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Strength, timing, setting and cause of mid-Palaeozoic extinctions

Michael R. House *

School of Ocean and Earth Science, Southampton Oceanography Centre, Southampton SO14 3ZH, UK

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Abstract

Much has been written over the last 20 yr on the Upper Kellwasser Event (Frasnian/Famennian or F/F boundary) as the major extinction event of the Middle Palaeozoic (Devonian) and as the fifth largest extinction event in the Phanerozoic; this opinion was based on analysis of family range data. These views are misleading. A current analysis of family extinction data, largely based on *The Fossil Record 2*, but updated in some respects, supersedes the data base of Raup and Sepkoski (1982) and shows that the Famennian has the highest total family extinction of marine taxa, with the Givetian in second and Frasnian in third place. If these new data are related to current (unreliable) estimated length of stages, then the severest extinction rates are: first, the Givetian at 14.2 family extinctions per Ma, secondly the Frasnian at 11.2 and thirdly the Eifelian at 6.8. Many short-term 'events' have been named for the Devonian based on short-term distinctive sedimentary and/or faunal perturbations. A review of these shows how they are often transgression/regression couplets, many with an association of anoxia and poor in benthos, or spreads of pelagic faunas, and some are phased and complex. Evidence is presented to suggest that the transgressive pulses correspond to warm temperatures which are terminated by cooling. Possible links with orbitally forced patterns are considered. A common explanation seems required, not just for the Kellwasser Event, but for all these events. The relation of the family stage extinctions, especially the Kačák, Taghanic, Kellwasser and Hangenberg Events, which are of much more limited duration, is discussed particularly in relation to new and more precise data of the extinction events known within these stages. In the absence of detailed studies for many groups, those that have been well documented may serve as a temporary proxy for others.

Keywords: extinction; Devonian; mid-Palaeozoic; Kellwasser; Frasnian/Famennian; Hangenberg; Taghanic

1. Introduction

In the last two decades it has been the Frasnian/Famennian boundary (F/F) extinctions which have been emphasised as a major mass extinction event of family taxa, and the fifth in importance of the Phanerozoic. The purpose of this paper is to look again at the extinction events in the Middle Palaeozoic (Devonian) and assess present knowledge on: their strength, that is the numbers of family taxa thought to be involved; their timing, in relation to detailed analysis of extinctions known within stages; to review and comment on their palaeogeographic setting; and to comment on the environmental and palaeoecological causes of the extinctions.

* Fax: +44-1703-596095.
E-mail address: mrhhouse@msn.com (M.R. House).

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That the F/F boundary level represents a faunal break has been long understood in general terms. It gave rise to the Frasnian and Famennian stage boundary division in the first place when those terms from the Ardennes were based on changes in neritic faunas. The corresponding break in pelagic facies, mainly using ammonoids and trilobites, was represented, especially in Germany, by the approximately similar Adorfian/Nehdenian and *Manticoceras*/*Cheiloceras* Stufen boundaries. All these terms were recognised in essence in the late 19th century although the formalising of the last was by Wedekind (1917). Particular current emphasis commenced with the assertion by McLaren (1970, 1982, 1983) that the F/F faunal break was a sudden mass extinction caused by bolide impact (although at that time the boundary was usually taken much higher, around the *crepida* Zone). The analyses of Phanerozoic family extinctions by Raup and Sepkoski (1982, and later publications by Sepkoski) gave the F/F boundary faunal break high Phanerozoic significance. There have been several subsequent reviews (McGhee, 1989, 1996; Schindler, 1990, 1993; Buggisch, 1991; Becker and House, 1994b; Walliser, 1986, 1996; Hallam and Wignall, 1997).

As a result of the need for precision in chronostratigraphic terminology, the International Commission on Stratigraphy, and its predecessor from 1960, has sought to define each stage by a Global Stratigraphic Section and Point (GSSP) by defining the base. These boundaries have to be formally ratified by the International Union of Geological Sciences (IUGS). All mid-Palaeozoic stage boundaries have now been defined and ratified by the IUGS and reviews have been published (Bultynck, 2000a,b). Most of these definitions have led to a need for the ranges of taxa to be reviewed partly because of the redefinitions of boundaries and partly through increased knowledge. This compilation uses *The Fossil Record 2* (Benton, 1993) organised by the Palaeontological Association which, by the time it was published, postdated most of the decisions. However, this paper stresses that there are many extinction events in the Devonian, and even within the Frasnian, so that the matter of which is the greatest extinction is not simple. Nor, in the matter of interpretation, is it likely that only one of these events will give all the answers.

2. History of analysis of extinction events

Quantitative analysis of palaeobiological events is fraught with problems. So far analyses have been primarily based on numerical studies of taxa and their ranges in time. It is sometimes argued that this does not take into account complex palaeoecological changes and breakdown in communities, but such do, of course, have a taxonomic element; but no satisfactory alternative means of analysis has been proposed. Studies using numerical taxonomic criteria commenced when John Phillips (1841) used taxon and range analysis to recognise, for the first time, the taxonomic attributes of the Palaeozoic (named by Adam Sedgwick), Mesozoic and Cainozoic eons (the last two named by Phillips, 1841, p. 160). Later Phillips (1860, p. 66) gave a diagramatic analysis of invertebrate taxa through time for the whole Phanerozoic.

Although diagrams illustrating relative morphological diversity later appeared, the modern studies date from the stimulation of the work of Newell (1952, 1982). Later, the writer published a chart of invertebrate generic diversity through the Phanerozoic, for major groups, based on the Treatise, Osnovy and Traité (House, 1963). The stratigraphic and taxonomic data base was thought so inadequate that he recommended to the Council of the Geological Society of London that an attempt be made to make a comprehensive review. This resulted in *The Fossil Record* (Harland et al., 1967). Notwithstanding the systematic statistical analyses given in this work by Cutbill and Funell (1967), this landmark contribution is rarely acknowledged. It formed the data base for an improved compendium of family ranges by Sepkoski (1982a, revised 1992) from which stemmed many important contributions (Sepkoski, 1982b, 1986, 1996, for example). The great range of contributions on evolutionary theory by Sepkoski and others using their data bases (see listing of Raup, 1999) cannot, however, be overemphasised and it has led to a flood of interesting and important contributions over the last two decades.

