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Extinction Patterns of the  
Paleozoic Stromatoporoidea

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# PART E, REVISED, VOLUME 4, CHAPTER 11B: EXTINCTION PATTERNS OF THE PALEOZOIC STROMATOPOROIDEA

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## INTRODUCTION

The Paleozoic stromatoporoids were greatly reduced in abundance and diversity in the middle of the Late Devonian epoch and became extinct at its end, in events that have been described as mass extinctions, owing to the disappearance of many groups of marine animals at the same time. These intervals of high rates of declining diversity in the Devonian period are clearly shown by graphs of family diversity published by RAUP and SEPKOSKI (1982): between the Frasnian and Famennian stages (F/F) and at the Devonian–Carboniferous boundary (D/C). Unfortunately, they have been named after intervals of dark shales and limestones in the western German succession, as the Kellwasser and Hangenberg events, on the unproven assumption that the anoxic environments that the sediments represent were worldwide in extent. Evidence of ubiquitous anoxia at these times is equivocal at best, so the terms should be confined to local use. No attempt is made in this chapter to review the vast literature on mass extinction, but possible causes common to events in which the stromatoporoids declined, and to other extinction events in life history, are discussed.

What is a mass extinction and at what level are such events to be separated from background extinction (HOFFMAN, 1989)? Are the causes of mass extinction different from, or did they operate on a different scale from, the causes that throughout geological time have carried away the great majority of organisms that have ever lived? HOFFMAN (1989) thought that no extraordinary causes needed to be postulated to explain mass extinctions but rather the coincidence of causes that operate all the time.

NEWELL (1967) suggested that there were six major episodes of accelerated extinction in the fossil record and favored a mechanism of regression to explain them. Most later work on characterizing mass extinctions has focused on the manipulation of various editions of SEPKOSKI's compilations (RAUP & SEPKOSKI, 1982; SEPKOSKI, 1996 [unpublished but see BAMBACH, KNOLL, & WANG, 2004, p. 523]; SEPKOSKI, 2002) to assess extinction patterns of the so-called big five events: (1) end-Ordovician; (2) Frasnian/Famennian; (3) end-Permian; (4) end-Triassic; and (5) end-Cretaceous. WANG (2003), WANG and MARSHALL (2004), and BAMBACH, KNOLL, and WANG (2004) concluded that the evidence for accelerated extinction as a cause of these diversity drops could only be established for three of these (1, 3, 5) and that the proportional decline in generic diversity for 2 and 4 was included in a continuum of background extinction rates. The D/C (Hangenberg) event that marks the final demise of the Paleozoic stromatoporoids is not one of the big five and is marked by only a minor decrease in the proportional diversity curve. BAMBACH, KNOLL, and WANG (2004) accounted for two-thirds of the diversity drop at the F/F boundary by origination failure and attributed only the remaining one-third to increase in extinction rate. The search for causes of marked diversity drops and extinctions in the fossil record now becomes as much one for mechanisms of origination failure as for catastrophic extinction disasters.

Most of the studies of mass extinctions have been based on counting of taxa (families and genera), but other methods for assessing the magnitude of extinction events have been proposed. McLAREN (1983) emphasized the extent of biomass loss as a measure

TABLE 1. Commonly recognized sequence of conodont zones in the Late Devonian–earliest Carboniferous succession (adapted from Sandberg, Morrow, & Ziegler, 2002).

Lower Carboniferous	⋮ <i>sulcata</i>
D/C	<i>praesulcata</i> <i>expansa</i> <i>postera</i> <i>tachytera</i>
Upper Devonian (Famennian)	<i>marginifera</i> <i>rhomboidea</i> <i>crepida</i> <i>triangularis</i>
F/F	<i>linguiformis</i> <i>rhenana</i> <i>jamieae</i> <i>hassi</i> <i>punctata</i> <i>transitans</i> ⋮
Upper Devonian (Frasnian)	

of the significance of mass extinctions. In particular, he drew attention to the demise of the Devonian reef facies in the F/F event. COPPER (1994) estimated that Frasnian reefs may have been ten times more extensive than modern ones and were reduced at the F/F event to insignificance. DROSER and others (2000) rated extinctions on the basis of four paleoecological levels, ranging from community-level changes to disappearances of whole ecosystems. They rated the changes at the F/F event as second, third, and fourth levels, but it is not clear how they would rate the D/C extinctions. MCGHEE and others (2004) rated the Late Devonian crises (which they considered together) as fourth in ecological severity of the big five and third in loss of marine familial diversity. They emphasized that the Late Devonian crisis was “. . . triggered in large part by a precipitous decline in speciation rates at the end of the Frasnian” (MCGHEE & others, 2004, p. 295).

Much of the discussion of the mid-Paleozoic extinctions involve reconstructions of the positions of the continents in Late Devonian time. Although many

paleogeographic maps have been published, the disposition of the continents at this time is still in doubt. Many paleontologists have rejected the widely distributed maps of SCOTSE and MCKERROW (1990; and, for example, [www.scotese.com](http://www.scotese.com)) on the basis that both Siberia and Laurussia are too far north and Paleotethys too open. STREEL and others (2000) adopted the map by HECKEL and WITZKE (1979), because it accounts for the distribution of palynomorphs better. MCGHEE (1996) discussed the uncertainties of mid-Paleozoic paleogeography at length.

The early literature on the mid-Paleozoic extinctions has been summarized in books by MCGHEE (1996), HALLAM and WIGNALL (1997), and HALLAM (2004). KOEBERL and MACLEOD (2002) have recently compiled a series of papers on mass extinctions (Geological Society of America Special Paper 356). Another series of papers presented at the Geological Society of America’s symposium in 2003 was issued by OVER, MORROW, and WIGNALL (2006) and contains an important paper by STOCK (2006) on stromatoporoid originations and extinctions.

