Geological Society of America
Special Paper 356
2002

# *Late Devonian sea-level changes, catastrophic events, and mass extinctions*

**Charles A. Sandberg***
*U.S. Geological Survey, Box 25046, MS 939, Federal Center, Denver, Colorado 80225-0046, USA*
**Jared R. Morrow**
*Department of Earth Sciences, University of Northern Colorado, Greeley, Colorado 80639, USA*
**Willi Ziegler**
*Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325, Frankfurt am Main, Germany*

## ABSTRACT

**Late Devonian history is explained through event stratigraphy comprising a sequence of 18 sea-level changes, catastrophic events, and mass extinctions. Generally rising sea level during the initial Frasnian Stage, beginning with the Taghanic onlap and ending with a sea-level fall and major mass extinction, was interrupted by several exceptionally rapid, very high rises of sea level. These rises may be related to a series of comet showers, as suggested by the coincidence of the Alamo Impact in Nevada and the older Amönau Event in Germany with two of the sea-level rises. The subcritical, off-platform marine Alamo Impact is demonstrated to have produced greatly different effects in deep water from those previously recorded on the carbonate platform.**

**The series of comet showers, most notably those around the Frasnian-Famennian boundary, evidenced by microtektites in widely separated regions, not only produced the late Frasnian mass extinction, but also induced global cooling. This cooling resulted in Southern Hemisphere glaciation. Generally falling sea level during the later Famennian Stage was interrupted by several warmer, interglacial episodes, evidenced by glacio-eustatic rises. Another, less severe mass extinction occurred during an abrupt sea-level fall near the end of the Famennian. This glacio-eustatic fall is interpreted to have resulted from a severe, terminal glacial episode.**

**Interpretation of Late Devonian history suggests that impacts and comet showers coincided with sea-level rises, whereas mass extinctions occurred during, not at the start of, sea-level falls.**

## INTRODUCTION

The Late Devonian Epoch, one of the most intensively studied of all the Paleozoic epochs, was a time of major sea-level changes and catastrophic events, some of which were impact related, and two mass extinctions, one of which was impact related. Detailed knowledge and dating of Late Devonian events resulted from a high-resolution biochronology, based primarily on conodont zonations (Sandberg and Ziegler, 1996) and supported in part by ammonoid, ostracod, and spore zonations. This detailed knowledge was gained by intensive biostratigraphic studies during the past two decades, inspired by the International Union of Geological Sciences Subcommission of Devonian Stratigraphy and by International Geological Cor-

---

*E-mail: sandberg@usgs.gov

Sandberg, C.A., Morrow, J.R., and Ziegler, W., 2002, Late Devonian sea-level changes, catastrophic events, and mass extinctions, *in* Koeberl, C., and MacLeod, K.G., eds., Catastrophic Events and Mass Extinctions: Impacts and Beyond: Boulder, Colorado, Geological Society of America Special Paper 356, p. 473–487.

relation Programme (IGCP) Projects on Global Bio-Events and Mass Extinctions (Kauffman and Walliser, 1990; Walliser, 1986, 1996a). The initial Late Devonian Frasnian Stage was a time of general transgression during the Taghanic onlap that began in the late Middle Devonian (Johnson et al., 1985). The final Famennian Stage was a time of general regression, probably due to Southern Hemisphere glaciation, interrupted by four major transgressions, probably related to interglacial episodes. Both the late Frasnian and late Famennian mass extinctions occurred during, not at the start of, rapid regressions that closely followed rapid transgressions. The stepwise late Frasnian mass extinction (Sandberg et al., 1988; Schindler, 1990a, 1990b; McGhee, 1996), one of the five greatest in Earth's history, is believed to have occurred as a result of environmental stresses that were related to not just one but to a series of multiple, noncritical impacts, beginning with the Alamo Impact (Morrow et al., 1998). The late Famennian mass extinction, however, is believed to have occurred at the culmination of stresses produced by alternating glacial and interglacial episodes (Sandberg et al., 1988).

## CONODONT BIOCHRONOLOGY

The Late Devonian was a time of many sea-level changes, catastrophic events, and two mass extinctions, knowledge of which is enabled mainly by means of a high-resolution conodont biochronology (Sandberg and Ziegler, 1996). The Devonian Period lasted 46 m.y., and comprises 57 conodont zones. The Late Devonian alone lasted 15 m.y., and comprises 32 of these zones (Fig. 1). The older Late Devonian Frasnian Stage, 5 m.y. long, contains 10 of these zones, whereas the younger Famennian Stage, 10 m.y. long, contains the other 22 zones. Two Frasnian zones are further divisible, and we intend to formally subdivide them in a later manuscript. Herein we informally recognize three subdivisions of the Early *rhenana* Zone: an early part, a middle part encompassing the entry and life span of the opportunistic species *Palmatolepis semichatovae*, and a late part apparently lacking this species. We also recognize two important subdivisions of the *linguiformis* Zone: an early part, encompassing the entry and life span of the nominal species *Palmatolepis linguiformis*; and an upper part, apparently lacking this species but containing *Pa. praetriangularis* and common *Ancyroides ubiquitus*.

Although the large number of recognized events might be considered to be an artifact of this detailed biochronology, we believe that the opposite is true. The multiple events that occurred during the Late Devonian caused the rapid evolution of conodonts and other marine organisms. This rapid evolution was punctuated first by the late Frasnian mass extinction (the so-called F-F or Kellwasser Event) and later by the late Famennian mass extinction (the so-called D-C or Hangenberg Event). *Palmatolepis* and two other pelagic genera, *Mesotaxis* and *Siphonodella*, are the principal taxa employed by the standard Late Devonian conodont zonation (Ziegler and Sandberg, 1990). However, only one species of *Palmatolepis, Pa. praetriangularis*, survived the late Frasnian mass extinction. This single species gave rise to the earliest Famennian species *Palmatolepis triangularis* and its more than 100 descendant species and subspecies during the Famennian. Later, only one of these descendant species, *Palmatolepis gracilis*, barely survived the late Famennian mass extinction, only to die out very early in the ensuing Early Carboniferous (Mississippian) Epoch.

## LATE DEVONIAN SEA-LEVEL CHANGES

The now widely accepted Late Devonian sea-level curve shown in Figure 2 was devised by Johnson et al. (1985) and improved for the western United States by Johnson and Sandberg (1989). This curve illustrates that a general transgression or sea-level rise began with the Taghanic onlap in the Middle Devonian (Givetian) Middle *varcus* Zone and continued through most of the Frasnian until just before the late Frasnian mass extinction within the *linguiformis* Zone (Fig. 1). The sea-level curve also demonstrates that a general Famennian regression occurred and was terminated by a second severe eustatic fall just before the start of the Early Carboniferous (Mississippian) Kinderhookian Stage. Sandberg et al. (1988) attributed this general Famennian regression to Southern Hemisphere glaciation that directly followed and may have resulted from the same catastrophic events that produced the late Frasnian mass extinction. This general regression was interrupted by four major sea-level rises that they attributed to interglacial episodes.

The Late Devonian sea-level curve was used by Sandberg et al. (1988, their Fig. 4) to illustrate that the late Frasnian mass extinction as well as the late Famennian mass extinction occurred during severe eustatic falls that immediately followed major eustatic rises. They also demonstrated by a series of three marine cross sections, two for the *linguiformis* Zone and one for the earliest Early *triangularis* Zone, how these sea-level changes dramatically altered not only conodont biofacies, but also sedimentation patterns. Furthermore, they documented these rapid changes of sea level sedimentologically not only at the Steinbruch Schmidt section in a deep-water, submarine-rise setting in Germany, but also at sections in inner shelf and outer shelf and slope settings in Belgium, Nevada, and Utah. Whereas it is well documented that a stepwise extinction began with the severe sea-level fall, the ultimate mass extinction took place well within this sea-level fall. The magnitude of this sea-level fall, which continued into the early Famennian, was demonstrated by a map showing that this regression caused the sea to retreat an average of 400 km westward from the Transcontinental arch in the western United States.

The occurrence of the two Late Devonian mass extinctions during sea-level falls was reemphasized by Sandberg and Ziegler (1991, 1992) at meetings of IGCP Project 216, dealing with Event Markers in Earth History and with Phanerozoic Global Bio-Events and Event Stratigraphy. This observation had been first made in relation to the Devonian-Carboniferous boundary

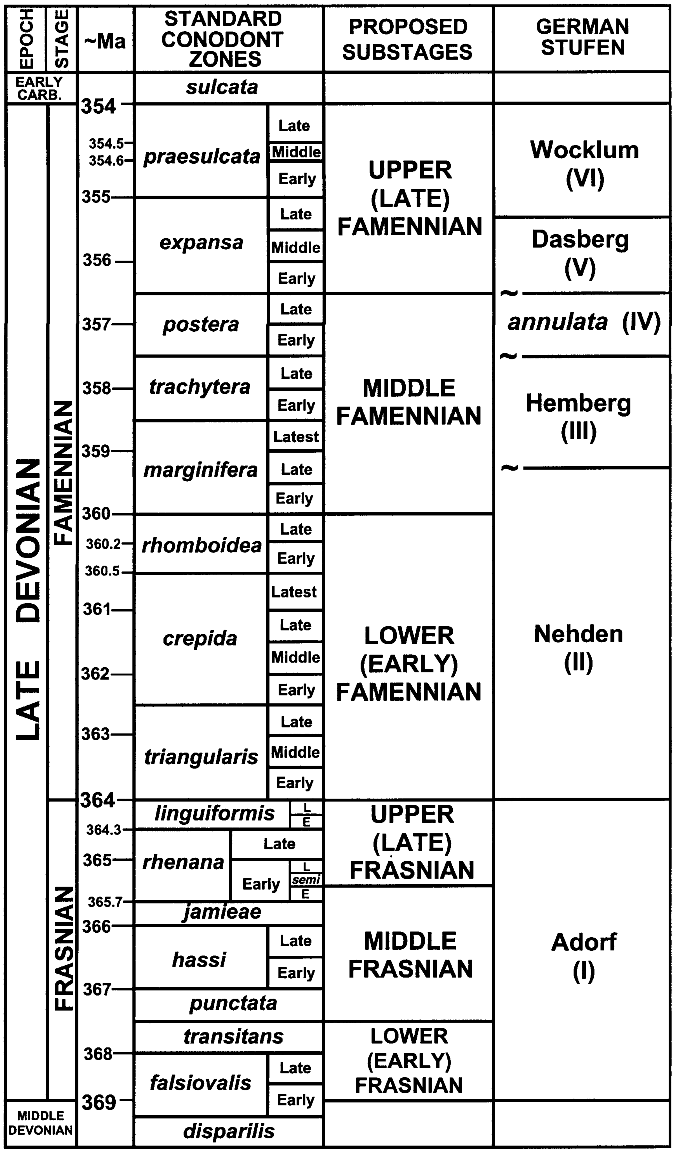

Figure 1. Late Devonian conodont zonation and approximate ages (after Sandberg and Ziegler, 1996). Substages proposed by Sandberg and Ziegler (1998); informal subdivisions of Early *rhenana* and *linguiformis* Zones are added. E is early part, L is late part, *semi* is *Palmatolepis semichatovae* interval, Carb. is Carboniferous.