The data base has been overtaken by a revision, by 89 group specialists, in *The Fossil Record 2* (Benton, 1993) which, with the addition of more recent data, is the compilation used here. Families refer to organic groups, or clades, which define units of closely defined morphology usually associated with discrete ecological preferences. They therefore contribute a double approach to evolutionary studies and reflect biotic diversification in both form and function. Attempts at similar generic compendia are probably beyond even the team assembled for *The Fossil Record 2*, but an attempt has been made by Sepkoski (1996). Many of the problems of generic analyses were discussed by Boucot (1990). Even precision in stratigraphical range is problematic for many families, and to achieve an acceptable quality data base for analysis of generic diversity at the level of conodont or ammonoid zones is unlikely and, unless linked to a reliable radiometric scale too unreliable to be useful. Sepkoski (1996) gave a generic analysis for the Frasnian using three divisions, but since formal substages are not yet defined for the Frasnian consistency is unlikely. However, the emphasis here on family data is only used to question the claims which have been made for it in relation to the Phanerozoic importance of the F/F boundary extinctions.

3. Terminology of mid-Palaeozoic extinction events

Many sedimentary perturbations associated with biotic change in the Devonian have been recognised and named specifically in the last 15 or so years. O.H. Walliser was responsible for much initial work. An attempt at an international comparison of Devonian sea-level changes, with anoxic tongues marked, was published by House in 1983. Later Walliser (1984a,b, 1985) used the term ‘event’ for these and others in the way which was then common among Cretaceous stratigraphers and he linked these to characteristic biota. In the current sense an ‘event’ is any horizon or unit characterised by a time-specific lithofacies and/or biofacies. Many are now known to be extremely widely distributed.

The main Devonian events now recognised are illustrated in Fig. 1. The use of a stratigraphical appelation (Upper Kellwasser Event, Choteč Event etc.), proposed by House (1985), using old names, serves to emphasise that most of the sedimentary perturbations had been recognised many years ago at levels which would now be given bed, unit or member status; the writer also was of the opinion that it was necessary to draw attention to the combination of distinct lithofacies with distinct faunal events. Palaeontological appelations suffer from the usual problem of changing fossil names, but, in particular, some of those applied referred to fossils appearing after, not in distinct lithofacies events (*Pinacites* appears within but is commonest after the Choteč Event), or before an event (*Cabrieroceras* or *C. rouvillei* appears before the Kačák Event), and some are inappropriate (*Manticoceras* appears long after the event after which it was named). However, the fundamental object was to draw attention to the association of all events with sediments interpreted as dysoxic or anoxic. This raises the problem of the necessity of seeking a common explanation of such similar events.

Some of the named events refer to unexplained widespread occurrences of a particular form (as platyclymenids with the Annulata Event). Others are associated with extinction, some of small scale, some of very large scale. Even single events are complex. In the Upper Kellwasser Event, some groups become extinct apparently with the onset of dysoxia, whilst others flourish in the dysoxic phase to become extinct at its close. The precise term F/F boundary extinction refers, in this case, only to the last. Thus House (1985) suggested most events could be divided into phases. This has been most clearly demonstrated in the detailed work of Schindler (1990) and Becker and House (1994b) on the Upper Kellwasser Event. It has been suggested by some that ‘event’ should therefore be given in plural form. But, by analogy, for example, with the First World War, the singular is correct since that war consisted of many skirmishes and battles, and some of these were before, others after the war itself.

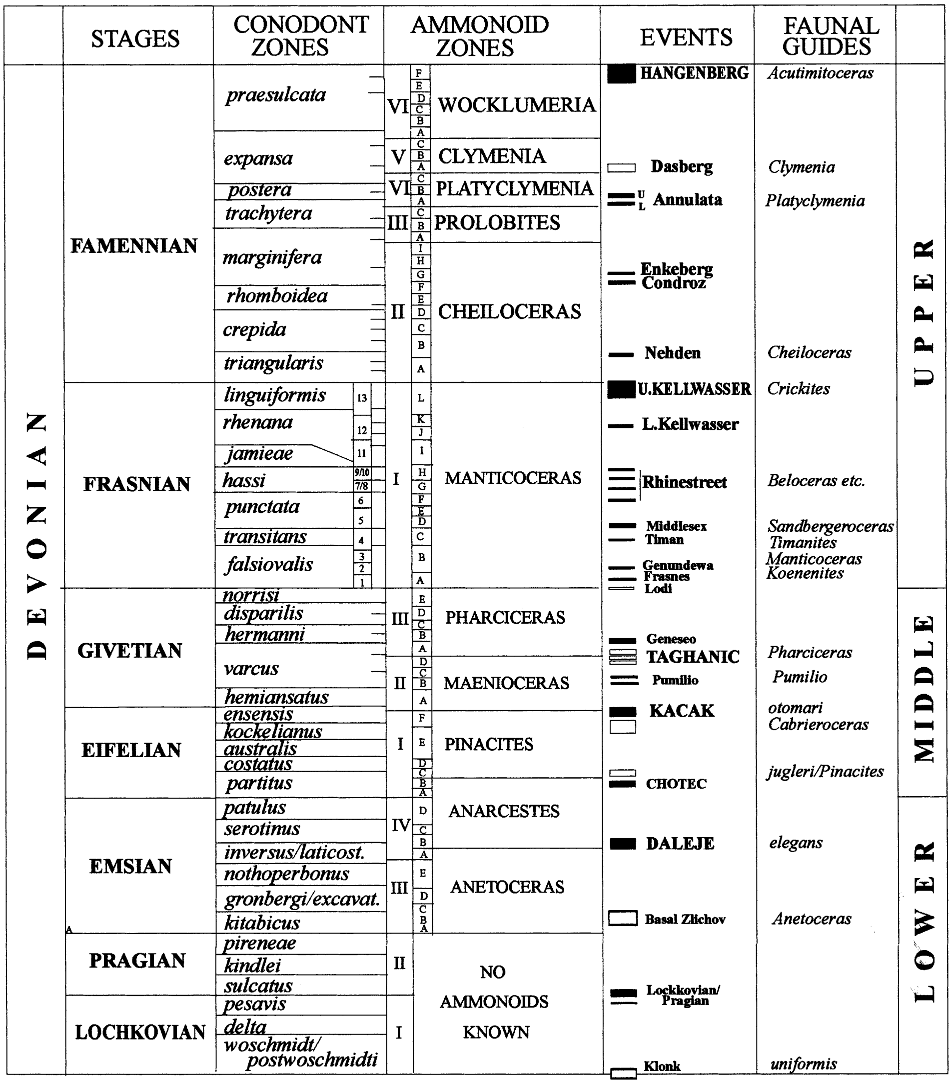


Fig. 1. Diagram showing the correspondence of the main 'events' recognised in the Devonian with the chronostratigraphic stages and with conodont and ammonoid zonations. Events characterised by short-term dysoxic or anoxic facies in their name areas are shown as black rectangles. Frasnian conodont zone correlation based on Klapper and Becker (1999).