## PHYSICAL EVIDENCE OF LATE DEVONIAN CONDITIONS

### TIME SCALES AND BOUNDARIES

Certain hypotheses of Late Devonian extinctions depend on the coincidence, or lack of coincidence, of physical and biostratigraphic events. Unfortunately, the dates of these events are not known precisely, and they change as research progresses, making older theories invalid. The extinctions that decimated the stromatoporoids are commonly said to occur at the Frasnian-Famennian boundary and at the end of the Devonian period. But these extinctions do not define the boundaries, and proving they occurred at the boundaries is difficult. The boundaries are defined for the convenience of conodont workers at the beginnings of the *triangularis* (F/F) and *sulcata* (D/C) zones respectively. The precise boundaries are set

in the Montagne Noir sections in France at certain convenient beds (for the D/C a ferruginous crust) that correspond closely to the conodont distributions. The commonly recognized sequence of conodont zones in the Late Devonian succession that are used to position events in the subsequent discussion are listed in Table 1 (SANDBERG, MORROW, & ZIEGLER, 2002). In most sections, the abrupt F/F changes in fauna occur just above the last beds bearing the youngest Frasnian conodont fauna of the *linguiformis* zone. WALLISER (1996) suggested that the D/C boundary is actually about half a million years younger than the Hangenberg shales that have been said to mark it. The age in years of the two events can only be estimated by making assumptions about the length of the conodont zones and extrapolating from dated ash beds or lavas. Commonly accepted values are 364 Ma and 354 Ma (GRADSTEIN & OGG, 1996; MCGHEE, 1996; STREEL & others, 2000), but dates as divergent as 376 Ma and 362 Ma have been suggested. The International Commission on Stratigraphy time scale of 2009 places the base of the Famennian (F/F) at  $374.5 \pm 2.6$  Ma, and the base of the Carboniferous (D/C) at  $359.2 \pm 2.5$  Ma. SELBY and CREASER (2005) place the D/C boundary at  $361 \pm 2.5$  Ma, on the basis of Re-Os dating of the Exshaw Shale.

#### STRATIGRAPHIC EVIDENCE

Great significance has been placed by Europeans on the occurrence at the F/F and D/C horizons of black shales and limestones of the Kellwasser and Hangenberg formations. The Kellwasser dark shales actually are divided into two parts by some beds of limestone. Conodonts of the *linguiformis* zone (latest Frasnian) occur just below the Kellwasser interval. WALLISER (1996) has been particularly enthusiastic about a worldwide anoxia indicated by these black shales. However, this euxinic facies by no means universally interrupts the carbonate facies at the F/F horizon, and in western Canada and Australia, where the interval is extensively exposed, no anoxic interval

interrupts the carbonate succession. In western Canada, dark, barren shales replace carbonates at the D/C horizon (Exshaw, Bakken, Chattanooga equivalents), but in much of eastern and arctic North America, long before the close of the Devonian period, the carbonate facies had given way to deltaic sandstones and siltstones. In the deltaic facies of the Upper Devonian there, black shales are so common that they are given no particular significance.

GELDSETZER, GOODFELLOW, and MCLAREN (1993) described the F/F contact on the Trout River in the Northwest Territories in detail. The beds below the contact are a stromatoporoid biostrome in the Kakisa Formation of *linguiformis* age. The contact is overlain by sandstone and is believed to represent an unconformity of lowermost *triangularis* age. In the southern Alberta Rockies (DAY & WHALEN, 2002), the F/F contact is underlain by stromatoporoid-bearing breccias in the Ronde Formation (of Kakisa age) and overlain by the Sassenach fine clastics (largely siltstones) in basal sections and on the shelf succession by the Palliser carbonates, whose basal beds appear to be of *crepida* age; i.e., the whole *triangularis* zone is missing on the shelf where the Sassenach is absent, owing to regression at this time. Apparently a regression at the F/F boundary withdrew the sea from the shelf area into the basins and was followed by a transgression in mid-Famennian time.

In the Canning Basin of western Australia, the F/F boundary is not marked by any conspicuous change in the stratigraphy that is indicative of transgression or regression (see COCKBAIN, 1989; BECKER & others, 1991). In southern China (WANG & others, 1991; MA & others, 2002), dark shales interrupt the carbonate successions in the *linguiformis* zone of the shallow-water facies but are not conspicuous in the marly deposits of deeper-water basinal sections. No equivalents of the Hangenberg facies occur in the D/C in southern China, and the boundary is within a bed of bioclastic

limestone (HALLAM & WIGNALL, 1997). In Guilin (South China), karst features at the F/F boundary have been interpreted as evidence of regression (CHEN & TUCKER, 2004).

### ISOTOPE VARIATIONS

At intervals suspected of recording extraordinary faunal events (so-called bioevents), geochemists note excursions from baseline values of the isotopes  $^{13}\text{C}$  and  $^{18}\text{O}$ . The most extensive compilation of these values for the whole of Phanerozoic time was that of VEIZER and others (1999). Globally, average  $\delta^{13}\text{C}$  values are low during the Devonian, compared to higher values in the Silurian and Carboniferous. Values also climb steadily through the Paleozoic toward the Permian. Values of  $\delta^{18}\text{O}$  also dip (to about  $-2$ ) during the Devonian but climb toward  $+2$  in the Carboniferous near its end. SALTZMAN (2005) indicated only minor positive excursions of  $\delta^{13}\text{C}$  values at the F/F boundary and larger ones at the D/C boundary, to about  $+5$ .

Global compilations are too broad to provide much information on immediate causes of Late Devonian extinctions. Isotope studies of local sections and short time intervals should be more helpful. In the western German sections, the black shale intervals show positive excursions of  $\delta^{13}\text{C}$  (HALLAM & WIGNALL, 1997). JOACHIMSKI and BUGGISCH (2002) examined conodont apatite for changes in C and O isotopes and reported  $\delta^{13}\text{C}$  excursions of about  $+3\%$  at the F/F boundary. They recorded positive swings in both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  in late *rhenana* and early *triangularis* times. GELDSETZER, GOODFELLOW, and MCLAREN (1993) recorded zigzag excursions in both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  across the F/F boundary on the Trout River. WANG and others (1991) reported  $\delta^{13}\text{C}$  shifts from  $+1\%$  to  $-2.5\%$  at the southern China boundary and concluded that this indicates a reduction in surface water biomass. STREEL and others (2000) summarized the evidence of  $\delta^{13}\text{C}$  as equivocal at the F/F boundary, and HALLAM and

WIGNALL (1997) indicated that there are no excursions of carbon isotopes at the D/C boundary.