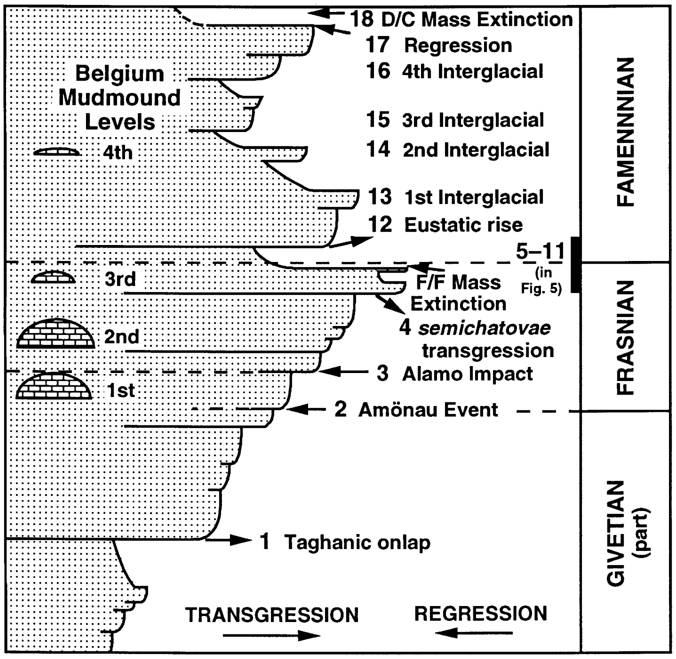

Figure 2. Late Middle to Late Devonian sea-level curve, showing positions of 18 sea-level changes, catastrophic events, and mass extinctions, which are more fully described in Table 1, and four levels of Belgium mudmounds. Events 5–11 are positioned in Figure 5 against more detailed sea-level curve for interval shown here by thick black bar. D/C is Devonian-Carboniferous, F/F is Frasnian-Femannian.

(Ziegler and Sandberg, 1984). Schindler (1990a, 1990b) effectively demonstrated not only the stepwise extinction during the late Frasnian sea-level fall, but also the concurrent introduction of new shallow-water faunas prior to the final mass extinction. The finding that a sea-level fall preceded the late Frasnian mass extinction was later corroborated biostratigraphically and sedimentologically by many other workers in other parts of the world (e.g., Goodfellow et al., 1989; Geldsetzer et al., 1993 [western Canada]; Matyjab and Narkiewicz, 1992 and Racki, 1998a [Poland]; Lazreq, 1992, 1999 [Morocco]; Girard and Feist, 1997 [southern France]; Ji, 1989 and Muchez et al., 1996 [southern China]; Schindler et al., 1998 [Germany]). Furthermore, a sequence stratigraphic study across the Frasnian-Famennian boundary (Morrow and Sandberg, 1997) substantiated the initial sedimentological analysis. In contradiction to overwhelming evidence presented by these and many other workers directly involved in Late Devonian studies, Hallam and Wignall (1999) misinterpreted, on the basis of a biased or incomplete literature survey, that the late Frasnian mass extinction had little support in sequence stratigraphic analysis and differed from the other four major mass extinctions in having occurred during a highstand or sea-level rise.

## LATE DEVONIAN EVENTS

The 18 major Late Devonian sea-level changes, catastrophic events, and two mass extinctions that we now recognize are positioned against the Late Devonian sea-level curve in Figure 2 and are listed with more detail in Table 1. We emphasize that this table, although having some events in common, does not revise or supplant the tabulation of 17–19 late Middle to Late Devonian eustatic and epeirogenic events in the western United States (Sandberg et al., 1989, 1997), which improved on earlier tabulations of only 13 such events in that region and around the "Old Red Continent" (Sandberg et al., 1983, 1986). These tabulations were matched by the recording of a similar sequence of mainly eustatic Late Devonian events

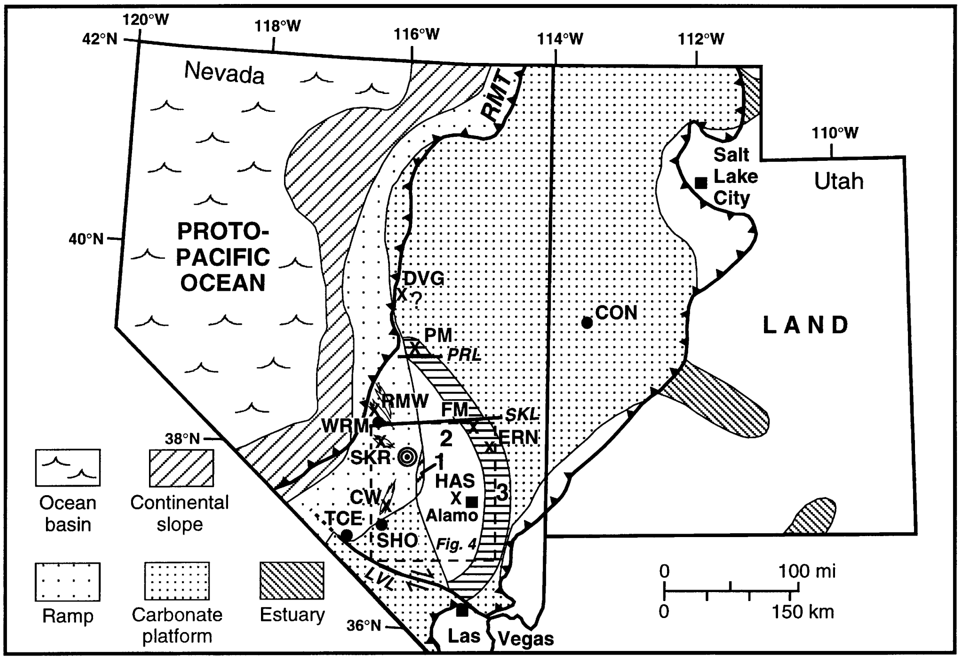

Figure 3. Paleotectonic map (partly restored) of Nevada and Utah during middle Frasnian *punctata* Zone, showing possible site of subcritical, oceanic Alamo impact (bullseye) and distribution of resulting Alamo Impact Breccia. Alamo Breccia Zones 1, 2, and 3 form semicircular pattern on ramp (Zone 1), outer carbonate platform (Zone 2), and peritidal, inner platform (Zone 3). Also shown are locations of four newly discovered deep-water channels of Alamo Breccia, some representing crater fill and some transporting breccia debris seaward. Selected major post-breccia structural features include RMT, latest Devonian to earliest Mississippian Roberts Mountains thrust, which significantly displaced Devonian transitional and oceanic facies; and three Tertiary lineaments that affected distribution of Alamo Breccia: LVL, Las Vegas lineament; SKL, Silver King lineament; and PRL, Pancake Range lineament. Important measured sections: CON, Little Mile-and-a-Half Canyon; CW, Carbonate Wash; DVG, Devils Gate; ERN, East Ridge North; FM, Fox Mountain; HAS, Hancock Summit (type locality of Alamo Breccia); PM, Portuguese Mountain; RMW, Rawhide Mountain West; SHO, Shoshone Mountain; SKR, Streuben Knob; TCE, Tarantula Canyon East; WRM, Warm Springs. Alamo Breccia localities are indicated (X) and other important data points are indicated by dots. Area of Figure 4 is shown by dashed rectangle.

in western Pomerania, Poland (Matyja, 1993). These earlier tabulations had a very different emphasis, however, from our global tabulation.

Herein, we explain more fully the 18 events summarized in Table 1 and discuss in detail the Amönau Event, Alamo Impact, and late Frasnian and late Famennian mass extinctions.

### *Taghanic onlap (Event 1)*

The Taghanic onlap (start of transgressive-regressive [T-R] cycle IIa of Johnson et al., 1985) marked the end of faunal provincialism, which had persisted since Early Devonian time and is well documented for conodonts and brachiopods (Johnson, 1970; Klapper and Johnson, 1980; Ziegler and Lane, 1987; Johnson and Sandberg, 1989). It also marked the start of an episode of cosmopolitanism, which continued uninterrupted until the late Frasnian mass extinction. This onlap and long episode of general sea-level rise began in the Middle Devonian Middle *varcus* Zone and was coincident with the Acadian orogeny, which produced a continental collision of Europe, and probably North Africa, with the present eastern side of North America. The Taghanic onlap ended with the rapid, eustatic sea-level fall and regression that coincided with the late Frasnian mass extinction near the end of the *linguiformis* Zone (Fig. 2).

### *Amönau Event (Event 2)*

The enigmatic Amönau Event occurred in the Rheinisches Schiefergebirge of central Germany coincident with a major pulse of the Taghanic onlap at the start of the Frasnian Stage within the late part of the Early *falsiovalis* Zone (Fig. 1). The event was recognized and named by Sandberg et al. (2000) on the basis of a reinterpretation of the Amönau Breccia. This so-called tuff breccia, containing large blocks derived from Devonian reefs mixed with basalt clasts and glass shards and found in two quarries near Wetter, Germany, was originally inter-

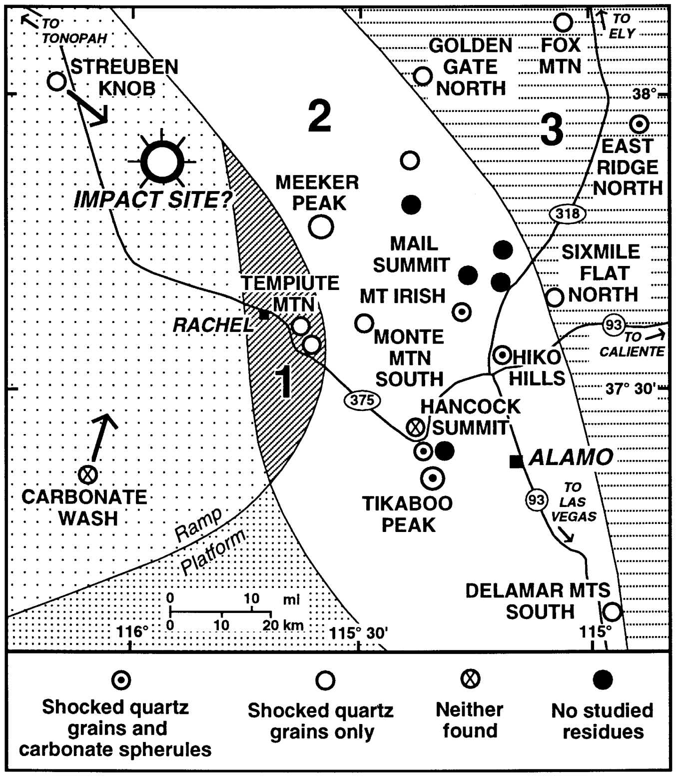

Figure 4. Northeast quadrant of distribution pattern of Alamo Breccia, southern Nevada, as indicated in Figure 3. Shown are inferred location of now buried, tectonically disturbed impact site; Zones 1, 2, and 3 of Alamo Breccia; probable direction of deep-water channels; and recovery of impact-fallout material at studied localities. Line bounding Zone 2 on west is position of Late Devonian *punctata* Zone shelf margin. Weak iridium anomaly was found at Meeker Peak. Mt—Mount, Mtn—Mountain, Mts—Mountains.

