wenlock they were prominent and widely distributed. The extinction had little long-term effect, and the biota was broadly similar to that of the Ordovician (Copper 1994, Copper & Brunton 1991).

## Preferential Survival of Groups with Simple Morphology

Documentation of the geologic history of morphological diversity in the various fossil groups is still in its infancy (see Foote 1997, 1999). Several taxonomists have suggested that groups with “simple morphology” preferentially survived the extinction. Examples include graptolites (Berry et al 1990), bryozoans (Anstey 1986), conodonts (Sweet 1990), and acritarchs (Duffield & Legault 1981).

## ZOOGEOGRAPHIC PATTERNS

Widespread genera of both brachiopods (Sheehan & Coorough 1990) and trilobites (Robertson et al 1991) have been shown to have preferentially survived the extinction. The more regions a given genus lived in during the Late Ordovician, the more likely it would be to survive the extinction. Brachiopods of the *Hirnantia* fauna were an exception, because the fauna was widespread during the Hirnantian (Figure 2) but had high levels of extinction. The second pulse of extinction hit the *Hirnantia* fauna particularly hard because it eliminated the cool-water habitat of the fauna. Preferential survival of broadly distributed groups is common to all of the major extinction events, regardless of their cause (Jablonski 1991).

The survival of so many widely distributed genera resulted in an extremely cosmopolitan fauna in the early Silurian. Because global biogeographic patterns are based on the evolution of distinctive higher taxa in isolated regions, it took until nearly the end of the Silurian Period for strong biogeographic provinces to redevelop.

## COMPARISON WITH OTHER MASS EXTINCTIONS

Few comparisons between mass extinctions have been made beyond simple taxonomic counts of disappearing groups (Table 1). Standardized methods for comparisons have only recently been developed (Droser et al 2000, Bottjer et al 2001). Comparisons with the Devonian mass extinction reveal that although taxonomic losses were greater in the Ordovician event, the ecologic consequences were greater

in the Devonian. Few dominant groups disappeared during the Ordovician event, but in the Devonian many groups, such as tabulate corals, stromatoporoids, conodonts, and biconvex brachiopods, disappeared or lost their dominant roles. Reefs recovered quickly after the Ordovician, but reefs declined during the Devonian event and did not recover in the Paleozoic (Copper 1994).

Sheehan et al (1996) compared the Ordovician and Cretaceous-Tertiary (K/T) extinctions. During the K/T event, most changes were related to the short-term loss of primary productivity consistent with loss of sunlight after an impact. Food chains that relied directly on food derived from photosynthesis suffered the greatest extinction. Many survivors were buffered from extinction by living in detritus-based food chains or by being starvation resistant. Ordovician extinction was high in food chains based on both living plants and detritus. Starvation-resistant Ordovician groups, such as brachiopods, found no refuge from extinction. In both extinctions, animals with wide geographic distribution had relatively low levels of extinction.

Schubert & Bottjer (1992) found stromatolite abundance increased after the Triassic extinction. Stromatolites were restricted by the activities of metazoans during the Cambrian and Ordovician radiations. The Triassic extinction reduced metazoan activity sufficiently to allow a resurgence of stromatolites. Recent field work (MT Harris, PM Sheehan, unpublished data) revealed a similar resurgence of stromatolites in the early Silurian Period of the Great Basin.

## SUMMARY

Two pulses of extinction correspond to the beginning and end of the Late Ordovician glaciation. At the beginning, global sea level declined nearly 100 m, and strong temperature gradients were established between the poles and the equator. Initiation of thermally driven deepwater circulation moved cold, oxygenated water into the deep ocean, which had been warm and had little turnover. At the end of the glaciation, sea level rebounded rapidly, the temperature gradient returned to prior levels, and deep oceanic circulation slowed. The glaciation had a very short duration, perhaps only half a million years (Brenchley et al 1994). The rapidity of the onset and decline of the glaciation probably contributed to the extinction by limiting the time available for evolutionary accommodation to the new environments.

At the onset of glaciation, as the seaways were drained, the initial extinction pulse hit shallow epicontinental sea faunas particularly hard. Cool temperatures in the open ocean contributed to the incursion of cool-water communities collectively known as the *Hirnantia* fauna. When the glaciation ended, sea level rise and warming and loss of oceanic mixing caused the second pulse of extinction, during which the *Hirnantia* fauna became extinct and many open marine faunas were annihilated.

With the loss of diversity, Silurian communities became much simpler and broader niched. Highly endemic faunas, which characterized the Late Ordovician, were replaced by faunas that were among the most cosmopolitan in the Phanerozoic. Recovery of taxonomic diversity and ecologic complexity took several

million years. Cosmopolitan zoogeographic patterns persisted through most of the Silurian.

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