### EVIDENCE OF IMPACTS

Evidence for the occurrence of asteroid or comet impacts at Late Devonian times of mass extinction comprises iridium anomalies, microtektites, impact breccia, and craters.

Two iridium anomalies have been recorded in the Late Devonian but have been dismissed as either being of insignificant magnitude to indicate a major event or as occurring at the wrong time. The first, at the F/F boundary in Guangxi, China (WANG & others, 1991) shows an Ir deflection of only about 0.21 ppbillion from that of adjacent strata. The second, at a bed rich in *Frutexitis* fossils in the Famennian of Western Australia, is generally considered to be caused by organic concentration of platinum group elements, rather than by an impact, and is not at either the F/F or D/C horizons.

Microtektites, the small globules of fused rock that have been considered indicative of impact events, have been found at the F/F boundary in Europe (at Hony, Belgium; CLAEYS & others, 1996) and South China, but, as WALLISER (1996) pointed out, these indicators are not uncommon in the insoluble residues extracted for conodont analyses throughout the Paleozoic. Since extraterrestrial matter of various calibers is continually raining through the atmosphere, the presence of some microtektites at any particular horizon is not, in itself, good evidence of a catastrophic event.

Craters and breccias provide more direct evidence of bolide impact. MCGHEE (1996, 2001) has proposed that the Siljan Crater in Sweden, the Flynn Crater in Tennessee, and the Alamo Crater and breccia in Nevada are evidence that impactors were the ultimate cause of the F/F extinctions. Although the Siljan, the largest of these craters at 52 km in diameter, was at one time thought to correspond in time to the F/F event, changes in

the time scale have since placed all the craters at approximately the time of the *punctata* zone, which is about 3 million years before the close of the Frasnian. To account for the time difference, MCGHEE (2001) applied a lag-time multiple impacts hypothesis to explain how these bolides could have been the ultimate cause of environmental changes that brought about the extinctions. TAPANILA and EKDALE (2004) reported that stromatoporoids overlie the breccia deposits from the Alamo event, and apparently the impact had no lasting effect on the stromatoporoid community. By 2006, MCGHEE recognized that all the known impact events appeared to postdate the F/F event, if more recent date estimates of approximately 376 Ma are valid. However, recent studies of the Siljan crater using laser argon dating (REIMOLD & others, 2005) give a date of  $377 \pm 2$  Ma, which is within the error limits of the 2005 date for F/F of the International Commission on Stratigraphy. Hypotheses linking impacts and extinction are frequently modified as different dates for the events are published.

There is no sure evidence of an impact or volcanic event associated with the D/C boundary; however, estimates of the times of impacts of the Charlevoix crater in Canada ( $357 \pm 15$  Ma) and the Woodleigh crater in Australia ( $359 \pm 4$  Ma) are within the range of estimates of the D/C boundary on the International Stratigraphic Commission Scale ( $359 \pm 2.5$  Ma) (MCGHEE, 2006).

The Woodleigh structure in the Carnarvon Basin of western Australia has been proposed as evidence of a Late Devonian impactor large enough to form a crater 120 km across (MORY & others, 2000). The size, nature, and date of this structure is controversial, and discussions and replies can be followed through papers in Earth and Planetary Science Letters (for example, REIMOLD & KOEBERL, 2000; RENNE & others, 2002).

#### EVIDENCE OF GLACIATION

Traces of glaciation near the paleopoles have been recognized generally as evidence of worldwide cooling. Considerable discus-

sion of the age of glacial deposits and glaciated surfaces in Brazil and North Africa has been summarized by STREEL and others (2000). Although they postulated cooling as a cause of the F/F extinction event, there is no evidence of glaciation at that time. However, evidences of miospore distribution, diamictites, and glaciated surfaces of latest Famennian age (D/C) are cited by STREEL and others (2000) as clear evidence of glaciation near the southern polar regions, close to Brazil and North Africa.

FISCHER (1984) pointed out that important climatic changes were taking place near the close of Devonian time when he defined his supercycles. The change from Earth's greenhouse condition to the icehouse condition, the end of the warm seas and extensive reefs of the early and middle Paleozoic, and the beginning of widespread and prolonged glaciation in the southern hemisphere took place in the Famennian but must have been relatively gradual.

#### LATE DEVONIAN DECLINE OF STROMATOPOROID DIVERSITY

Not all investigators agree that the Paleozoic stromatoporoids became extinct at the end of the Devonian period. MISTIAEN (1984, 1994) has proposed that, with the changing ocean environments of the Sandberg Supercycle, the stromatoporoids merely lost the ability to secrete a carbonate skeleton until they reappeared as the Mesozoic stromatoporoids. He suggested that the changing Late Devonian marine environment caused stromatoporoid skeletons to decrease in density during Famennian time and eventually to disappear at its end.

That stromatoporoids persisted into earliest Carboniferous time (Tournaisian) has also been reported. The stromatoporoids originally reported from the Tournaisian of China have since been reassigned to latest Famennian. SMITH (1932) described *Labechia carbonaria* from early Carboniferous beds in England, but the name was preoc-

TABLE 2. Species and generic diversity of stromatoporoids (new).