preted by Bender et al. (1984, p. 31) to have resulted from "erosional destruction of a reef during a period of volcanic activity." Sandberg et al. (2000) found that the presumed volcanic explosion at Amönau was coincident with another tuff breccia at Donsbach, 38 km to the southwest, and a bentonite bed at Blauer Bruch near Bad Wildungen, 40 km to the northeast. Thus, subaerial volcanism, which might have resulted from an impact on a submarine rise, began simultaneously across a 78-km-long transect of the Rheinisches Schiefergebirge. At the same time, a stratigraphic hiatus was produced by deposition of exhalative hematite at Martenberg, 40 km northwest of Blauer Bruch. Subsequent field work suggested that a 170-m-thick debris flow near Günterod (Huckriede, 1992) could be part of the same event. All three known breccias might represent post-impact crater fill. However, we emphasize that evidence for an impact has not yet been found because of the scarcity of exposures, except in a few quarries and stream cuts, in this region of predominantly highly weathered slate hills. The Amönau Event is meaningful, however, as a harbinger of later, well-documented catastrophic events and mass extinctions that shaped Late Devonian history.

### *Alamo Impact (Event 3)*

The biochronologically dated, well-documented Alamo Impact in southern Nevada (Fig. 3) is especially significant because of its possible relationship to the younger Frasnian mass extinction and to several other, radiometrically dated Late Devonian impacts. The Alamo Impact has been dated by conodonts in beds below, within, and above the resulting breccia as having occurred during the early Frasnian *punctata* Zone (Fig. 1), ~3 m.y. before this mass extinction within the latest Frasnian *linguiformis* Zone (Sandberg and Warme, 1993; Sandberg and Morrow, 1998). Because of the number of other Late Devonian impacts, such as the Flynn Creek in Tennessee and the Siljan in southern Sweden, we suggest that the Alamo Impact may have been part of a comet shower or the first—or second, if the Amönau Event proves to be impact related—of a series of comet showers. These showers would explain the demise of three successively less extensive and biotically less diverse reef levels in Belgium (Fig. 2), and the progressive weakening of marine communities before their final extinction. The timing of the Alamo Impact coincides with the demise of the first reef level. Unfortunately, the other Devonian impacts have been dated by different radiometric methods and are difficult to relate to one another and to the Alamo Impact.

Even though the location of its crater is uncertain because of later tectonic dismemberment and burial beneath valley fill and volcanics, the Alamo Impact has been documented on the basis of many different criteria. Originally, the occurrence of three zones of megabreccia in a semicircular distribution pattern, 200 km in diameter and located mainly on a shallow carbonate platform, and the presence of a weak iridium anomaly were documented by Warme and Sandberg (1995). They illustrated an example of the shocked quartz grains, identified by Leroux et al. (1995), which occur abundantly within turbidites in the upper part of the megabreccia. Localities at which shocked quartz grains have been recovered in all three zones, as well in a deep-water channel farther west (Morrow et al., 1998), as reported herein, are shown in Figure 4. Impact-related injected dikes and sills within the 300 m of strata below the Alamo Breccia at Tempiute Mountain, which may be located close to the eastern crater rim, have been described and illustrated (Warme and Sandberg, 1995; Sandberg et al., 1997). Impact-fallout, zoned, carbonate spherules within the breccia were recognized by Warme and Kuehner (1998). Like the shocked quartz grains, these spherules occur in small blocks within coarse turbidites in the upper part of breccia. Shocked quartz grains were found within the turbidites, as well as within the contained blocks, and in the cores of spherules. Localities where both shocked quartz grains and carbonate spherules occur in Zones 2 and 3 are shown in Figure 4. The final line of evidence, which also permits estimation of the crater depth, is the presence in these same blocks of common, ejected Middle Ordovician and possibly older conodonts, which were blasted from strata 1.5 km or more below the Late Devonian seafloor

TABLE 1. LATE DEVONIAN EVENTS

| Number | Event |
|---|---|
| 18 | Late Famennian mass extinction within eustatic fall; loss of many Devonian species including Lazarus fauna |
| 17 | Start of major eustatic fall at climax of Southern Hemisphere glaciation; biotic decline begins |
| 16 | Eustatic rise at start of 4th interglacial episode; Etroeungt Lazarus fauna suddenly appears in Northern Hemisphere |
| 15 | Eustatic rise at start of 3rd interglacial episode; *annulata* black basinal shales deposited in Germany |
| 14 | Eustatic rise at start of 2nd interglacial episode; Baelen mudmound formed in Belgium |
| 13 | Eustatic rise at start of 1st interglacial episode; *Cheiloceras* dark shales deposited |
| 12 | Eustatic rise, producing initial post-extinction biotic radiation |
| 11 | Carbonate-platform margins collapse due to glacioeustatic lowering of seas; widespread coarse tsunamite breccias result |
| 10 | Storms and (or) tsunami scour or remove Frasnian-Famennian boundary beds in France, Germany, and Nevada |
| 9 | Late Frasnian mass extinction within eustatic fall; widespread layer of abiotic extinction shale deposited; start of Southern Hemisphere glaciation |
| 8 | Rapidly increased shallowing; storm deposits; stepwise extinction of some deep-water species as shallow-water species move into deeper water; spore floras change |
| 7 | Eustatic fall; start of global cooling; reduction in number and diversity of deep-water faunas |
| 6 | Continued eustatic rise; stratification of water column, resulting in widespread basinal anoxia; start of rapid evolution of deep-water entomozoan ostracods |
| 5 | Eustatic rise producing dysoxia in deep basins; start of events leading to mass extinction |
| 4 | Major *semichatovae* transgression producing biotic changes and stress |
| 3 | Alamo Impact in Nevada, coinciding with eustatic rise and demise of 1st level of Belgian mudmounds |
| 2 | Amönau Event, coinciding with onset of impact-induced(?) volcanic activity in central Germany and with eustatic rise at start of Frasnian |
| 1 | Taghanic onlap at start of plate-tectonic movements in Northern Hemisphere; end of faunal provincialism |

(Sandberg, 1998; Morrow et al., 1998). The recovery of rare reworked Ordovician conodonts within the groundmass of the breccia was reported by Warme and Sandberg (1995).

More complete descriptions of these lines of evidence were given by Warme and Kuehner (1998) and Morrow et al. (1998, 1999). Warme and Kuehner (1998) and Warme and Chamberlain (2000), however, interpreted the impact site to be on the shallow-water carbonate platform, rather than in deeper water off the platform margin, as interpreted by Morrow et al. (1998, 1999). Our current study of deep-water channels, several of which contains shocked quartz grains, provides further support for a deeper water impact site.

Our interpretation of the deeper water site of the subcritical Alamo Impact is best explained by reference to our partly restored *punctata* Zone paleotectonic map (Fig. 3) showing the three partial rings of Alamo Breccia in relation to the coeval platform, ramp, and continental slope. The innermost ring, Zone 1, a 130-m-thick turbidite, was deposited by crater fill that poured seaward off the Late Devonian carbonate-platform margin. The middle ring, Zone 2, deposited on the shallow carbonate platform, consists of a lower debrite of huge, seaward-sliding blocks evolving upward into several normally graded, coarse- to fine-grained turbidites resulting from the ensuing megatsunami. The outer ring, Zone 3, consists of stranded, locally isolated, high-water-line megatsunami deposits on the peritidal inner carbonate platform and adjacent Late Devonian shoreline. These rings are now truncated and/or segmented by several generally east-west-trending strike-slip lineaments, the three most critical of which are shown in Figure 3.

Warme and Kuehner (1998) and Warme and Chamberlain (2000), misinterpreting the stratigraphy of rocks enclosing the Alamo Breccia, tried to show that, if the impact were entirely on the carbonate platform, structural reinterpretation of the Timpahute Range would produce three complete rings. However, our recent study of deeper water channels and of Zone 1 show that these contemporaneous Alamo Breccia deposits overlie a different suite of older Devonian rocks than those that underlie the breccia on the carbonate platform. We now realize that the pattern of rings need not be completely circular even if the original crater and crater rim were circular. The Zone 2 ring is a shallow-water deposit, whereas the Zone 3 ring is peritidal to nonmarine. Given the early Frasnian paleogeography, which shows progressively deeper water toward the proto-Pacific Ocean basin on the west (Fig. 3), it is physically impossible for these rings to be completed by very shallow water and land to the west, even if the impact had been on the carbonate platform. In direct contradiction to the complete-ring interpretation of Warme and his coworkers, we have discovered four deep-water channels (Fig. 3), in several of which we recovered shocked quartz grains. These channels are interpreted to form a pattern radiating from the probable crater site, very much like the pattern shown by Ormö and Lindström (2000) for the Early Ordovician marine Lockne crater in Sweden. Thus, we now interpret the Alamo Impact depositional phenomena to form two different patterns, depending on paleotectonic setting, and theorize that the western rim of the crater is located farther west and downslope, perhaps below the Roberts Mountains thrust.

The northeast quadrant of the Alamo Breccia deposits (enlarged in Fig. 4) focuses on the evidence for our interpretations and shows some of the more important localities. We interpret that the Streuben Knob channel, containing shocked quartz grains, flowed craterward from the western crater rim. Conversely, we interpret that the Carbonate Wash channel, containing blocks of carbonate-platform rocks but no shocked quartz grains, represents crater fill from the shattered platform margin. We also record, for the first time, the occurrence of carbonate spherules in Zone 3 at East Ridge North.