Then there is the question of scale. It seems clear that some events, notably the Choteč, Kačák, Taghanic, Kellwasser Events, were associated with many extinctions. Much of this has still to be documented in detail, as the discussion below will show. But a gradation of scale is already apparent. Also the terms 'mass extinction' and 'crisis' have been introduced. For the first, some consensus will emerge on the order of taxonomic loss appropriate for the term 'mass extinction' to give it value, perhaps 10% extinction for families, perhaps 30% for genera might be appropriate. Perhaps that is the current situation for the end Ordovician, end Permian and end Cretaceous extinctions. Relevant here is the discussion and analysis of generic extinction data by MacLeod (2001, Fig. 2), but note that his raw data on extinctions do not appear to have been subjected to the necessary correction for rate, and that the available scales are probably too vague (in the

TAXON	SIL.	DEVONIAN							VIS.
	PRD	LOK	PRA	EMS	EIF	GIV	FRA	FAM	TOU
PROTOZOA	2	0	0	0	0	0	2	2	
PORIFERA	0	0	1	0	1	0	3	1	
STROMATOPOROIDS	1	1	0	0	0	0	6	6	
TABULATA etc	3	2	1	2	7	2	3	0	
RUGOSA etc.	0	4	1	3	6	18	3	5	
GASTROPODA etc	0	0	1	3	1	6	1	1	
NAUTILOIDEA	5	4	0	1	5	5	2	12	
AMMONOIDEA	0	0	0	4	0	6	9	24	
COLEOIDEA	0	0	0	3	0	0	0	0	
BIVALVIA	1	0	0	2	2	3	1	0	
TENTACULITIDA etc	0	3	0	0	1	1	4	3	
ANNELIDA	2	0	0	0	0	0	3	0	
TRILOBITES, EURYPTS etc	5	1	5	5	2	5	8	3	
CRUSTACEA pars	1	0	0	0	1	0	0	3	
OSTRACODA	1	1	0	0	2	0	2	4	
BRACHIOPODA	6	6	6	7	12	14	15	2	
BRYOZOA	1	0	0	1	0	4	1	2	
ECHINODERMATA	0	3	2	7	3	5	4	2	
GRAPTOLITHINA	1	1	0	1	0	0	0	0	
MISCELLANEA	0	0	0	0	1	1	0	0	
CONODONTA	1	1	1	0	0	1	0	3	
EXTINCT IN STAGE	30	27	18	39	44	71	67	73	
TOTAL FAMILIES IN STAGE	466	468	479	504	498	493	449	449	444
EXTINCT/TOTAL X 100	6.4	5.8	3.8	7.7	8.8	14.4	14.9	16.3	

Fig. 2. Table showing extinctions of invertebrate marine families for each stage of the Devonian. Data essentially taken from Benton (1993) with some corrections.

Palaeozoic) to enable this to be done. Then there is the term 'crisis', or as some may prefer 'crises', which introduces a subjective and sensational element into the terminology. And what is the distinction between a crisis and a catastrophe? In English, these emotive terms seem best relegated to popular science writing and journalism.

It has been suggested (Walliser, 1996) that the events (as for example on Fig. 1) are 'global'. It is true that the environmental and sedimentological effects of some events are known over wide areas of the globe, but none is global in the sense that they have been demonstrated in many areas on all continents. Since half the Devonian globe was probably ocean, global distribution will never be proven. It is only the extinctions associated with events that can be said to be global, and these only if the evidence has been tested over very wide areas. If, however, climatic change comes to be shown to be a major factor causing events, especially if driven by orbital forcing or time-constrained tectonic or volcanic events, then global effects would be expected.

4. Strength of mid-Palaeozoic extinction events

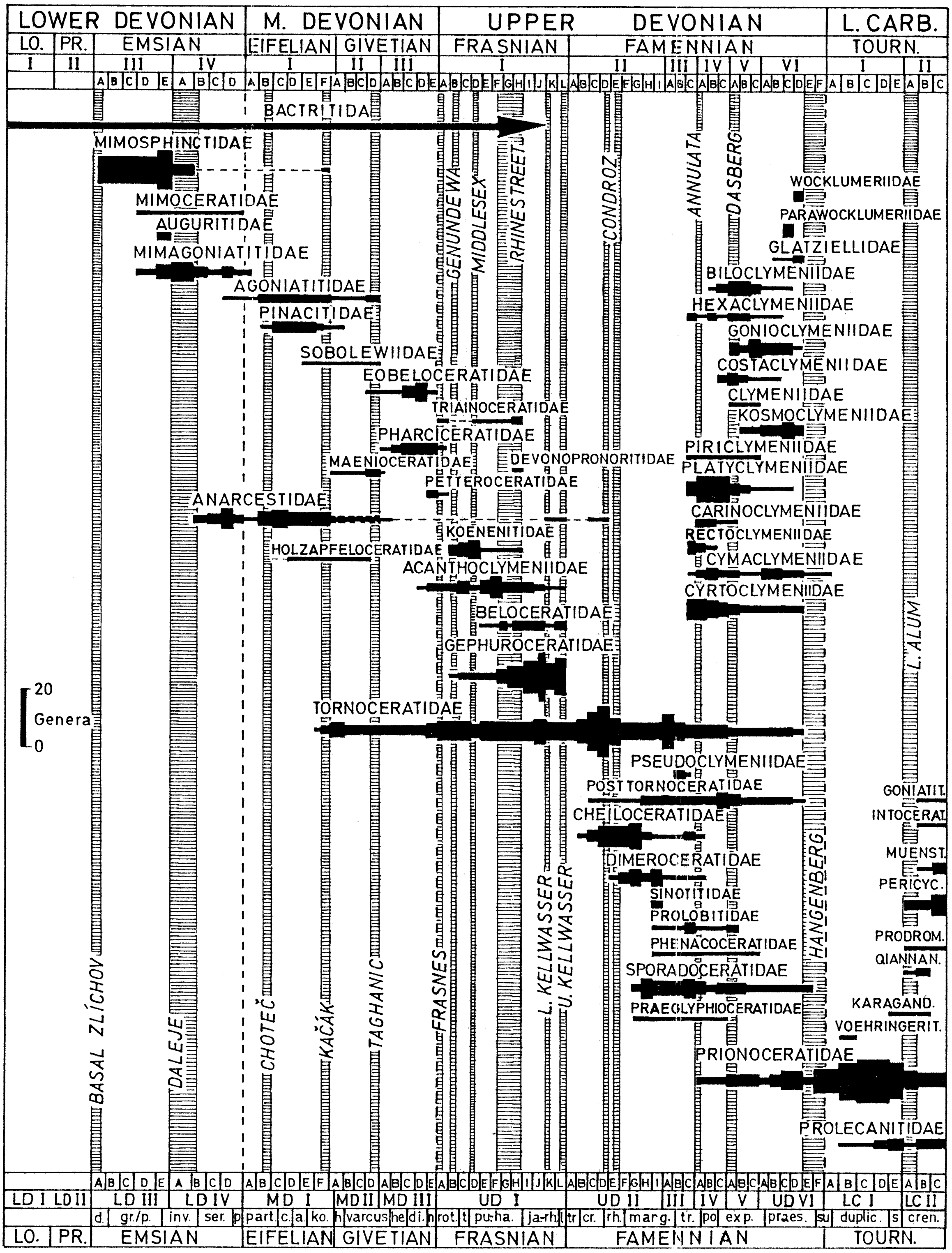
By 1860 Phillips had recognised, using taxon analysis, the importance of the end Permian and end Cretaceous extinctions. A century later the analysis of Cutbill and Funell (1967, fig. 18) suggested that the greatest family level taxon losses were, approximately and in decreasing order of importance, near the Cretaceous/Tertiary boundary, near the Permian/Triassic boundary, near the Devonian/Carboniferous (D/C) boundary, and near the Late Ordovician boundary. An analysis of Sepkoski (1982b) using the percentage of marine families eliminated gives, in decreasing order, so-called mass extinction periods in the Late Permian (50% loss), Late Ordovician (22% loss) Late Devonian (21% loss), Late Triassic (20% loss) and late Cretaceous (15% loss). Two problems made interpretation difficult. Extinctions cannot be regarded alone, but need to be analysed in relation to originations (as Cutbill and Funnell recognised in 1967) since many taxa arise by evolution from earlier taxa without a meaningful extinction intervening. Secondly any diversity changes need to be related to the time over which they happened. Raup and Sepkoski (1982) recognised that a time element was needed to make a correction for different time periods of stratigraphic units and they therefore divided the supposed extinction totals by the supposed time interval. For the present purpose, new estimates of marine invertebrate family extinction in Devonian stages, based largely on data from Benton (1993), stage by stage, are as follows: Pridolian, 30; Lochkovian, 27; Pragian, 18; Emsian, 39; Eifelian, 44; Givetian, 71; Frasnian, 67; Famennian, 73. On Fig. 2 these data are also given as a percentage of the total known families during the stage. R.T. Becker informs the writer that the three Emsian coleoid families are not now accepted in which case the Emsian total is reduced to 36; this is corrected for in the rate given below.