Area	Author and date	Givetian			Frasnian			Famennian		
		sp.	gen.	s/g	sp.	gen.	s/g	sp.	gen.	s/g
Afghanistan	Mistiaen, 1985	34	19	1.8	18	10	1.8	3	3	1.0
Belgium	Lecompte, 1951*	56	11	5.1	61	11	5.5	4	3	1.3
Poland	Kazmierczak, 1971	32	12	2.7	19	12	1.6	—	—	—
Czech Republic	Zukalova, 1971 <sup>§</sup>	16	8	2.0	56	17	3.3	8	7	1.1
Western Australia	Cockbain, 1984	—	—	—	25	12	2.1	2	2	1.0
Western Canada	Stearn+	24	16	1.5	37	20	1.9	5	5	1.0

\*Famennian data: Conil (1961); <sup>§</sup>Famennian data: Friakova and others (1985); + new compilation.

cupied, and SOKOLOV (1955, p. 111 and pl. 90, see caption) suggested, in renaming the fossil as *L. smithi*, that it was a chaetetid. The cystose structure of labechiids is duplicated in many types of rugose and tabulate corals, and fragments of these can easily be mistaken for a labechiid stromatoporoid. At present, no post-Famennian stromatoporoids, in the sense of the term used here, are confirmed.

Most accounts of Late Devonian faunas describe the decline in diversity of not only the stromatoporoids but also of many other groups approaching the F/F crisis. STEARN (1982) identified the peak of diversity of the stromatoporoids in Givetian reefs and outlined the decline in diversity through the Frasnian worldwide and in local sections (1982, 1987). On a worldwide basis, STEARN (1987) recognized a Frasnian generic diversity of 37 and a late Famennian diversity of between 20 and 24 genera (see also *Treatise Online*, Part E, Revised, Volume 4, Chapter 11A, Fig. 1–2).

The difference in taxonomic diversity between Givetian and Frasnian stromatoporoid faunas is not as obvious as between Frasnian and Famennian stromatoporoids, when monographic treatments of particular basins are tabulated. The number of species and genera in Givetian, Frasnian, and Famennian beds derived from various monographs (and therefore taxonomically consistent) for well-studied faunas within larger areas (i.e., not just local sections) is listed in Table 2.

Obviously, some paleontologists have different taxonomic philosophies and distinguish more morphologic variants as different

species within genera; hence the wide variation shown in the ratio of species to genera (s/g) in Table 2. As a result, the number of genera appear to be the better measure of diversity for comparison between different studies. In most areas, the difference in generic diversity between Givetian and Frasnian faunas is insignificant. In Afghanistan, the taxonomic diversity decreases through the Devonian, but in the Czech Republic, it increases into the Frasnian. For the few areas where a comparison of Frasnian with Famennian faunas is possible, the drop in diversity from an average of about a dozen Frasnian genera to two or three in the Famennian is striking.

STOCK (2006) tabulated the diversity changes in seven Devonian successions from around the world and noted that in nearly all the sections, generic diversity fell during the Frasnian and into the Famennian. Origination and extinction of stromatoporoid genera were also tabulated from the taxonomic review of STEARN and others (1999). For the first four stages of the Devonian, originations exceeded extinctions, but from the Eifelian time to the end of the period, the rate of origination steadily declined and the rate of extinction increased, reaching a maximum in the Frasnian. STOCK (2006) also plotted overall generic diversity by stage through the Devonian. Diversity reached a peak in Eifelian time and declined slightly through Givetian to Frasnian time, but the difference between Emsian and Frasnian diversity is less than 10%, or only three genera. Famennian diversity was only half the diversity in the Eifelian.

The question of whether the decrease in diversity of stromatoporoid genera in Late Devonian time could be owing to the Signor-Lipps effect (SIGNOR & LIPPS, 1982) should be assessed. This effect produces an apparent decline in diversity toward abrupt extinctions and is caused by the decreased likelihood of collecting rare and poorly preserved species of fossils at the ends of their ranges. The effect is minimal for fossils of abundant animals and those with skeletons that are likely to be preserved, such as the stromatoporoids. It has largely been adduced in the interpretation of ranges of fossils in local sections rather than in regional and global diversity studies extending over tens of millions of years, as for the stromatoporoids.

Early and middle Famennian stromatoporoid faunas are known from the Czech Republic, Australia, and western Canada. They are much reduced in diversity from late Frasnian fauna but contain such typically Frasnian genera as *Amphipora*, *Stachyodes*, *Stromatoporella*, *Syringostroma*, *Gerronostroma*, and *Stromatopora*. In Australia (COCKBAIN, 1984), Famennian rocks contain *Clathrocoilona* and *Stromatopora* (STEARN, HALIM-DIHARDJA, & NISHIDA, 1987, suggested this is a *Trupetostroma*). By mid-Famennian time, stromatoporoids had recovered to the extent that they were building small reefs in the carbonates of western Alberta.

The most remarkable feature of the Famennian faunas in North America, Russia, Kazakhstan, Siberia, and southern China, however, is not the presence of survivors of the F/F decline but the abundance and diversity of the order Labechiida. The typical genus of these faunas is *Stylostroma*, but the labechiid root stock branched into as many as 13 genera in southern China. If these Chinese genera are subtracted from the Famennian generic diversity total, the decrease in diversity at the F/F interval becomes 86%. The distribution of the labechiid and nonlabechiid communities in the late Famennian has been discussed in the sections dealing with

paleobiogeography (*Treatise Online*, Part E, Revised, Volume 4, Chapter 14). Assemblages of nonlabechiids only, labechiids only, and mixed assemblages are separated geographically in late Famennian (Strunian) rocks, and they first appear to be localized around the equatorial Paleotethys ocean. On the basis of this distribution, STEARN (1987) suggested that the labechiids became dominant in the Famennian because they were more tolerant of cool water.

The abundance and diversity of the labechiids in latest Famennian rocks is more remarkable because the family is rare in nearly all other Devonian stromatoporoid faunas. WEBBY and ZHEN (1997) have reviewed the scattered occurrences in Lower and Middle Devonian rocks (Mid-Devonian England, Queensland; Lower Devonian Urals, Queensland, northeastern Russia), but the major monographs on Givetian and Frasnian stromatoporoids contain no mention of labechiids. STEARN (1983) did describe a *Labechia* sp. from rocks of Emsian age in the Canadian Arctic, but ST. JEAN (1986) has suggested that this may be a misidentification of a cystose structure in *Syringodictyon*. YAVORSKY (1957) has described five species of *Labechia* from beds he identified as being of Frasnian age, southern Urals, and, if these beds are confirmed in age, they are a unique assemblage.