### Semichatovae *transgression (Event 4)*

The *semichatovae* transgression (Event 4) was an abrupt, but short-lived major deepening event (Fig. 2). This event corresponds to the start of T-R cycle IId of Johnson et al. (1985). This transgression carried *Palmatolepis semichatovae*, an opportunistic representative of a pelagic genus, far onto shallow carbonate platforms, normally uninhabitable for *Palmatolepis*, throughout the world. This species composes 70%–100% of *Palmatolepis* populations on the carbonate platform, but <10% of such populations in deep basins (Sandberg et al., 1989). This population migration is unique among all organisms in the Late Devonian record. Although the *semichatovae* transgression did not directly terminate the second level of Belgian Late Devonian mudmounds, it is recorded by an abrupt sedimentologic change, possibly associated with the onset of volcanism, between the second and third levels (Sandberg et al., 1992). We offer no explanation for this globally recorded, exceptionally high, very rapid eustatic rise, but ponder whether, like the Alamo Event, it could be impact related.

### *Late* rhenana *Zone eustatic rise (Event 5)*

This eustatic rise, shown as the next sea-level spike above the *semichatovae* transgression in Figure 2, followed a eustatic fall late in the Early *rhenana* Zone and early in the Late *rhenana* Zone. It equaled Event 4 in intensity and resulted in the demise of the third level of Belgian Late Devonian mudmounds. Event 5 deepening, which produced dysoxia in most marine basins, was the start of a series of events leading to the late Frasnian mass extinction, as illustrated in the detailed Late Devonian sea-level curve (Fig. 5). As in the case of Event 4, we ponder whether Event 5 could be impact related. Regardless, the close timing of two such catastrophic floodings undoubtedly weakened and destabilized marine populations, so that they more easily succumbed to the late Frasnian mass extinction during a major eustatic fall.

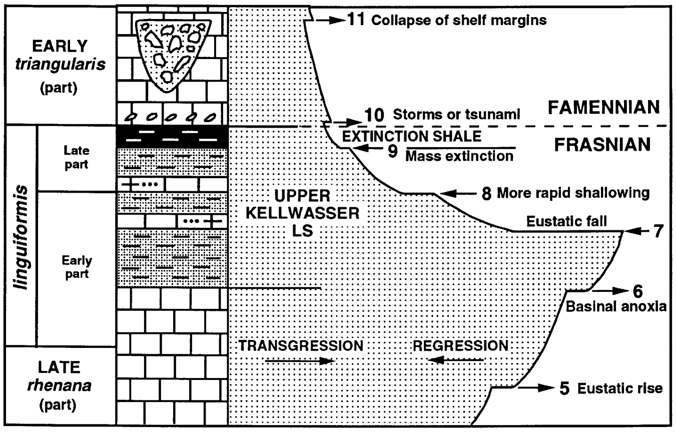

Figure 5. Detailed Late Devonian sea-level curve across Frasnian-Famennian stage boundary and generalized pattern of sedimentation related to late Frasnian mass extinction. Events 5–11 are more fully described in Table 1. Conodont zonation is at left and position of Upper Kellwasser Limestone (LS) is at right of lithologic column.

### Linguiformis *Zone anoxia (Event 6)*

Deepening continued uninterrupted from the Late *rhenana* into the *linguiformis* Zone. Eventually, well within the *linguiformis* Zone, the oceans deepened so considerably that even in most epicontinental seaways, the water column became stratified into aerobic, dysaerobic, and anaerobic layers. The resulting basinal anoxia was recognized by the overstepping of black carbonaceous shale and chert over lighter colored carbonate rocks, as exemplified within several stratigraphic sections in Nevada, Belgium, and Germany (Sandberg et al., 1988). The most important, readily accessible reference sections for faunal, sedimentologic, geochemical, and geomagnetic studies of Events 6 to 9 are Devils Gate, Nevada, and Steinbruch Schmidt, Germany.

Conodont abundances decreased by at least 80% as a result of the basinal anoxia, but few if any significant deeper water extinctions occurred at that time. In fact, deep-water entomozoan ostracod populations continued to thrive and evolve (Buggisch et al., 1978; Groos-Uffenorde and Wang, 1989; Groos-Uffenorde and Schindler, 1990). Nevertheless, the anoxic events were considered to be the actual cause of the Frasnian-Famennian faunal crisis by Joachimski and Buggisch (1993), who based this interpretation on a positive $\delta^{13}C$ excursion and an increase in organic carbon burial.

However, the deepening during Event 6 changed marine conditions on the shallow shelf areas and carbonate platforms, even where obvious lithologic evidence of the event is lacking (Bratton et al., 1999). Many workers have previously used the highest occurrences of colonial and large solitary corals or of *Amphipora* biostromes in shallow-water or peritidal settings, respectively, to approximate the end of the Frasnian in the absence of definitive conodont evidence (e.g., Geldsetzer et al., 1993). However, it is more likely that these Frasnian corals and biostromes disappeared concurrently with the increased deepening in Event 6 within the *linguiformis* Zone, if they had not already been decimated or terminated earlier, concurrently with the start of deepening and demise of the third level of Belgian mudmounds in the Late *rhenana* Zone (Event 5). Similarly, extinctions of some species of shallow-water atrypid and gypidulid brachiopods, commonly attributed to the late Frasnian mass extinction (Event 9), may actually have occurred earlier, during Events 5 and 6.

### **Linguiformis** ***Zone eustatic fall pulses (Events 7 and 8)***

A severe eustatic fall (Event 7) followed by a pulse of even more rapid shallowing (Event 8) preceded the late Frasnian mass extinction terminating the *linguiformis* Zone (Fig. 5). The sedimentologic and oxygenation changes accompanying these pulses were described in detail by Sandberg et al. (1988), so only the drastic conodont faunal changes are summarized here. Stepwise extinction and genetic mutations of almost all species of the deep-water genus *Palmatolepis* accompanied the pulses of falling sea level. These changes are exemplified by the two most important taxa, *Palmatolepis linguiformis* and *Pa. rhenana rhenana. Palmatolepis linguiformis*, the entry of which defines the start of the *linguiformis* Zone (Ziegler and Sandberg, 1990), died out at Event 8. Consequently, we now informally divide the *linguiformis* Zone into early and late parts, with and without this key species (Fig. 5). Bizarre, oddly shaped mutants, illustrated by Ziegler and Sandberg (1990, 2000), preceded the demise of *Pa. rhenana rhenana* within the late part of the *linguiformis* Zone. Contemporaneous with these changes were major changes in shallower water conodont faunas, as exemplified by two important species, *Icriodus alternatus* and *Ancyroides ubiquitus. Icriodus alternatus*, which had been a minor constituent of all conodont faunas during Event 5 and totally absent from deep-water faunas during Event 6, resurged to compose 30% or more of all deep- and shallow-water faunas during Event 7. *Ancyroides ubiquitus*, which is a further aid to identification of the late part of the *linguiformis* Zone, evolved from *As. uddeni* late within the early part of the *linguiformis* Zone and survived the late Frasnian mass extinction only to die out early in the Early *triangularis* Zone.

The stepwise extinction and changes in conodont faunas during Events 7 and 8 are matched by equally significant stepwise extinctions and changes in other groups, as described by Schindler (1990a, 1990b). The stepwise extinctions involve trilobites in Event 6, gephuroceratid ammonoids and some entomozoan ostracods in Event 8, and finally homoctenids, which like *Ancyroides ubiquitus*, barely survived Event 9. Concurrently with these extinctions, a large bivalve *Buchiola* invaded shallower water strata during Event 8.

### ***Late Frasnian mass extinction (Event 9)***

Biological and geochemical studies of the late Frasnian mass extinction, one of the five greatest in the Phanerozoic record, have increased exponentially since its recognition by McLaren (1967 [personal commun.], 1970, 1982). The literature has grown so voluminous that only the more recent references and the most relevant older references can be cited here. Comprehensive bibliographies listing most of the other equally significant studies up to the date of publication were presented by Sandberg et al. (1988), McGhee (1996), and Hallam and Wignall (1999). By combining this vast amount of knowledge contained in these studies with our own investigations of the late Frasnian mass-extinction (Event 9), we can now answer with confidence the important questions of what happened, and when and where this happened. These answers pertain mainly to the marine realm. Admittedly, we know little about the effect of the extinction on the landmasses, except for some studies of palynomorphs and estuarine fish. We can, however, partly answer the question of how the mass extinction took place, but the remaining question of why remains equivocal. We attempt to explain the merits of the opposing arguments as to whether this was an Earth-bound or an impact-related event.

The late Frasnian mass extinction, or Kellwasser Crisis (Schindler, 1990a, 1990b), decimated most groups of marine organisms, as thoroughly summarized by Walliser (1996b), but apparently did not entirely wipe out any of them. Although the mass extinction affected the Earth's tropical and subtropical regions, which encompassed most of the areas of studied Devonian rocks, we know little about the temperate and polar regions. Apparently these regions as well as the deep ocean basins provided refuges for survivors or unaffected species that later repopulated the Famennian oceans. For example, although reef-building Devonian corals and large shallow-water solitary rugose corals were wiped out, small deep-water corals must have survived, because they are recorded in early Famennian rocks. Either their descendants or large rugose corals that survived in some unknown refuge produced a Lazarus fauna, containing large rugose corals late in the Famennian (Event 16). Likewise, although reef-building bulbous stromatoporoids were wiped out, descendants returned to produce large, pillow-shaped colonies in the late Famennian.

There are many other examples of the existence of survivors in other groups; we cite here only a few prime examples. Among the conodonts, all but one species of the pelagic genus *Palmatolepis* became extinct (Sandberg et al., 1988). The lone survivor *Pa. praetriangularis*, which had evolved just before the mass extinction, gave rise to the myriad of Famennian species, which in diversity far surpassed their Frasnian relatives. Regarding the mass extinction of ostracods (Lethiers and Casier, 1999), investigations of a single locality, Devils Gate, Nevada, documented their near mass extinction (Casier et al., 1996), the survival of some species (Casier and Lethiers, 1998a), and their eventual recovery (Casier and Lethiers, 1998b). The extinction of brachiopod faunas was effectively summarized by Racki (1998a). From our own studies at Devils Gate and elsewhere in Nevada, we note that although gypidulid and atrypid brachiopods were essentially wiped out, other groups such as the cyrtospiriferids and rhynchonellids were unaffected and occur profusely in post-extinction beds. A single possible atrypid survivor, *Peratos* sp., in the Famennian of Morocco was illustrated by Schindler (1990a). Likewise, possible homoctenid survivors high in the lower Famennian of South China were illustrated by You (2000), but the possibility of their reworking from the Frasnian or oldest part of the Famennian cannot be ruled out.