To assess average extinction rates, Raup and Sepkoski (1982) used radiometric periods then available for the Devonian stages and total family extinction data. But that was before revision of chronostratigraphic boundaries for many Devonian stages which changed the length of some stages, so recent dates will be stratigraphically better defined. There have also been revisions of the radiometric scales (Tucker et al., 1998; Williams et al., 2000). Several authors have commented on stratigraphic ranges of error in recent scales. At present, setting that problem aside, one set of the published data (Compston, 2000; fig. 16b) gives the following times for stage length in million years: Lochkovian, 4.5; Pragian, 4; Emsian 15.5; Eifelian, 6.5; Givetian, 5; Frasnian, 6; Famennian, 14.5. Another scale given by Compston (2000, p. 1144) may perhaps indicate the lack of reliability in Devonian scales at present.

If one accepts these dates, and accepts the family extinctions as meaningful and accurate (and the writer has doubts on these), the effect of these is to make the dominant extinction in Devonian stages to fall in the Givetian, not the Frasnian. The actual figures, for family extinctions per million years, are: Lochkovian, 6; Pragian, 4.5; Emsian, 2.3; Eifelian, 6.8; Givetian, 14.2; Frasnian, 11.2; Famennian, 5.0.

Some current literature frequently infers that extinctions took place at the corresponding 'events' (basal Lochkovian, basal Pragian,

Fig. 3. Diagram plotting generic diversity of Devonian ammonoid families through time against the ammonoid and conodont zonal scales and indicating the main events discussed in the text (after Becker and House, 2000).


LOWER DEVONIAN
M. DEVONIAN
UPPER DEVONIAN
L. CARB.
LO.
PR.
EMSIAN
EIFELIAN
GIVETIAN
FRASNIAN
FAMENNIAN
TOURN.
BACTRITIDA
MIMOSPHINCTIDAE
MIMOCERATIDAE
AUGURITIDAE
MIMAGONIATITIDAE
AGONIATITIDAE
PINACITIDAE
SOBOLEWIIDAE
EOBELOCERATIDAE
TRIAINOCERATIDAE
PHARCICERATIDAE
MAENIOCERATIDAE
DEVONOPRONORITIDAE
PETTEROCERATIDAE
ANARCESTIDAE
KOENENITIDAE
HOLZAPFELOCERATIDAE
ACANTHOCLYMENIIDAE
BELOCERATIDAE
GEPHUROCERATIDAE
TORNOCERATIDAE
PSEUDOCLYMENIIDAE
POSTTORNOCERATIDAE
CHEILOCERATIDAE
DIMEROCERATIDAE
SINOTITIDAE
PROLOBITIDAE
PHENACOCERATIDAE
SPORADOCERATIDAE
PRAEGLYPHIOCERATIDAE
PRIONOCERATIDAE
PROLECANITIDAE
WOCKLUMERIIDAE
PARAWOCKLUMERIIDAE
GLATZIELLIDAE
BILOCLYMENIIDAE
HEXACLYMENIIDAE
GONIOCLYMENIIDAE
COSTACLYMENIIDAE
CLYMENIIDAE
KOSMOCLYMENIIDAE
PIRICLYMENIIDAE
PLATYCLYMENIIDAE
CARINOCLYMENIIDAE
RECTOCLYMENIIDAE
CYMACLYMENIIDAE
CYRTOCLYMENIIDAE
GONIATIT.
INTOCERAT.
MUENST.
PERICYC.
PRODROM.
QIANNAN.
KARAGAND.
VOEHRINGERIT.
20
Genera
0
BASAL ZLÍCHOV
DALEJE
CHOTEČ
KAČÁK
TAGHANIC
FRASNES
GENUNDEWA
MIDDLESEX
RHINESTREET
L. KELLWASSER
U. KELLWASSER
CONDROZ
ANNULATA
DASBERG
HANGENBERG
L. ALUM
LD I
LD II
LD III
LD IV
MD I
MD II
MD III
UD I
UD II
III
IV
V
UD VI
LC I
LC II
d.
gr./p.
inv.
ser.
p
part.
c.
a.
ko.
h
varcus
he
di.
h
rot.
t
pu-ha.
ja-rh.
l
tr
cr.
rh.
marg.
tr.
po
exp.
praes.
su
duplic.
s
cren.