In summary, stromatoporoid diversity declined slightly from Eifelian time toward an ecological crisis at the end of the Frasnian stage; then the widespread reef facies of Frasnian time was greatly restricted and many genera became extinct. This drop was the result of a major decline in rate of origination since the middle of the Devonian Period and a less significant increase in the rate of extinction. During latest Devonian time, a few surviving Frasnian genera accompanied a resurgent labechiid order to form small reefs scattered in most of the continental blocks until the end of Famennian time. The remaining stromatoporoid stock went extinct at the D/C boundary. The F/F boundary marks an important ecological

change, and the D/C boundary an important taxonomic one.

## RESPONSE OF OTHER TAXA TO LATE DEVONIAN EVENTS

In assessing the nature of the environmental changes that determined faunal changes during F/F and D/C times, a survey of the changes in other taxonomic groups is useful. The numerous papers on the radical changes at F/F seem to have overshadowed and depreciated the changes that took place at D/C. Shallow-water faunas were not as much affected at D/C, but goniatites and hemipelagic ostracodes lost much of their diversity (WALLISER, 1996).

Summaries of the groups affected by both episodes can be found in the works of BUGGISCH (1991), WALLISER (1996), MCGHEE (1996), HALLAM and WIGNALL (1997), and HALLAM (2004), and these are not repeatedly cited in the following discussion. MCGHEE (1996) estimated that 14%–30% of families, 50%–60% of genera, and 70%–80% of species became extinct in the Late Devonian mass extinctions, between late *rhenana* and middle *triangularis* zones (i.e., the Kellwasser interval). MCGHEE and others (2004) place familial diversity loss of marine faunas at 21%.

The calcareous Foraminifera were in their initial interval of radiation in Givetian and Frasnian times, and their shells are common in Frasnian grainstones. They suffered a rapid decline at F/F from 30 to 2 genera. MCGHEE (1996) made much of the abundance of hexactinellid sponges in the Devonian shelf sediments of New York as evidence of invasion of deep cool-water taxa, but this occurrence is very local, perhaps unique, and can hardly have worldwide significance. SORAUF and PEDDER (1986) considered the fate of the abundant Frasnian rugosans at F/F. They recorded that only 5 of the 47 genera of late Frasnian rugose corals survived into the Famennian. There is some evidence that deeper-water genera survived to radiate into shallow environments. Whether D/C had a significant effect on rugosans is contro-

versial. Tabulate corals were in decline in the Late Devonian and represented largely by branching forms such as *Thamnopora*. They were greatly reduced by the F/F change but little affected by D/C.

Bivalves and bryozoans both seem to have been little affected by either of the Late Devonian crises.

Cricoconarids had a precipitous decline at F/F, reducing from 6 genera to 1 genus. As they are generally regarded as pelagic in habitat and commonly preserved in dark shales, their decline is difficult to relate to some hypotheses of changing sea levels and rising anoxia. Ammonoids seem to have been facing crises throughout their history. As a result, investigators attach little significance to the fact that they declined in Frasnian time and recovered in the Famennian. However, about 85% of the goniatites became extinct at D/C. FEIST (1991) documented the general decline of the trilobites in the Frasnian from a high of diversity in the Eifelian. Very few new trilobite genera were added in Frasnian time, and the trilobites were never again a significant part of shallow-water faunas in late Paleozoic time.

Brachiopods have been regarded as holding the key to climate change at this time, owing to the work of COPPER (1977, 1994) on South American faunas. The diversity of Frasnian brachiopods declined toward the F/F; the number of genera reduced from 92 in the Frasnian to 23 in the Famennian. Thirty of the 33 families lost at this point were tropical forms. The orders Pentamerioidea and Atrypaidea became extinct in Frasnian time (the latter in early *linguiformis* time). Orthids and strophomenids were greatly affected, but spiriferids and rhynchonellids were not. STIGALL RODE (in STIGALL RODE & LIEBERMAN, 2006) has studied changes in the brachiopod community at the Devonian biodiversity crisis using environmental niche modelling.

STREEL and others (2000) documented miospores. Their diversity shows a peak in the Givetian of about 58 species and a decline from Frasnian to Famennian from

51 to 23 species. Plant macrofossil diversity shows a similar decline. Chitinozoans survived the F/F but became extinct at the end of a long decline at D/C. Acritarch diversity collapsed at D/C rather than at F/F. Ostracode history gives no clear signal, and their distribution and decline has been interpreted in various ways.

In summary, most fossil groups responded to Late Devonian environmental change by decreasing in diversity; most survived the two (or more) crises, but the stromatoporoidea did not. The extinctions, largely at the family and lower taxonomic levels, extended over a considerable period of time; MCGHEE (2001) suggested from late *rhenana* to mid-*triangularis* times.

### CAUSES OF LATE DEVONIAN EXTINCTIONS

Paleontologists have suggested many causes to explain mass extinctions. McLAREN (1983) suggested that we should recognize a hierarchy of causes leading us to some ultimate cause; that is, if anoxia is the immediate cause of the extinction of shallow-water faunas, was the anoxia caused by transgression, was the transgression caused by ice-cap melting, was the melting caused by climate change, and was the warming caused by an increase in CO<sub>2</sub> in the atmosphere? The problems of identifying causes and distinguishing them from triggers in the interpretation of the stratigraphic record has been examined by CLELAND (2001) and commented on by KILTY (2002) and BAILEY (2002). BAILEY (2002, p. 953) concluded that in stratigraphic interpretation: "The attempt to establish causality within reasonable doubt is for the most part futile and when attempted likely to be misleading." Earth systems are so complex and inter-related that retracing the whole chain of causation for events of hundreds of millions of years ago seems impossible, and we should be cautious of simplistic solutions.