Having discussed what happened and where it happened, we now answer the question of when the mass extinction happened. From the conodont evidence and the international decision to locate the base of the Famennian at the start of sedimentation following the extinction, Event 9 can be dated as the final Frasnian event at the end of the late part of the *linguiformis* Zone (Fig. 5). This extinction apparently took place within a sedimentologically calculated interval of 20 k.y. or less (Sandberg et al., 1988), just prior to 364 Ma, which is the conodont biochronologic date assigned to the start of the Famennian (Sandberg and Ziegler, 1996). The mass extinction occurred during a long, catastrophic eustatic sea-level fall that immediately followed two closely spaced, rapid sea-level rises (Sandberg et al., 1988; Fig. 5).

Our findings contradict the conclusion reached by Hallam and Wignall (1999) that the late Frasnian mass extinction differed from the other four major Phanerozoic mass extinctions in having occurred during a sea-level rise rather than during a sea-level fall. Their conclusion was based on an incomplete literature survey that resulted in several incorrect assumptions. First, they assumed that *Icriodus* was restricted to shallow-water facies in the Frasnian. This is incorrect for two reasons. At least one species, *Icriodus symmetricus*, preferred moderately deep water settings and is uncommon in shallow-water settings. They assumed that the species *Icriodus alternatus*, the proliferation of which they challenged, inhabited only shallow-water settings. In fact, it also inhabited many preextinction, deep-water settings such as around the black smoker at the famous Martenberg section in Germany and the submarine rise at Steinbruch Schmidt, where it makes up 4% of youngest Late *rhenana* Zone faunas (Ziegler and Sandberg, 1990). Hallam and Wignall (1999, p. 226) stated that because of the shallow-water Frasnian occurrence of *Icriodus*, conodont workers assumed that "it had a similar facies distribution in the basal Famennian" and that the proliferation of the conodont *Icriodus* did not signal sea-level changes but rather a filling of vacant ecospace by lucky survivors. In addition to being inaccurate for several reasons, these are self-contradictory statements. The proliferation of *Icriodus* began during Events 7 and 8, not during the mass extinction (Event 9). The earliest Famennian conodont biofacies distribution of *Icriodus* in comparison to Frasnian and younger Famennian patterns was depicted by Sandberg et al. (1997, their Table 1). Sandberg et al. also showed that the "*Icriodus*" in later Famennian biofacies was not a true *Icriodus* but rather reiterative, homeomorphic shallow-water species of *Pelekysgnathus*, as documented by Sandberg and Dreesen (1984). Third, they assumed that the *Icriodus* bloom was the sole evidence on which the sea-level fall was based. They ignored the many documented sedimentologic and megafaunal changes that accompanied the *Icriodus* bloom prior to the mass extinction. The findings redocumented herein are supported by the findings of an overwhelming consensus of specialists who have studied the Frasnian-Famennian boundary globally (e.g., Goodfellow et al., 1989; Schindler, 1990a, 1990b; Lazreq, 1992, 1999; Matyja and Narkiewicz, 1992; Muchez et al., 1996; Girard and Feist, 1997; Racki, 1998a; Schindler et al., 1998).

Our scenario to partly explain how and why the late Frasnian mass extinction happened involves our sequence of Events 1–8. We agree with McGhee (1981, 1988), that the marine ecosystem had collapsed and reef and mudmound communities had been destroyed well before the mass extinction occurred. Applying the association of sea-level rises with the known Alamo Impact and enigmatic Amönau Event to other unexplained sea-level rises, we theorize that the Frasnian was a time when the Earth was subjected to a number of subcritical oceanic impacts produced by a series of comet showers. The two short, catastrophic rises that immediately preceded the mass extinction were particularly devastating to marine communities. Thus, the final event that triggered the mass extinction could have been another group of small, subcritical impacts. Following Sandberg et al. (1988), we interpret that one of these impacts could have been in the Southern Hemisphere, possibly close to Australia and China, and that this impact produced a global cooling and subsequent Southern Hemisphere glaciation during the Famennian (Caputo, 1985). A strong $\delta^{13}C$ anomaly associated with a weak iridium anomaly has been found at the Frasnian-Famennian boundary in southern China (Wang et al., 1991). Younger, early Famennian microtektites reported there by Wang (1992) were interpreted by Claeys and Casier (1994) as being possibly reworked. Evidence of another possible impact site is provided by the finding of iridium enrichments in the boundary interval in western New York State (Over et al., 1997). Even more compelling evidence for a third impact site is the finding by Claeys and Casier (1994) of microtektite-like glass precisely at the boundary layer at the Hony railroad cut, Belgium, which was previously measured and used to interpret the mass extinction by Sandberg et al. (1988). The Siljan Impact in Sweden was suggested as the possible source for the Belgian microtektites (Claeys and Casier, 1994).

Several respected investigators of the Frasnian-Famennian boundary interval disagree for different reasons with an impact origin for the extinction (e.g., Copper, 1986; McGhee et al., 1986; Joachimski and Buggisch, 2000; Racka and Racki, 2000; Racki, 1998b, 1999). Whereas we agree with Copper (1986) regarding most stepwise floral and faunal extinctions, we do not agree that continental suturing took place between the

Frasnian and Famennian, or that the diverted, cold polar currents would have been dysaerobic. According to our sequence of events, continental suturing—i.e., the Acadian orogeny—would have already occurred in Event 1, concurrent with the onset of cosmopolitanism. In addition, using the modern analog, Antarctic waters are known to be not dysaerobic, but well oxygenated and teeming with biota. McGhee et al. (1986) concluded that no geochemical evidence existed at Steinbruch Schmidt, Germany, for an impact during the Kellwasser Event. They analyzed the entire Upper Kellwasser Limestone, which incorporates Events 6–9. However, the relevant extinction layer (Event 9) at this locality is a possibly slumped or tectonically squeezed 5 cm interval. If this interval were to be properly analyzed geochemically, it should be done by means of a core hole well back from the cliff face. In all fairness, McGhee (1996) later thoroughly summarized and gave equal weight to all opposing theories, but seemingly favored an impact origin for the late Frasnian mass extinction. Although Joachimski and Buggisch (2000) tentatively reported, on the basis of $\delta^{18}O$ shifts, a 7 °C decrease in tropical surface-water temperature, this does not negate an impact. The large decrease could have been produced by the impact-related global cooling postulated by Sandberg et al. (1988) or even by an ancient El Niño-La Niña cycle. Racki (1998b, 1999) reverted to a Variscan plate tectonic explanation for the biotic crisis, but added the possibility of volcanic-hydrothermal processes, while not excluding minor cometary strikes. Regardless of the ultimate solution for the cause of Event 9, we concede that given the preexisting weakness of marine communities, the triggering mechanism for the extinction could have been relatively minor.

### *Violent post-extinction currents (Event 10)*

At most studied sections where the Frasnian-Famennian boundary can be precisely pinpointed in carbonate-platform, shelf, and slope settings in Belgium, France, Germany, Nevada, and Utah, but where a dark-colored extinction shale is not preserved, there is convincing evidence of immediate post-extinction scour. For example, in a slope sequence at Burg Berg, Germany (Ziegler and Sandberg, 1990; new data herein), initial sampling of a bed only 5 cm thick yielded a mixed *linguiformis* and Early *triangularis* Zone conodont fauna. However, vertically slabbing this bed disclosed that it comprised three thin layers. Horizontally slicing a slab and individually analyzing each layer revealed that the lower, medium gray micrite layer and the medial, dark gray micrite layer both contained a fauna that we now assign to the early part of the *linguiformis* Zone. The medial layer is scoured and channeled by a chaotically bedded, sandy, finely conglomeratic, grayish orange wackestone upper layer yielding an Early *triangularis* Zone fauna. Detailed sedimentologic analysis of boundary beds elsewhere produces similar results. At Hony, Belgium, unusual pentagonal crinoid columnals not recorded in older beds of this middle-shelf sequence attest to the occurrence of storms that carried these remains shoreward from deeper water (Sandberg et al., 1988). At the Frasnian-Famennian global stratotype section and point (GSSP) at Coumiac, France, a stratigraphic gap was found to encompass the youngest part of the *linguiformis* Zone and oldest part of the Early *triangularis* Zone (Sandberg et al., 1988; Ziegler and Sandberg, 1996). Even in the unbroken boundary sequence of a submarine-ridge setting at Steinbruch Schmidt, the first layer deposited during the earliest part of the Early *triangularis* Zone contains pink stained synsedimentary micrite pebbles probably related to rip-up by tsunami or storm currents. Only at Devils Gate, Nevada (Sandberg et al., 1988), are thick slope sequences deposited during both the late part of the *linguiformis* Zone and the earliest part of the Early *triangularis* Zone fortuitously preserved. From our study of these and many other boundary sequences worldwide, we conclude that the immediate post-extinction world was wracked by storms and/or tsunamis. This would accord with microtektites found at the boundary layer in Belgium (Claeys and Casier, 1994) and the reworking of microtektites in southern China (Wang, 1992) into higher layers.

### *Collapse of carbonate-platform margins (Event 11)*

The last of the seven events associated with the late Frasnian mass extinction was the collapse of carbonate-platform margins (Fig. 5), which occurred as a result of continued regression, accelerated by the lowering of oceans with the onset of Southern Hemisphere glaciation. During this regression, the Late Devonian seaway offlapped the Transcontinental arch and regressed more than 400 km westward in the western United States (Sandberg et al., 1988, Fig. 2). This drastic lowering, probably exceeding 100 m, shallowed or exposed the margins of carbonate platforms, dead Frasnian mudmounds and reefs, and submarine ridges, and caused their collapse. This catastrophic event, which is represented by debris-flow deposits and tsunamites in some regions, is also responsible for the removal by tsunamis of older deposits of the Early *triangularis* Zone in most other regions. Hence, researchers generally record that the Early *triangularis* Zone is highly condensed. This phenomenon is best exemplified by the excellent exposure at Devils Gate, Nevada (Sandberg et al., 1988, 1997). There, a thick breccia deposit, interpreted as a tsunamite, is preserved in a channel. In one measured section at this locality, the channel overlies 4.5 m of Early *triangularis* Zone deposits, but in another, only 200 m along strike, it truncates them. This tsunamite consists mainly of slabs of Early *triangularis* Zone shallow-water deposits removed from the proto-Antler forebulge on the west. Its distal edge is preserved at Coyote Knolls, Utah (Sandberg et al., 1988, 1997). Similar debris-flow breccias have been recorded in Poland (Matyja and Narkiewicz, 1992) and Morocco (Walliser et al., 1989).

### *Middle* **triangularis** *Zone biotic radiation (Event 12)*

Post-extinction adaptive radiation of the surviving biota began during the eustatic rise (start of T-R cycle IIe of Johnson et al., 1985; Fig. 2) that occurred in the middle of the Middle *triangularis* Zone. This eustatic rise has been documented by later researchers in most regions of the world. We interpret that it occurred as the initial pulse of Southern Hemisphere glaciation waned and cold waters from a melting ice cap were gradually released to the oceans. The burgeoning of faunas is best exemplified by conodont and brachiopod populations, but little is known about the effects on other groups such as the surviving corals and stromatoporoids.