Zlíchov+Daleje, Kačák, Taghanic, Kellwasser and Hangenberg respectively) but many authors have shown in detail the importance of intra-stage extinction. McGhee (1989, 1996), for example, considered this in a general way in relation to the Frasnian as, using ammonoid data, and data from other groups, did House (1985, 1989), and this has been covered, in varying detail, for corals (Oliver and Pedder, 1994; Pedder, 1982; Sorauf and Pedder, 1986), for stromatoporoids (Stearn, 1987), trilobites (Feist, 1991; Chlupáč, 1994; Chlupáč et al., 2000), and for brachiopods (Copper, 1998; Racki, 1998; Brice et al., 2000). The problem of declining groups within stages is developed further in the next section. With regard to the late Frasnian extinctions, there has been a surprising tendency for some authors to add 'mass extinction' and 'global' to the titles of their papers without presenting any evidence to support their assertions.

It is relevant to comment on the contribution of Signor and Lipps (1982) which is widely quoted. If there are extinction events within a stage before a major extinction event, then a simple statement of sampling error relating to the main event is not appropriate. Sampling error will always be important for very rare taxa. But, because of the great effort expended by the SDS over many years to reach the new GSSP definitions, it is probably true to say, for the Devonian, that intervals immediately before and after boundary events have been much more thoroughly sampled than other intervals. This should also be borne in mind in relation to the search for possible bolide, impact, or cometary ejectimenta where some boundary levels, and event horizons, have been searched far more rigourously than most levels.

It is the view of the writer that, in order to assess the strength of extinction events, it is necessary to discriminate between the several extinction events known to occur within stages and not to assume that one event in each stage is responsible. Comments on this matter are considered next.

5. Timing of mid-Palaeozoic extinction events

The conodont and ammonoid zonations give zonal scales, each with about 60 divisions, for the Devonian. Currently these form the most precise scale available for analysing extinction and diversification events (Figs. 1–3) and locally they may be refined farther. When drawing attention to marker fossils associated with events, Walliser (1984a,b, 1985) linked these within stages in a general way. In naming the events after sedimentological perturbations, and their association with detailed evolution of ammonoids, House (1985) tried to tie the events with ammonoid and conodont zones in more detail. The events of the Lower Devonian were reviewed by Chlupáč (1986) who commented on Barrandian events in detail; this was most appropriate because the name-giving 'type' sections of House (1985) were mostly in Czechia. Taxon variation through the Devonian for many groups was attempted by House (1989) and Becker (1993b) analysed ammonoid extinction data in relation to events more fully. For the late Frasnian extinctions there has been a burgeoning literature with a review by McGhee (1996) and, for brachiopods, a synthesis (Racki and Baliñski, 1998). Others have been listed above. The most important recent review of 'global' events in the Devonian was given by Talent et al. (1993) and Walliser (1996). There have been many important papers analysing particular events and these are referred to below in a review which is intended to supplement and update previous work.

5.1. Lower Devonian

5.1.1. Klonk Event, Silurian/Devonian (S/D) boundary event

The S/D boundary is drawn in bed 20 of a succession at Klonk, near Suchomasty, Czechia, in a sequence of micritic limestones and shales. The Klonk Event name appears to date from Jeppsson (1998) and should perhaps be only applied to bed 20. It represents a faunal boundary of international significance which was recognised when it was selected as the first GSSP, defining the S/D boundary when its palaeontological and other attributes were described with international areas with which it was correlated (Martinsson, 1977). The considerable list of family extinctions

(Fig. 2) of the Pridolian is not yet related exactly to the boundary. Current statements on the significant faunal changes are given by Chlupáč and Kukal (1988), Chlupáč et al. (1998) and Chlupáč and Hladil (2000). This is a significant faunal event, but no sedimentological characteristics define it in other areas at present.

5.1.2. Basal Pragian Event

This is the Lochkovian/Pragian boundary event of Walliser (1996). It is associated with the changes at the basal Pragian GSSP (Chlupáč, 2000). At the type locality in Czechia it is recognised by a change from dark shales to lighter Pragian carbonates, interpreted as a deepening. Faunal changes are significant, and the local boundary was formally used by some to define the S/D boundary before the IUGS decision to place the GSSP much earlier. Again this is a significant faunal event, but no sedimentological features define it in other areas at present.

5.1.3. Basal Zlíchov Event

This event (Chlupáč and Kukal, 1988) is rather later than the GSSP for the base of the Emsian established in the Zinzil'ban Gorge, Uzbekistan (Yolkin et al., 1997, 2000), where it is associated with evidence for deepening. The palaeontological changes, especially for conodonts, were thought to be sufficient for international definition. On a broader scale, the boundary is marked by a gradual loss of the pelagic graptolites and their later replacement, pari passu, in the pelagic realm by the coiled ammonoids a little above the boundary. This marks a good example of Arembourg's 'evolutionary relay' and is major Palaeozoic example of changed occupancy of the same ecological environment. In North America the eustatic changes are characterised by a slow replacement of endemic brachiopod genera by Old World genera (Johnson, 1986). Fig. 3 shows an evolutionary diagram of the Devonian ammonoids (Becker and House, 2000) from their entry just above this event. Henceforth this ammonoid record serves as a good framework for the consideration of later extinction events; notice that the width indicated for events is in part to emphasise some levels and in part for graphic convenience. In no case is a period in years known for these events. Current views on the precise assignment to conodont and ammonoid zones, however, are conveniently indicated.

5.1.4. Daleje Event

Named by House (1985), this corresponds to an unnamed event in Walliser (1984a,b, Fig. 3; it should be noted that this publication was not available when House wrote his paper, published in January 1985) and to the *gracilis* or *cancellata* Event. This event has been reviewed by Chlupáč and Kukal (1988) and Walliser (1996). A broad international rise of sea level is recognised at this time. If the Emsian comes to be divided into two substages, the boundary is likely to be associated with this event. For ammonoids, most noticeable is the near-loss of the loosely coiled mimosphinctids and Teicheroceratidae.