In the search for causes of mass extinctions, the most powerful tool is selectivity: the difference in ecologic requirements

between the organisms becoming extinct and those surviving. For example, if species that lived in the tropics become extinct, while cool-water species survive and occupy formerly tropical environments, then cooling temperatures are almost certainly part of the complex of causes.

Although many discrete causes of Late Devonian diversity decline have been suggested, they can be grouped into three general hypotheses: (1) extraterrestrial influences, impactors, or cosmic rays; (2) sea level changes and accompanying anoxia; (3) climate change, notably cooling, shown by and giving rise to Southern Hemisphere glaciation.

### BOLIDE IMPACT HYPOTHESES

Extraterrestrial matter continually impacts the atmosphere, and larger particles rain down on the Earth's surface. The evidence for this is usually widely distributed in marine sediments and is unlikely to have significant effect on marine life. The search for extraterrestrial causes, or triggers, for mass extinction is a search for anomalies in the rate at which this evidence is introduced into the marine record. The extent of the anomaly required for an extensive extinction has not been clearly defined but is usually stated in terms of the diameter of the impactor; i.e., a 10 km impactor should do the job. The question of how many microtektites, or shocked quartz grains, demand our attention as causes or triggers, goes unanswered. The search for these signatures of impact at the F/F and D/C has yielded little evidence and that which has been adduced has been efficiently refuted (HALLAM, 2004, p. 76).

The evidence for bolide impact has been reviewed above and, apart from the occurrence of breccias, is not compelling. Coincidence of impact date of major sites with biostratigraphic events is difficult to establish. MCGHEE (2001) suggested that multiple impacts in early to middle Frasnian time (approximately *transitans* zone) would

have produced an anomalous warm period in the general cooling trend of Late Devonian time associated with the transition from greenhouse to icehouse conditions. He proposed that the immediate cause of F/F extinctions was the abrupt return to the general cooling of oceans as the anomalously high CO<sub>2</sub> concentrations caused by the impacts was absorbed in the rapidly spreading plant community. Application of the multiple impact hypothesis to Late Devonian extinctions seems to be a final attempt to rescue the bolide hypothesis from rejection.

Suggestions that radiation from space may have caused mass extinctions can be traced back to SCHINDEWOLF (1954), who suggested that cosmic rays from a supernova explosion caused the end-Permian extinction. A similar hypothesis has been proposed more recently by Adrian MELOTT (see HECHT, 2003) that gamma rays from an exploding star caused the Late Ordovician event. SHAVIV and VEIZER (2003) have drawn attention to the probable effect of cosmic ray flux as a determinant of Phanerozoic climate but do not apply their model to extinction causes.

### ANOXIA, TRANSGRESSION, AND REGRESSION

The coincidence of the Kellwasser and Hangenburg intervals of dark shales and limestones with the extinctions in Europe has convinced many geologists there that the spread of anoxia over continental shelves through transgression was an immediate cause of the biota changes. A corollary hypothesis is that the mid-Paleozoic oceans were chronically unventilated at depth, and it was this anoxic water spreading over the carbonate shelves that poisoned so many animals adapted to shallow, oxygenated waters (such as stromatoporoids). The hypothesis is also connected to the burial of large quantities of organic carbon in these dark shales and consequent drawdown of atmospheric CO<sub>2</sub> and decrease in temperature. JOACHIMSKI and BUGGISCH (2002) attributed positive excursions in

δ<sup>13</sup>C as evidence of 20%–30% increase in burial of organic carbon in the ocean and hence a drawdown of atmospheric CO<sub>2</sub>. MURPHY, SAGEMAN, and HOLLANDER (2006), who studied two black shale intervals in the Devonian of New York that they correlated with the Lower and Upper Kellwasser horizons, recorded in them a positive δ<sup>13</sup>C excursion of 4‰ to 5‰. On the basis of this and changes in the C:N:P ratio of buried organic matter, they postulated that eutrophication of the water column was important in causing extinctions. BRATTON, BERRY, and MORROW (1999) studied the geochemistry of an anoxic interval in the Great Basin of the southwestern United States and concluded that it marked neither the end of the Frasnian nor the *linguiformis* zone, but ended about 0.1 million years before F/F. The interpretation of the positive shift in δ<sup>13</sup>C at the F/F boundary in some sections has been difficult to explain. ERWIN (2006) discussed various alternatives for similar changes at the end-Permian extinction.

MCGHEE (1996) pointed out that intervals of dark, organic-rich shales, much like the Hangenburg and Kellwasser, are common at many levels within the Late Devonian successions around the world, and the great majority have not been associated with extinctions or radical faunal changes. In addition, local anoxia is easy to accept, but worldwide oceanic anoxia is more difficult to model.

If the incursions of anoxic water onto shelves is taken as evidence of rise of sea level, then sea level must have fallen rapidly thereafter to account for the widely recognized regression at the beginning of Famennian time (STREEL & others, 2000; JOACHIMSKI & BUGGISCH, 2002; STOCK, 2006). In western Canada, for example, the F/F appears to be a disconformity formed by widespread regression from the carbonate shelf environments. Such regression would have restricted shallow-water habitats and might have led to increased competition between shallow-water benthic organisms and thus extinctions. BUGGISCH (1991) has

constructed a complex cyclic model of rising and falling sea levels and anoxic shelves to explain the upper and lower Kellwasser intervals. His sequence can be summarized as follows: transgression → anoxia on shelves → organic carbon sequestering → decrease in atmospheric CO<sub>2</sub> → icehouse → glaciation → regression → erosion of organic C → increase in atmospheric CO<sub>2</sub> → greenhouse → increased organic production → transgression, and so on. MAY (1997) postulated that the Kellwasser and five other previous Devonian bioevents were all caused by rapid transgression of anoxic waters over the shelves. RACKI (1998) reminded us that rapid sea level changes can also be caused by tectonic events such as rifting, but commonly the postulated sea level changes are attributed to Late Devonian glaciation.