### *First interglacial episode (Event 13)*

Early Famennian global warming caused further melting of the Southern Hemisphere ice cap and raised ocean temperatures to such a degree that the first interglacial episode ensued in the middle of the Middle *crepida* Zone (Fig. 1). This produced a major transgressive interruption of the general Famennian regression (Fig. 2) and a great sedimentologic and biotic change. This change, termed the *Cheiloceras* Event (Walliser, 1985) after the ammonoid genus, was first recognized in Germany by the overstepping of black shale over lighter colored carbonate rocks. It flooded shelf areas with deeper water, resulting in deposition of red-stained nodular cephalopod limestone in Belgium and producing similar sedimentologic changes throughout Europe and Morocco (Dreesen, 1989). In basinal sections in Germany and Morocco, especially where the intervening, lowest part of the Famennian is greatly condensed, the *Cheiloceras* black shale is recognized as a third Kellwasser Event or is included in the Kellwasser facies (e.g., Wendt and Belka, 1991). In Nevada, Event 13 resulted in the expansion of the Late Devonian Pilot basin and in the overstepping of shallow-water, carbonate-platform facies of the Guilmette Formation by the moderately deep water, cephalopod-bearing, nodular West Range Limestone.

### *Second interglacial episode (Event 14)*

The second major transgression to interrupt the general Famennian regression resulted from the second interglacial episode in the Early *marginifera* Zone (Fig. 1). This sea-level rise resulted in deposition of the Baelen mudmound, representing the fourth level of Belgian mudmounds and the only well-documented Famennian mudmound anywhere (Dreesen et al., 1985). Unlike the Frasnian stromatoporoid- and coral-rich Belgian mudmounds, the Baelen mudmound was structurally bound by cyanobacteria and algae and overgrown by thickets of crinoids and sponges. However, the few known global occurrences of early Famennian small, deep-water corals may be related to this event. In Nevada, Event 14 resulted in the deepening and further expansion of the Pilot basin. Concurrently, the great Palliser bank and its equivalents, extending from Alberta to Nevada, developed on the outer margin of the carbonate platform (Sandberg et al., 1989).

### *Third interglacial episode (Event 15)*

The third interglacial episode, although not as pronounced as the second, has been recognized in several regions, but it is best represented by the overstepping of black shale over carbonate rocks in Germany. There, it has been termed the *annulata* Event, after the ammonoid *Platyclymenia annulata*. Faunal changes accompanying this event were described by Walliser (1996b), who accepted its conventional dating as Late *trachytera* Zone. Ziegler and Sandberg (2000) tentatively redated the *annulata* Event as the next younger, Early *postera* Zone. In western North America, Event 15 is represented by the major transgression that resulted in deposition of the Trident Member of the Three Forks Formation and its lateral equivalents. The Trident Member and its deep-water equivalents in Nevada and California contain the ammonoid *Platyclymenia americana*, but the Trident has yielded only a nonpalmatolepid conodont fauna previously assigned roughly to the *trachytera* Zone (Sandberg et al., 1989). The age of these rocks, like the *annulata* Event, may need to be reevaluated.

### *Fourth interglacial episode (Event 16)*

The fourth interglacial episode resulted in the final Famennian transgression, initiating T-R cycle IIf of Johnson et al. (1985), beginning in the Early *expansa* Zone. Like the transgression resulting from the second interglacial episode (Event 14), the fourth was a major eustatic event. Because of the accompanying important faunal changes, Events 14 and 16 are both employed for defining the proposed Famennian substages (Fig. 1). Event 16 introduced the shallow-water Etroeungt fauna into the Northern Hemisphere in widely separated areas, such as Utah and Arizona, northern France and southern Belgium, and the southern Urals. The Etroeungt fauna was a Lazarus fauna, characterized by the enigmatic reappearance of large clisiophyllid and caninoid corals, probably descended from supposedly extinct Frasnian rugose corals but for which there is no intervening Famennian record. As a result of extreme global warming and warm ocean currents, these corals must have been introduced from an unknown refuge, possibly in the Southern Hemisphere or in Asia. Stromatoporoids, occurring in large pillow-shaped colonies, also mysteriously reappeared at this time.

In addition to causing a rapid acceleration in conodont evolution, Event 16 also produced major changes in megafaunas, particularly the brachiopods and armored fishes. Among the brachiopods, first the highly diverse Percha fauna, including unusually large species such as *Paurorhyncha endlichi*, evolved. This fauna was followed in the next younger Middle *expansa* Zone by the diverse Louisiana Limestone fauna, which contains many forerunners of Carboniferous genera, such as *Syringothyris*. Among the fish, some of the largest known arthrodires inhabited the warm seas. The unusually large size of both the megafauna and conodonts supports the interpretation that Event 16 was a warm, tropical, interglacial episode in the Northern Hemisphere.

### *Middle* **praesulcata** *Zone eustatic fall (Event 17)*

A major eustatic fall (Ziegler and Sandberg, 1984), probably associated with a resurgence of Southern Hemisphere glaciation (Caputo, 1985), began in the Middle *praesulcata* Zone and continued into the Early Carboniferous. The Middle *praesulcata* Zone eustatic fall (Event 17) and the ensuing mass extinction (Event 18) have been collectively termed the Hangenberg Event and were discussed in detail by Walliser (1996b). The initial pulse of this eustatic fall is evidenced in every studied section globally by a short stratigraphic interval wherein the pelagic siphonodellid conodont biofacies is replaced by a shallow-water protognathodid biofacies. Where initially recognized in a closely sampled, condensed carbonate sequence at the Trolp Quarry, near Graz, Austria, this gap amounts to only 5 cm. The gap is interpreted to indicate that sea level dropped so catastrophically at the start of the eustatic fall that the pelagic species *Siphonodella praesulcata* was forced to retreat from epicontinental seas to the ocean basins, and hence left no trace in a short interval of uppermost Devonian rocks of all continents. In the United States, the eustatic fall is characterized by regressive sandstones that retreated seaward from the Transcontinental arch; the upper part of the Sappington Member of the Three Forks Formation to the west and the Berea Sandstone to the east. Both units contain the diagnostic latest Famennian *Retispora lepidophyta* spore flora. The continuing eustatic fall induced a stepwise mass extinction of pelagic conodont species and the disappearance of the Etroeungt coral fauna, which reappeared again at different times during the Early Carboniferous.

### *Late Famennian mass extinction (Event 18)*

The late Famennian (or D-C), mass extinction (Event 18) occurred during the eustatic sea-level fall that continued across the Devonian-Carboniferous boundary. As suggested by Sandberg et al. (1988), we interpret this mass extinction to be the terminal event of the Devonian Southern Hemisphere glaciation. However, Caplan and Bustin (1999, p. 148) concluded that climatic glacial cooling led to a “D-C mini-glaciation in Gondwana,” thus inferring that Event 18 was an initial, not a terminal, glacial event. They also concluded that the global faunal crisis occurs “at the base of a globally extensive black, organic-rich mudrock.” This statement is contradicted by the study of Ziegler and Sandberg (1984), who evaluated the most continuous D-C boundary sections in North America, Austria, Germany, the southern Urals, and South China, and showed that the black extinction shale is only locally preserved as at some localities in Germany and South China. More commonly the sea-level fall is represented by a hiatus or discontinuity or is masked within shallow-water deposits, as at the selected GSSP in the Montagne Noire, southern France (Ziegler and Sandberg, 1996).

Event 18 was not as intense as the late Frasnian mass extinction and is not included among the five major Phanerozoic mass extinctions. It caused the demise of the dominant pelagic conodont genus *Palmatolepis*; only a single species, *Palmatolepis gracilis*, survived into the Early Carboniferous. However, many shallow-water conodont genera, including *Protognathodus*, which had evolved shortly before the mass extinction, lived well into the Carboniferous. Likewise, shallow-water Carboniferous-type latest Famennian brachiopods, including the widespread *Syringothyris* fauna, were unaffected by the mass extinction and continued to flourish. Thus, it is likely that the late Famennian mass extinction affected mostly pelagic, as well as benthic and nektobenthic organisms, as suggested by Caplan and Bustin (1999). The Etroeungt coral fauna probably disappeared before the final mass extinction. As was the case in the early Famennian, following the late Frasnian mass extinction, only generally small, deep-water corals are known in the earliest Carboniferous.

## CONCLUSIONS

Late Devonian geologic history comprises two very different but related parts. The initial Frasnian Stage was a time of generally rising sea level, accentuated by several catastrophic rises and punctuated by a mass extinction that occurred during a drastic, abrupt sea-level fall. The later Famennian Stage was a time of generally falling sea level, interrupted by several glacio-eustatic rises and terminated by a less severe mass extinction during another abrupt sea-level fall.

The most reasonable explanation for the catastrophic pulses of eustatic sea-level rise during the Frasnian and the ensuing late Frasnian mass extinction is a series of comet showers. This is suggested by a large number of known and possible impacts, such as the Siljan and Flynn Creek impacts. These are radiometrically dated by different methods and so cannot be positively correlated with one another. However, compelling evidence for relating the catastrophic rises to comet showers is provided by the biochronologically dated, well-documented Alamo Impact, which accompanied such a major rise. The off-platform, subcritical Alamo Impact is reinterpreted to have produced a greatly different sedimentary pattern in deep water from that previously recorded on the carbonate platform. The rises associated with the Alamo Impact shower and later comet showers altered or terminated three levels of Belgian mud-mounds, progressively diminished their size, and decimated reef communities. As a result, the global ecosystem was weakened and thus susceptible to the terminal Frasnian sea-level fall, which accompanied the mass extinction.

A logical explanation for the generally falling Famennian sea level is Southern Hemisphere glaciation resulting from global cooling that was induced by comet showers occurring just before, and possibly just after, the late Frasnian mass extinction. These showers are evidenced by microtektites found at and just above the Frasnian-Famennian boundary in widely separated areas. The four major pulses of sea-level rise that interrupted the general fall are attributable to glacio-eustatic rises during warm interglacial episodes. Each rise is associated with increased biotic abundance and diversity, resulting from the many more hospitable niches provided by warmer oceans. The mass extinction just before the end of the Famennian occurred during the sea-level fall produced by the terminal Devonian glacial episode.