None of the Lower Devonian events referred to above can be regarded as mass extinctions and they are all low level events. Nor do they have the same association with well defined anoxic pulses which characterises most later events. If one takes the periods in Ma for stages given above and the new totals for family extinctions given in Fig. 2, then family extinction totals/period in Ma $\times$ 100, in all cases lies well below 10 family extinctions per million years.

5.2. Middle Devonian

5.2.1. Basal Choteč Event

The Emsian/Eifelian boundary and Lower/Middle Devonian series boundary has its GSSP near Wetteldorf in the Eifel, Germany (Ziegler, 2000). Just above this level is the Choteč Event, first named by House (1985), but the apellation given more precision by Chlupáč and Kukal (1988). Walliser (1984a,b, 1985) used the term *Pinacites* or *jugleri*, but *P. jugleri* is most abundant above the event. This is an event documented in Central Europe (Chlupáč et al., 2000; Walliser, 1996), Southern Europe and North Africa (Becker and House, 1994a). In Morocco, Klug et al. (2000) indicate two associated anoxic layers. It is not so far demonstrated to be global but *Pinacites* is known from Alaska and British Columbia, as far south as Mauritania in Africa and across Asia to China (Becker and House, 1994a), but most of these areas need to be tested for the subjacent lithology of the event. It has distinctive faunal characters but is not known to be a major extinction event. Whether some of the family extinctions of the late Emsian should more properly be assigned here is uncertain.

However, the event has the first clear characters of many of the later Devonian events. The typical lithology is of dark micrites rich in planktonic or nektonic pelagic faunas with evidence of deepening and a lithology and restricted benthonic fauna suggestive of sea floor dysoxia or anoxia. The presence of the giant bivalve *Panenka*, one of the rare benthos, suggests a stress environment.

5.2.2. Kačák Event

Named by House (1985), this is, at least in part, the *otomari* or *rouvillei* Event of Walliser (1984a,b, 1985). The distinctive characteristics have been made known through work to designate a basal Givetian GSSP (Walliser et al., 1995; House, 1996; Walliser, 2000), that level now being drawn high within it at Mech Irdane, Morocco. The event in the Czech area has been described by Budil (1995) and German equivalents have been thoroughly monographed (Schöne, 1997). This event is clearly developed as several successive phases, documented in the quoted works. *Nowakia otomari* and *Cabrieroceras* of the *rouvillei/crispiforme* Group start earlier and long survive the event. *Maenioceras*, a novelty group, appears within it. Much work is still needed to document how many of the estimated 44 family extinctions in the Eifelian fall within the stage and how they relate to this event. In other words, the excellent detailed work of Schöne (1997) needs to be replicated in other regions of the world to correct any bias provided by local events. The high Eifelian extinction rate of 6.8 family extinctions/Ma may apply only to a short time within the Choteč and Kačák Events. If ever a precise radiometric or orbital forcing timescale is available, then a specific extinction event may prove to be one of the more important in the Devonian, as suggested by the stage extinction rating of fourth in the system.

The matter of precise definition of this event has been appositely raised by Walliser (1996), complications arising because of the phased nature of the faunal and lithological changes. It seems to the writer that such a debate, for this and other events, has largely been overtaken by the work of Crick and Ellwood in their magnetostratigraphic (MSEC) studies discussed later, and also perhaps the geochemical signatures which may be recognised (Joachimski et al., 2001). Given the precision, and apparent ease of correlation of MSEC anomalies, these may provide the best framework for analysing the phases and defining the boundaries, particularly if climatically driven by orbital forcing.

5.2.3. Lower and Upper Pumilio Events

These are named after the stratigraphic units, the Pumilio Beds, and hence still carry the fossil name. These are dark to black lumachelles full of micromorphic brachiopods which have been traced from Germany to North Africa. Lottmann (1990) gives a thorough review. There has been no documentation of extinctions associated with them outside the Europe/North Africa region. The events have been interpreted as marking a widespread tsunami event. Their nature, however, suggests a transgressive pulse and if, as later argued, most of these events are related to Milankovitch controlled temperature heterodynes, then the possibility of unusual events enabling a widely dispersed spat fall seems a more reasonable explanation.

5.2.4. Taghanic Event

This is the *Pharciceras* or *Thaganic* (*sic*, a misspelling) Event of Walliser (1996). When this event was named (House, 1985), the break between the *Maenioceras* and *Pharciceras* Stufen was the defining palaeontological event, the loss of the Sobolewiidae, Holzapfeloceratidae, Agoniatitidae and Maenioceratidae being critical. In North America this corresponded with the contrast between the upper Hamilton (with agoniatitids and, following discoveries of G. Kloc, now with maenioceratids) and the Upper Tully Limestone with pharciceratids. The Tully Limestone has been recognised since the work of J.M. Clarke in the late 19th century as transgressive, a view