STOCK (2006) attributed the fall in diversity of stromatoporoid faunas in Frasnian time to the transgression of the Transcontinental Arch in North America and consequent mixing of faunas from the Eastern Americas realm and Old World realms. Whether the arch was an effective barrier to stromatoporoids from Eifelian to late Frasnian time, or if its flooding had more than a local effect on world faunas, remains to be proven.

HALLAM (HALLAM & WIGNALL, 1997; HALLAM, 2004) strongly supported anoxia as a cause of mass extinctions. He postulated that a late Frasnian regression was followed by a Famennian transgression flooding the continents with anoxic waters that until then had been confined to the deep oceans.

In a similar hypothesis, KUMP, PAVLOVA, and ARTHUR (2005) suggested that during intervals of oceanic anoxia, the chemocline separating sulfidic deep waters from oxygenated surface waters could have risen to the surface, killing much marine life and introducing lethal doses of H<sub>2</sub>S into the atmosphere in Late Devonian time. Another hypothesis advanced by BAMBACH, KNOLL, and SEPKOSKI (2002) postulated that large quantities of CO<sub>2</sub> introduced into the atmosphere from an anoxic ocean's depths

would more seriously affect invertebrates of lower metabolism and activity (such as stromatoporoids) than those with higher metabolic rates and would lead to less successful survival of such an event. The release of methane (CH<sub>4</sub>) from hydrates in the deep continental shelves by fall of sea level or rise of temperature has been proposed to account for the positive excursions of δ<sup>13</sup>C at extinction boundaries (ERWIN, 1993, 2006) and deleterious effects on the environment by increasing the greenhouse effect.

In conclusion, oscillations of sea level in Late Devonian time have certainly been documented, but their effects as controls on diversity and extinction are not obvious.

## GLACIATION IN THE SOUTHERN HEMISPHERE

When rapid transgressions and regressions occur in the geological record, stratigraphers turn to the growth and melting of continental ice sheets for explanation. The spread of ice beginning in mid-Carboniferous time over much of the southern hemisphere in the icehouse phase of the late Paleozoic has been accepted since early in the 20th century, but the identification of Late Devonian glaciation has been controversial. The evidence of diamictites and striated surfaces in northeastern Brazil dated palynologically has recently been reviewed by STREEL and others (2000). They concluded that glaciation there, and possibly in North Africa, is well supported by stratigraphic evidence at D/C but not at F/F. Still, to justify the extinctions at F/F, they postulated a short glacial interval within a generally warm climate. The general cause of the cooling that brought on the glaciations is so-called sinking of the greenhouse gas CO<sub>2</sub>, in both marine organisms and rapidly spreading land vegetation. STREEL and others (2000) pointed out that, at present, the productivity in plant-matter mass on land is three times that of the sea, but this does not mean that it was so in Devonian time.

## GLOBAL COOLING

The fractionation of oxygen isotopes is dependent on temperature, and excursions in  $\delta^{18}\text{O}$  have been used as a proxy for temperature. GONG and XU (2003) warned, however, that  $^{18}\text{O}$  excursions can also be caused by changes in sea-water salinity. Temperature has also been used as a proxy for the extent of continental ice sheets, and the extent of ice has been used as a proxy for sea level. For example, STREEL and others (2000) suggested that the  $\delta^{18}\text{O}$  positive excursions at F/F can be correlated with a drop of sea level of 180 m, owing to the trapping of water in polar ice. In contrast, JOACHIMSKI and BUGGISCH (2002) suggested that  $\delta^{18}\text{O}$  values of  $-1\text{‰}$  indicate warm sea temperatures of about  $26^\circ\text{C}$  at this time. For comparison, recall that the steady decrease of water temperatures from Eocene time to the present leading to the Ice Age is represented by a  $\delta^{18}\text{O}$  from about  $0\text{‰}$  to  $+4\text{‰}$ . VEIZER and others (1999) correlated a positive swing of  $^{18}\text{O}$  with Late Ordovician glaciation and suggest that the rise in the Late Devonian may be correlated with a similar phenomenon at that time. The extensive  $\delta^{18}\text{O}$  determinations on mid-Paleozoic brachiopods published by BRAND (1989) gave unrealistic seawater temperatures in the  $36^\circ\text{C}$  to  $54^\circ\text{C}$  range, which have been largely dismissed by later investigators as being influenced by diagenesis of his samples.

On the basis of oxygen isotopes from conodonts, JOACHIMSKI and BUGGISCH (2002) denied evidence of extensive Late Devonian ice sheets. The ocean temperatures for late Frasnian time derived from  $\delta^{18}\text{O}$  values of  $-1\text{‰}$  are warm, about  $32^\circ\text{C}$ ; the two excursions in the oxygen isotope curves near the F/F boundary indicate temperatures falling to about  $26^\circ\text{C}$ . This decrease in temperature is comparable to that which accompanied the Pleistocene glaciation ( $4\text{--}8^\circ\text{C}$ ). However, they attributed the Late Devonian extinctions to general and episodic cooling and ultimately to the burial of organic carbon in so-called sinks and

decrease in atmospheric  $\text{CO}_2$ . JOACHIMSKI, VON BITTER, and BUGGISCH (2006) discussed the significance of  $\delta^{18}\text{O}$  to sea level changes in the Pennsylvanian cyclothems and suggested that a change of  $+1.7\text{‰}$  would be equivalent to a temperature decrease of  $7^\circ\text{C}$ , if explained solely by temperature, and could have resulted in sea level falls of more than the 120 m experienced during Pleistocene glaciations.