## ACKNOWLEDGMENTS

Peter Bender and Jens Ormö assisted our current study of the Amönau Breccia. Alan K. Chamberlain, Hans-Christian Kuehner, and, especially, John E. Warme helped immeasurably with our earlier interpretations of Alamo Breccia sedimentology and the Alamo Impact. Roland Dreesen contributed significantly to our study of Belgian mudmounds and to our understanding of Belgian Devonian event stratigraphy. Raymond C. Gutschick has collaborated with Sandberg since 1962 in studying the uppermost Famennian rocks of the western United States and introduced him to the Upper Devonian of Michigan and Indiana. Forrest G. (Barney) Poole has collaborated with Sandberg since 1968 in regional Devonian studies of the western United States and has contributed his considerable expertise on the geology of Nevada. Eberhard Schindler provided helpful comments on an early version of our manuscript. We thank Hans-Peter Schönlaub and an anonymous reviewer, whose comments helped improve our final manuscript.

Acknowledgment is made to the donors of the Petroleum Research Fund, administered by the American Chemical Society, for support of J.R. Morrow's contribution to this research.

## REFERENCES CITED

Bender, P., Hühner, G., Kupfahl, H.-G., and Voutta, U., 1984, Ein Mitteldevon/Oberdevon-Profil bei Amönau auf Bl. 5018 Wetter (Hessen): Geologisches Jahrbuch Hessen, v. 112, p. 31–65.

Bratton, J.F., Berry, W.B.N., and Morrow, J.R., 1999, Anoxia pre-dates Frasnian-Famennian boundary mass extinction horizon in the Great Basin, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 154, p. 275–292.

Buggisch, W., Rabien, A., and Hühner, G., 1978, Biostratigraphische Parallelisierung und Faziesvergleich von oberdevonischen Becken- und Schwellen-Profilen E Dillenburg: Geologisches Jahrbuch Hessen, v. 106, p. 53–115.

Caplan, M.L., and Bustin, R.M., 1999, Devonian-Carboniferous Hangenberg mass extinction event, widespread organic-rich mudrock and anoxia: Causes and consequences: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 148, p. 187–208.

Caputo, M.V., 1985, Late Devonian glaciation in South America: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 51, p. 291–317.

Casier, J.-G., and Lethiers, F., 1998a, Les ostracodes survivant à l'extinction du Dévonien supérieur dans la coupe du Col de Devils Gate (Nevada, U.S.A.): Geobios, v. 30, no. 6, p. 811–821.

Casier, J.-G., and Lethiers, F., 1998b, The recovery of the ostracod fauna after the Late Devonian mass extinction: The Devils Gate Pass section example (Nevada, USA): Comptes rendus de l'Académie des Sciences, Serie 2, Sciences de la Terre et des Planetes, Earth and Planetary Sciences, v. 327, p. 501–507.

Casier, J.-G., Lethiers, F., and Claeys, P., 1996, Ostracod evidence for an abrupt mass extinction at the Frasnian/Famennian boundary (Devils Gate, Nevada, USA): Comptes rendus de l'Académie des Sciences, Serie 2a, Sciences de la Terre et des Planetes, Earth and Planetary Sciences, p. 415–422.

Claeys, P., and Casier, J.-G., 1994, Microtektite-like glass associated with the Frasnian-Famennian boundary mass extinction: Earth and Planetary Science Letters 122, p. 303–315.

Copper, P., 1986, Frasnian/Famennian mass extinction and cold-water oceans: Geology, v. 14, p. 835–839.

Dreesen, R., 1989, The "*Cheiloceras* Limestone", a Famennian (Upper Devonian) event-stratigraphic marker in Hercynian Europe and northwestern Africa: Bulletin de la Société Belge de Géologie, v. 28, no. 2, p. 127–133.

Dreesen, R., Bless, M.J.M., Conil, R., Flajs, G., and Laschet, C., 1985, Depositional environment, paleoecology and diagenetic history of the "Marbre rouge à crinoïdes de Baelen" (Late Upper Devonian, Verviers syclinorium, eastern Belgium): Annales de la Société Géologique de Belgique, v. 108, p. 311–359.

Geldsetzer, H.J., Goodfellow, W.D., and McLaren, D.J., 1993, The Frasnian-Famennian extinction event in a stable cratonic shelf setting: Trout River, Northwest Territories, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 104, p. 81–95.

Girard, C., and Feist, R., 1997, Eustatic trends in conodont diversity across the Frasnian-Famennian boundary in the stratotype area, Montagne Noire, Southern France: Lethaia, v. 29, p. 329–337.

Goodfellow, W.D., Geldsetzer, H.H.J., McLaren, D.J., Orchard, M.J., and Klapper, G., 1989, The Frasnian-Famennian extinction: The current results and possible causes, *in* McMillan, N.J., Embry, A.F., and Glass, D.J., eds., Devonian of the World: Calgary, Canadian Society of Petroleum Geologists Memoir 14, v. 3, p. 9–21.

Groos-Uffenorde, H., and Wang, S.-Q., 1989, The entomozoacean succession of South China and Germany (Ostracoda, Devonian): Courier Forschungsinstitut Senckenberg, v. 110, p. 61–79.

Groos-Uffenorde, H., and Schindler, E., 1990, The effect of global events on entomozoan Ostracoda, *in* Whathey, R., and Maybury, C., eds., Ostracoda and global events: London, Chapman and Hall, p. 101–112.

Hallam, A., and Wignall, P.B., 1999, Mass extinctions and sea-level changes: Earth Sciences Reviews, v. 48, p. 217–250.

Huckriede, H., 1992, Das Barytlager von Günterrod in der Dillmulde (Rheinisches Schiefergebirge, Deutschland): Eine allochthone Scholle in givetischen Debris-Flow-Sedimenten: Geologisches Jahrbuch Hessen, v. 120, p. 117–144.

Ji, Q., 1989, On the Frasnian-Famennian mass extinction event in South China: Courier Forschungsinstitut Senckenberg, v. 117, p. 275–301.

Joachimski, M.M., and Buggisch, W., 1993, Anoxic events in the late Frasnian—Cause of the Frasnian-Famennian faunal crisis?: Geology, v. 21, p. 675–678.

Joachimski, M.M., and Buggisch, W., 2000, The Late Devonian mass extinction—Impact or earth-bound event? [abs.], *in* Catastrophic events and mass extinctions: Impacts and beyond: Houston, Texas, Lunar and Planetary Institute, LPI Contribution No. 1053, p. 83–84.

Johnson, J.G., 1970, Taghanic onlap and the end of North American Devonian provinciality: Geological Society of America Bulletin, v. 81, p. 2077–2105.

Johnson, J.G., Klapper, G., and Sandberg, C.A., 1985, Devonian eustatic fluctuations in Euramerica: Geological Society of America Bulletin, v. 96, p. 567–587.

Johnson, J.G., and Sandberg, C.A., 1989, Devonian eustatic events in the Western United States and their biostratigraphic responses, *in* McMillan, N.J., Embry, A.F., and Glass, D.J., eds., Devonian of the World: Canadian Society of Petroleum Geologists Memoir 14, v. 3, p. 171–179.

Kauffman, E.G., and Walliser, O.H., eds., 1990, Extinction events in Earth history, *in* Proceedings of the IGCP Project 216 "Global Biological Events in Earth History": Heidelberg, Germany, Springer-Verlag, Lecture Notes in Earth Sciences, v. 30, 432 p.

Klapper, G., and Johnson, J.G., 1980, Endemism and dispersal of Devonian conodonts: Journal of Paleontology, v. 54, p. 400–455.

Lazreq, N., 1992, The upper Devonian of M'rirt (Morocco): Courier Forschungsinstitut Senckenberg, v. 154, p. 107–123.

Lazreq, N., 1999, Biostratigraphie des conodontes du Givétien au Famennien du Maroc central: Biofaciès et événement Kellwasser: Courier Forschungsinstitut Senckenberg, v. 214, 111 p.

Leroux, H., Warme, J.E., and Doukhan, J.-C., 1995, Shocked quartz in the Alamo Breccia, southern Nevada: Evidence for a Devonian impact: Geology, v. 23, p. 1003–1006.

Lethiers, F., and Casier, J.-G., 1999, Autopsie d'une extinction biologique: Un exemple: La crise de la limite Frasnien-Famennien (364 Ma): Comptes rendus de l'Académie des Sciences, Serie 2, Sciences de la Terre et des Planetes, Earth and Planetary Sciences, no. 329, p. 303–315.

Matya, H., 1993, Upper Devonian of Western Pomerania: Acta Geologica Polonica, v. 43, no. 1–2, 94 p.

Matyja, H., and Narkiewicz, M., 1992, Conodont biofacies succession near the Frasnian/Famennian boundary: Some Polish examples: Courier Forschungsinstitut Senckenberg, v. 154, p. 124–147.

McGhee, G.R., Jr., 1981, The Frasnian-Famennian extinctions: A search for extraterrestrial causes: Field Museum of Natural History Bulletin, v. 52, no. 7, p. 3–5.

McGhee, G.R., Jr., 1988, The Late Devonian extinction event: Evidence for abrupt ecosystem collapse: Paleobiology, v. 14, no. 3, p. 250–257.

McGhee, G.R., Jr., 1996, The Late Devonian mass extinction: The Frasnian/Famennian crisis: New York, Columbia University Press, 303 p.

McGhee, G.R., Jr., Orth, C.J., Quintana, L.R., Gilmore, J.S., and Olsen, E.J., 1986, Late Devonian "Kellwasser Event" mass-extinction horizon in Germany: No chemical evidence for a large-body impact: Geology, v. 14, p. 776–779.

McLaren, D.J., 1970, Presidential address: Time, life, and boundaries: Journal of Paleontology, v. 44, p. 801–815.

McLaren, D.J., 1982, Frasnian-Famennian extinctions: Geological Society of America Special Paper 190, p. 477–484.

Morrow, J.R., and Sandberg, C.A., 1997, Sequence stratigraphy across the F-F (mid-Late Devonian) boundary, central Great Basin; a conodont-based "reality check": Geological Society of America Abstracts with Programs, v. 29, no. 2, p. 41.

Morrow, J.R., Sandberg, C.A., Warme, J.E., and Kuehner, H.-C., 1998, Regional and possible global effects of sub-critical Late Devonian Alamo Impact Event, southern Nevada, USA: Journal of The British Interplanetary Society, v. 51, p. 451–460.

Morrow, J.R., Sandberg, C.A., and Ziegler, W., 1999, Recognition of mid-Frasnian (early Late Devonian) oceanic impacts: Alamo, Nevada, USA, and Amönau, Hessen, Germany [abs.]: European Science Foundation—Alfred Wegener Institute IMPACT Workshop, Oceanic Impacts: Mechanisms and Environmental Perturbations, Bremerhaven, Germany, Berichte zur Polarforschung 343, p. 66–69.

Muchez, P., Boulvain, F., Dreesen, R., and Hou, H.F., 1996, Sequence stratigraphy of the Frasnian-Famennian transitional strata: A comparison between South China and southern Belgium: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 123, p. 289–296.