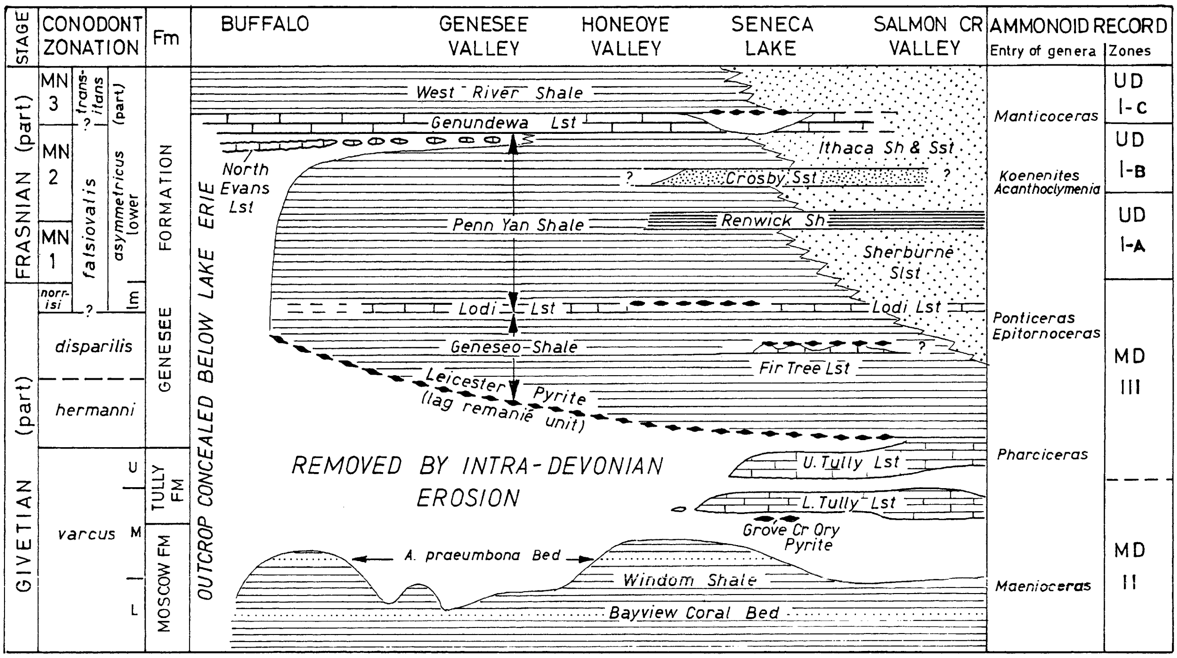


Fig. 4. Diagram showing the setting of the Tully Limestone and the Taghanic Event in the name area of upstate New York. Based on an early diagram of Huddle (1981) modified by Baird and Brett (1986) and Kirchgasser et al. (1994). Here updated, with the generous collaboration of W.T. Kirchgasser, to show ammonoid zones and goniatite occurrences.

also taken by Cooper and Williams (1935), Cooper et al. (1942) and House and Kirchgasser (1993). The entry of carbonates suggests transgressive migration landward of the Hamilton zone of clastics with the exotic faunas (for New York), including *Hypothyridina*; scutelluids and *Pharciceras* indicate links with open global waters. The tongues of *Hypothyridina*-bearing levels transgress eastwards into neritic or terrestrial clastic facies which includes the Gilboa Forest. The date of the Upper Tully level with *Pharciceras* is late Middle *varcus* Zone (not *hermanni-cristatus* Zone as given by Walliser, 1996), that is, Late Givetian on the new definition.

In New York the Taghanic is a phased event, but is not associated with anoxic-appearing sediments. Several phases are linked to this event and these are illustrated in Fig. 4. There is a break between the top Hamilton and Lower Tully Limestone, a break below the Upper Tully Limestone, and then a break with the succeeding, transgressive black anoxic shales of the Geneseo possibly at the base of the *hermanni* Zone. This last event Day (1996b) recognises in Iowa, and Aboussalam and Becker (2001), in Morocco, correlate it with the extinction of Maenioceratidae and Agoniatitidae and with the entry of multilobed pharciceratids.

The Tully Limestone units have distinct beds and at one level in the Upper Tully the Borodino reef is developed. Dutro (1981) revised and documented the changes and extinctions in brachiopod faunas within the Tully Limestone, but similar precision does not appear to have been attempted elsewhere, apart from the work of Brice et al. (2000) in the Boulonnais, and that of Day (1996a,b) in North America. In a review of possible formal subdivision of the Givetian, Aboussalam and Becker (2001) give a discussion on international correlation of the phases discussed above. They also give evidence that equivalents of the Tully interval in Morocco have styliolinites and dark micrites which are the more usual signatures for mid-Devonian events.

The Taghanic Event covers a long time span, perhaps several eccentricity cycles, and it is clear that major extinctions are associated with it, even if ranges are not yet well enough known to link them with the phases suggested above. The basal transgressive pulse was named the Taghanic Onlap by Johnson (1970), and an early attempt to trace the international extent was made by House (1975a,b) and to assess its effect. Laurussian evidence was reviewed by Johnson et al. (1985, 1986). More recently evidence has been given for its effect in northern Russia (House et al., 2000a) and Western Australia (Becker et al., 1993; Becker and House, 1997). For corals Scrutton (1997, p. 201) has documented this as a major extinction period, and some 18 rugosan families appear to have become extinct. For trilobites the extinction has been emphasised by Feist (1991) who documents four families lost at about this interval. The Benton (1993) data give 14 brachiopod families extinct here, and details of the many genera affected have been listed by Brice et al. (2000) who draw the extinction level at the end of the Givetian, presumably through lack of more detailed biostratigraphy. What is badly needed is a systematic documentation of the international situation for all taxa against the conodont and ammonoid zonal scales.

5.3. Upper Devonian

5.3.1. Frasnes Event

Much additional work has been done since this event was named (House, 1985) when it was intended to reflect the Pharciceras/*Manticoceras* Stufe boundary (although *Manticoceras* enters later), the base of the Lower *asymmetrica* Zone and the transgression in the early Frasnes Group of the Ardennes. The extinction of the last Petteroceratidae and Pharciceratidae (House et al., 2000c) is now known to fall above the GSSP level within Upper Devonian UD I-A and apparently within the former Lower *asymmetrica* Zone (within Montagne Noire zone MN 1). But evidence of the forms lost is limited by their distribution from North Africa to Central and Eastern Asia (Becker and House, 2000). In New York the level must be above the Lodi Limestone, a calcareous pelagic intercalation in the earliest Penn Yan Shale

Ebert (1993) named the Ense Event for facies changes at the base of the Lowermost *asymmetrica* Zone which he related to the transgression IIb of Johnson et al. (1985, 1986) and gave a detailed analysis of faunal events. This appears to be the same as the Frasnes Event.

Since the collapse of Middle Devonian reef carbonates was thought to commence with the Taghanic Event, House (1983) attempted a correlation of the reef pulses then known in Western Canada and the Ardennes with the sedimentary cycles of New York. This was repeated with more conodont data by Johnson et al. (1985, 1986). The reefs appear to have been initiated by transgression, which often then proceeded faster than reef growth leading to reef extinction. To test whether these transgressive pulses were international, detailed biostratigraphical analysis was undertaken in Western Australia (Becker et al., 1993; Becker and House, 1997) and in northern Russia (House et al., 2000a). Similar work for North Africa is still unreported in detail. Many of the Frasnian episodic deepening events discussed below showed an equivalence but there is also evidence of local epeirogenic signatures.

5.3.2. Genundewa, Timan, Middlesex and Rhinestreet Events

In the early Frasnian the entry of internationally known koenenitids is in the upper Penn Yan of New York. The Genundewa Limestone of New York is interpreted as transgressive anoxic facies pelagic styliolinites with a meagre benthos (House and Kirchgasser, 1993). The true *Manticoceras* enters and this occurs in conodont zone MN 3, and ammonoid zone UD I-B. Thus the use of *Manticoceras* as a faunal guide for the Frasne Event is inappropriate.

Later, but not yet shown in the New York West River Shale, which succeeds the Genundewa, is the international spread of *Timanites* (in MN 4 and UD I-C), after which the Timan Event is named (Becker and House, 1997). Since the name genus occurs rarely from Western Canada, the Timan (House et al., 2000a), and the Canning Basin (Becker et al., 1993) a transgressive pulse is indicated and the typical facies in many of these regions are again dark to black limestones or shales.