The hypothesis that global cooling was one of the main causes of Late Devonian extinctions, which was first clearly stated by COPPER (1986), has been supported since by more and more evidence. COPPER'S conclusions grew out of studies of South American brachiopods (1977). These cold-water faunas displaced the tropical brachiopods in Late Devonian time, clearly signalling a cooling event. Originally, COPPER (1986) suggested that the cooling was caused by the movement of the continents and closing of the Frasnian equatorial ocean (Paleotethys). Later, COPPER (1994) suggested that reefs and calcareous plankton have a great capacity to sink  $\text{CO}_2$  and cause climatic change.

That global cooling,  $\text{CO}_2$  in the atmosphere, sea level changes, and even glaciation are connected with the burial of organic carbon at the beginning of the Icehouse Earth is a common thread in many recent hypotheses. The increase in removal of  $\text{C}_{\text{org}}$  from recycling to the atmosphere, as evidenced by organic-rich sediments and positive  $\delta^{13}\text{C}$  excursions, is most commonly attributed to the spread of plants upon the land (ALGEO & SHECKLER, 1998) but may also have been related to ocean anoxia, slowing the decay of marine organic matter and sequestering it in black shales.

MCGHEE (2006) based his discussion of extinction hypotheses on a model of falling global temperatures, starting at the beginning of the Givetian and culminating in late Famennian glaciation. The ultimate cause of the cooling was falling atmospheric  $\text{CO}_2$  content, owing to the rise of vascular plants. MCGHEE postulated that this steady

cooling trend was interrupted by a brief, sharply defined, warmer greenhouse interval in late Frasnian time, caused by impacts or volcanic phenomena (flood basalts), whose collapse led to F/F extinctions. The climatic changes could have been episodic to explain the series of pulses that MCGHEE identified in late Frasnian extinctions. Similar episodic extinction events have not been identified in the history of the stromatoporoidea.

STEARN (1987) suggested that general cooling of Late Devonian climates led first to widespread F/F drop in diversity and abundance of the stromatoporoidea, the rise of the cool-water tolerant labechiids, and eventually to the demise of the whole class (D/C). COPPER (1994) has suggested that the greater effect of F/F events on the corals than on the stromatoporoidea means that the former were more sensitive to environmental change than the latter.

CLARKE (1993) commented on the role of temperature alone in causing extinction of marine organisms. He emphasized changes in seasonality in interrupting reproductive cycles as being more important than changes in temperature. The latter are more likely to cause changes in the distribution of organisms than their extinction. He noted that humans, as warm-blooded animals, may see colder temperatures as detrimental, while many marine invertebrates thrive in frigid waters.

Not all models of Late Devonian temperatures postulate overall steady cooling of the atmosphere during this interval, and several postulate warm seas in Frasnian and Famennian time. Until a detailed temperature curve is agreed upon, hypotheses linking temperature and extinction will continue to be subject to modification. TWITCHETT (2006) has summarized studies of mass extinctions and concluded that climate change is the only reasonable explanation for most of these events.

## CONCLUSIONS

That changing conditions as the Devonian Period came to an end were challenging to shallow-water faunas is clearly evident;

that they were catastrophic is harder to prove (HALLAM, 2004). The appeal of the so-called New Catastrophism has led many to seek an extraordinary event or events and a unique cause to explain the deteriorating marine environment of Late Devonian time. In consideration of GOULD's (1985, 1989) proposal that contingency and, in particular, randomly caused episodes of mass extinction are the fundamental controls on the history of life, paleontologists have concentrated on the study of these time intervals. Certainly, the attention given by media and public to the abrupt extinction of the dinosaurs coincident with an extraordinary astronomical event has focused attention on other similar incidents in life history and suggested similar abrupt scenarios. But there is no reason why each of the big five extinction events should have the same cause; on the contrary, marked differences in the stratigraphic record at the five boundaries suggest just the opposite. The evidence for each event must be weighed separately. For example, although the coincidence in time with extinction events at the end of the Cretaceous and Permian of extensive flood basalts in India and Siberia, respectively, has been suggested as a cause of the extinctions, no such extensive extrusions coincide with the Devonian extinctions. The evidence for each extinction event in the geologic record must be weighed separately.

Extinctions at all hierarchical levels: orders, families, genera, and species, took place continuously throughout life history, as the changing environmental determinants became inhospitable to this or that organism. As the cycles of change in limiting environmental parameters such as (in the marine environment) temperature, salinity, oxygenation, nutrient level, depth, and illumination, took place, different organisms with different sensitivities to these parameters became extinct. When conditions adverse to marine life in a few of the parameters coincided in time, several groups became extinct; at those rare times when adverse conditions coincided in most of them, then what has

been called a mass extinction occurred. If this is the case, then not only are such episodes inevitable at random times in the history of life, but they have no immediate single cause, only multiple causes. The model is further complicated by the intimate interrelationships of the ecological determinants, so that looking for a single trigger in this web of causes is frustrating. JABLONSKI (2000, and references therein) argued that large-scale ecologic systems (such as the mid-Paleozoic reef complexes) have an inherent resistance to perturbations and require an external extraordinary event to disrupt them. A hypothesis of multiple coincident causes has also been discussed by ERWIN (1993, 2006).

All the major mechanisms of Late Devonian extinction that have been proposed have evidence in their favor and evidence against them. That we will ever be able to reconstruct the events of hundreds of millions of years ago seems unlikely. What seems likely is that some combination and interaction of climate change, anoxia, sea level variation, and sinking of carbon dioxide resulted in environmental instability beyond the capability of much of the warm-water marine benthos to accommodate. Whether extraterrestrial influences had any effect as a trigger remains to be proven. RACKI (2006) has summarized many of these arguments and provided an extensive bibliography.

Only a likely scenario can be postulated. Deteriorating marine conditions associated with temperature fall slowly affected the rate of origination of stromatoporoids from Givetian to Famennian time. The ultimate cause of such global climatic change is unlikely to be determined from paleontological or stratigraphical studies. This decline in originations was intensified into widespread extinctions in the F/F and D/C intervals by changes in sea level, causing habitat loss and locally catastrophic flooding of anoxic waters onto shelf environments. By the end of the Devonian, stromatoporoids were unable to withstand further stress and became extinct.

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