Ormö, J., and Lindström, M., 2000, When a cosmic impact strikes the sea bed: Geological Magazine, v. 137, no. 1, p. 67–80.

Over, D.J., Conaway, C.A., Katz, D.J., Goodfellow, W.D., and Gregoire, D.C., 1997, Platinum group element enrichments and possible chondritic Ru:Ir across the Frasnian-Famennian boundary, western New York State: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 132, p. 399–410.

Racka, M., and Racki, G., 2000, Geochemical aspects of the Frasnian-Famennian mass extinction: The Polish example [abs.], *in* Catastrophic events and mass extinctions: Impacts and beyond: Houston, Texas, Lunar and Planetary Institute, LPI Contribution No. 1053, p. 174.

Racki, G., 1998a, The Frasnian-Famennian brachiopod extinction events: A preliminary review: Acta Palaeontologica Polonica, v. 43, no. 2, p. 395–411.

Racki, G., 1998b, Frasnian-Famennian biotic crisis: Undervalued tectonic control?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 141, p. 177–198.

Racki, G., 1999, The Frasnian-Famennian biotic crisis: How many (if any) bolide impacts?: Geologisches Rundschau, v. 87, p. 617–632.

Sandberg, C.A., 1998, Tiny teeth shed light on ancient comets: U.S. Geological Survey News Release, March 20, 1998, 2 p.

Sandberg, C.A., and Dreesen, R., 1984, Late Devonian icriodontid biofacies models and alternate shallow-water conodont zonation, *in* Clark, D.L., ed., Conodont biofacies and provincialism: Geological Society of America Special Paper 196, p. 143–178.

Sandberg, C.A., Gutschick, R.C., Johnson, J.G., Poole, F.G., and Sando, W.J., 1983, Middle Devonian to Late Mississippian geologic history of the Overthrust Belt region, western United States: Denver, Colorado, Rocky Mountain Association of Geologists, Geologic Studies of the Cordilleran Thrust Belt, v. 2, p. 691–719.

Sandberg, C.A., Gutschick, R.C., Johnson, J.G., Poole, F.G., and Sando, W.J., 1986, Middle Devonian to Late Mississippian event stratigraphy of Overthrust belt region, western United States, *in* Bless, M.J.M., and Streel, M., eds., Late Devonian events around the Old Red continent: Société Géologique de Belgique Annales, v. 109, pt. 1, Special volume "Aachen 1986", p. 205–207.

Sandberg, C.A., and Morrow, J.R., 1998, Role of conodonts in deciphering and dating Late Devonian Alamo Impact Megabreccia, southeastern Nevada, USA [abs.], *in* Bagnoli, G., ed., Seventh International Conodont Symposium (ECOS 7): Bologna-Modena, Italy, Abstracts volume, p. 93–94.

Sandberg, C.A., Morrow, J.R., and Warme, J.E., 1997, Late Devonian Alamo Impact Event, global Kellwasser Events, and major eustatic events, eastern Great Basin, Nevada and Utah: Brigham Young University Geology Studies, v. 42, pt. 1, p. 129–160.

Sandberg, C.A., Morrow, J.R., and Ziegler, W., 2000, Possible impact origin of the enigmatic early Late Devonian Amönau Breccia, Rheinisches Schiefergebirge, Germany [abs.], *in* Catastrophic events and mass extinctions: Impacts and beyond: Houston, Texas, Lunar and Planetary Institute, LPI Contribution No. 1053, p. 187.

Sandberg, C.A., Poole, F.G., and Johnson, J.G., 1989, Upper Devonian of Western United States, *in* McMillan, N.J., Embry, A.F., and Glass, D.J., eds., Devonian of the World: Canadian Society of Petroleum Geologists Memoir 14, v. 1, p. 183–220.

Sandberg, C.A., and Warme, J.E., 1993, Conodont dating, biofacies, and catastrophic origin of Late Devonian (early Frasnian) Alamo Breccia, southern Nevada: Geological Society of America Abstracts with Programs, v. 25, no. 3, p. 77.

Sandberg, C.A., and Ziegler, W., 1991, Extreme falls of sea level accompanied late Frasnian (F/F) and late Famennian (D/C) mass extinctions in the Late Devonian [abs.]: Calgary, International Union of Geological Sciences, Joint Meeting of IGCP Projects 216, 293, and 303, Event Markers in Earth History, Programs and Abstracts, p. 63.

Sandberg, C.A., and Ziegler, W., 1992, Late Devonian conodont evolution and post-crisis recoveries [abs.]: Göttingen, Germany, International Union of Geological Sciences, IGCP Project 216, Fifth International Conference on Global Bioevents, Phanerozoic Global Bio-Events and Event-Stratigraphy, Abstracts volume, p. 92.

Sandberg, C.A., and Ziegler, W., 1996, Devonian conodont biochronology in geologic time calibration: Senckenbergiana Lethaea, v. 76, p. 259–265.

Sandberg, C.A., and Ziegler, W., 1998, Comments on proposed Frasnian and Famennian Subdivisions (Document submitted to IUGS Subcommission on Devonian Stratigraphy Meeting in Bologna, Italy): Subcommission on Devonian Stratigraphy Newsletter No. 15, p. 43–46.

Sandberg, C.A., Ziegler, W., Dreesen, R., and Butler, J.L., 1988, Late Frasnian mass extinction: Conodont event stratigraphy, global changes, and possible causes, *in* Ziegler, W., ed., 1st International Senckenberg Conference and 5th European Conodont Symposium (ECOS V), Contribution 1: Courier Forschungsinstitut Senckenberg, v. 102, p. 263–307.

Sandberg, C.A., Ziegler, W., Dreesen, R., and Butler, J.L., 1992, Conodont biochronology, biofacies, taxonomy, and event stratigraphy around middle Frasnian Lion Mudmound (F2h), Frasnes, Belgium: Courier Forschungsinstitut Senckenberg, v. 150, 87 p.

Schindler, E., 1990a, The late Frasnian (Upper Devonian) Kellwasser Crisis: Lecture Notes in Earth Sciences, v. 30, p. 151–159.

Schindler, E., 1990b, Die Kellwasser-Krise (hohe Frasne-Stufe, Ober-Devon): Göttinger Arbeiten Geologie und Paläontologie, Göttingen, no. 46, 115 p.

Schindler, E., Schülke, I., and Ziegler, W., 1998, The Frasnian/Famennian boundary at the Sessacker Trench section near Oberscheld (Dill Syncline), Rheinisches Schiefergebirge, Germany: Senckenbergiana Lethaea, v. 77, no. 1–2, p. 243–261.

Walliser, O.H., 1985, Natural boundaries and Commission boundaries in the Devonian: Courier Forschungsinstitut Senckenberg, v. 75, p. 401–408.

Walliser, O.H., ed., 1986, Global bio-events, *in* Proceedings of the First International Meeting of the IGCP Project 216 "Global Biological Events in Earth History": Lecture Notes in Earth Sciences, v. 8, Heidelberg, Germany, Springer-Verlag, 442 p.

Walliser, O.H., ed., 1996a, Global events and event stratigraphy in the Phanerozoic: Results of international interdisciplinary cooperation in the IGCP Project 216 "Global Biological Events in Earth History": Heidelberg, Germany, Springer-Verlag, 333 p.

Walliser, O.H., 1996b, Global events in the Devonian and Carboniferous, *in* Walliser, O.H., ed., Global events and event stratigraphy in the Phanerozoic: p. 225–250.

Walliser, O.H., Groos-Uffenorde, H., and Schindler, E., 1989, On the Upper Kellwasser Horizon (boundary Frasnian/Famennian): Courier Forschungsinstitut Senckenberg, v. 110, p. 247–255.

Wang, K., 1992, Glassy microspherules (microtektites) from an Upper Devonian limestone: Science, v. 256, p. 1546–1549.

Wang, K., Orth, C.J., Attrep, M., Jr., Chatterton, B.D.E., Hou, H., and Geldsetzer, H.H.J., 1991, Geochemical evidence for a catastrophic biotic event at the Frasnian/Famennian boundary in South China: Geology, v. 19, p. 776–779.

Warme, J.E., and Chamberlain, A.K., 2000, Primary ejecta, tsunami reworking, tectonic dismemberment: Reconstructing the Late Devonian Alamo Breccia and crater, Nevada [abs.], *in* Catastrophic events and mass extinctions: Impacts and beyond: Houston, Texas, Lunar and Planetary Institute, LPI Contribution No. 1053, p. 238.

Warme, J.E., and Kuehner, H.-C., 1998, Anatomy of an anomaly: The Devonian catastrophic Alamo impact breccia of southern Nevada: International Geology Review, v. 40, p. 189–216.

Warme, J.E., and Sandberg, C.A., 1995, The catastrophic Alamo breccia of southern Nevada: Record of a Late Devonian extraterrestrial impact: Courier Forschungsinstitut Senckenberg, v. 188, p. 31–57.

Wendt, J., and Belka, Z., 1991, Age and depositional environment of Upper Devonian (early Frasnian to early Famennian) black shales and limestones (Kellwasser facies) in the eastern Anti-Atlas, Morocco: Facies, v. 25, p. 51–90.

You, X.L., 2000, Famennian tentaculitids of China: Journal of Paleontology, v. 74, no. 5, p. 969–975.

Ziegler, W., and Lane, H.R., 1987, Cycles in conodont evolution from Devonian to mid-Carboniferous, *in* Aldridge, R.J., ed., Palaeobiology of conodonts: British Micropalaeontological Society, p. 147–163.

Ziegler, W., and Sandberg, C.A., 1984, Important candidate sections for stratotype of conodont based Devonian-Carboniferous boundary, *in* Paproth, E., and Streel, M., eds., The Devonian-Carboniferous boundary: Courier Forschungsinstitut Senckenberg, v. 67, p. 231–239.

Ziegler, W., and Sandberg, C.A., 1990, The Late Devonian standard conodont zonation: Courier Forschungsinstitut Senckenberg, v. 121, 115 p.

Ziegler, W., and Sandberg, C.A., 1996, Reflexions on Frasnian and Famennian Stage boundary decisions as a guide to future deliberations: Newsletters on Stratigraphy, v. 33, p. 157–180.

Ziegler, W., and Sandberg, C.A., 2000, Utility of palmatolepids and icriodontids in recognizing Upper Devonian Series, Stage, and possible Substage boundaries, *in* Bultynck, P., ed., Subcommission on Devonian Stratigraphy: Recognition of Devonian series and stage boundaries in geological areas: Courier Forschungsinstitut Senckenberg, v. 225, p. 335–348.

MANUSCRIPT ACCEPTED BY THE SOCIETY MARCH 22, 2001

Printed in the U.S.A.