A later transgression in New York gave rise to the name Middlesex Event (Becker et al., 1993; House and Kirchgasser, 1993), characterised, at its type locality, by black anoxic shales and the goniatite *Sandbergeroceras* (in MN 4/5, level uncertain in New York, UD I-D). This represents a transgressive pulse thought to be recognised also in the Timan (Domanik deepening), Morocco and the Canning Basin (Becker and House, 2000).

The black shales of the Rhinestreet Shale in New York represent one of the major dysoxic black shale developments of the Devonian. Several transgressive pulses are developed within it, as shown by Sutton (1963), but the stratigraphical range is great (MN 6 to MN 11, UD I-F–I) and details still have to be elucidated. The base is taken as what Johnson had intended as the base of T-R cycle IId (Johnson et al., 1985, 1986), that is the base of the Rhinestreet Shale. But recently other levels have been used for the base of IId including the much higher *semichatovae* transgression (MN 11) (Sandberg et al., 2000). We have recognised the basal Rhinestreet Event both in Morocco and Western Australia (Section 366; Becker et al., 1993).

None of these faunal breaks represents mass extinctions but they represent significant faunal change on the ammonoid evidence. However, before considering the Kellwasser events, some comment is required on the way in which these episodic transgressive events, and the associated extinctions of reefs have an effect on the history of Frasnian extinctions generally. For example, Feist (1991) shows reduction of genera within the mid-Frasnian and the loss of, for example, the Dechenellinae and Tropidocoryphinae before the Upper Kellwasser Event. Details of the fallout of trilobite species over the same period are given by Chlupáč et al. (2000) and of genera by Chlupáč (1994). Day (1998), in reviewing atrypid decline in North America, shows a loss of many genera over the same period and specifically refers to stepped decline over what is the period of the Rhinestreet Events. Atrypid decline has also been considered by Copper (1998), and the coral decline has been documented using an older conodont zonation by Sorauf and Pedder (1986).

5.3.3. Lower Kellwasser Event

This dysoxic level has been separated in recent years and well documented by Schindler (1990, 1993) who gives sections for several areas in Germany, France and Morocco. In those areas, generally the Upper is better developed than the Lower. But in New York, the supposed Lower Kellwasser equivalent, the Pipe Creek Shale, of black paper shales, is much thicker than the restricted equivalents of the Upper Kellwasser. Then, Wendt and Belka (1991) used the term Kellwasser Member in Morocco for a wide swathe of the Frasnian styliolinites. Irregularities in the extent of anoxic sediments are not unexpected reflecting local anoxic basins. For ammonoids, this level (UD I–early K) is an extinction event and several new forms enter above it (Becker, 1993b; Becker and House, 1994a). Schindler (1990, 1993) considered the period including both Kellwasser events as a 'Krise', but for reasons given earlier, as well as comparison with the proximity of other Devonian 'events', this seems inappropriate.

5.3.4. Upper Kellwasser Event

Much has been written on the interpretation of this event (Buggisch, 1991; Schindler, 1990, 1993; Joachimski and Buggisch, 1993; Becker and House, 1994b; McGhee, 1996; Walliser, 1996; Joachimski, 1997; Hallam and Wignall, 1997; Racki, 1998, 1999) and of the environmental changes (Copper, 1986, 1998). The GSSP for the F/F boundary is at Coumiac (Klapper et al., 1993; House et al., 2000b). A fundamental review of German and other areas famous for the events was given by Schindler (1990). Some ammonoids, which are abundant within these dysoxic and dark limestones, become extinct at the regression closing the event (the F/F boundary event itself). By contrast trilobite families are lost with the onset of the transgression and anoxia (Feist in House et al., 2000b and Chlupáč et al., 2000), or a regression at the lower boundary. Contrary to former views, the tentaculitids and *Homoctenus* long survived the event (You, 2000). Clear definition enables the F/F boundary to be traced on all continents except southern polar regions. In New York, the Upper Kellwasser level (Over, 1997) shows less prominently than the supposed Lower Kellwasser level (the Pipe Creek Shale) where the sea-level curve over these events by Smith and Jacobi (2001) seems preferable to those of Johnson et al. (1985, 1986). In the Canning Basin the sections are in oxic facies (Becker et al., 1991), however, there is a short event interval of up to 1.8 m at McWhae Ridge, and 1.1 m at Windjana Gorge, where the boundary has been located using conodonts (by G. Klapper) but no macrofauna is known; this interval is not obviously dysoxic. It is unfortunate that data for most invertebrate groups, linked to the standard zonation scales, are not as detailed as those for the ammonoids (Fig. 3). To provide this should be a major future aim of the SDS. For the ammonoids, however, Frasnian data can be plotted in more detail and the results are shown below. It should be observed that generic data include cases where one genus evolved into another, as in the sequence *Probeloceras*, *Naplesites*, *Mesobeloceras*, *Beloceras*, so the forms may become extinct but the lineage continues. This is one of the reasons why clade (in this case family) data are to be preferred to generic data.

The extinction figures for ammonoid families and genera through the Frasnian for ammonoids, plotted against the zonal divisions UD I-A–L, give the following results:

	Families	Genera
L	2	11
K	0	0
J	1	6
I	0	3
H	2	3
G	0	2
F	0	4
E	0	2
D	0	1
C	0	2
B	0	1
A	2	2

Thus, for family level extinctions, two other levels (the Frasnes and Rhinestreet Events) would appear to be as important as the Upper Kellwasser Event, which in this case means the close of the event, the true F/F boundary, the genera being common within the dysoxic phase of the Upper Kellwasser Limestone and its equivalents. Notice that over twice the number of generic extinctions are earlier in the stage than the Upper Kellwasser Event. Notice also the importance of the fine stratigraphic division possible. Such factors control the definition and understanding of 'mass extinctions'.

5.3.5. *Nehden and Condroz Events*

The Nehden Event (House, 1985) refers to the widespread transgression in the earliest Famennian associated with black shales. It is not a discrete event, and it is characterised, not by extinction, but by the associated radiation of the Cheiloceratidae (Fig. 2), well documented by Becker (1993a) and probably also the rise of the rhynchonellids. The Condroz Event (Becker, 1990, 1993a) corresponds to an extinction level at which many tornoceratids and cheiloceratids are lost.

5.3.6. *Condroz and Enkeberg Events*

Both these events fall within the Nehdenian. The Condroz event was named by Becker (1993a,b): it is marked at the top of UD II-D and sees the extinction of over one third of ammonoid genera. The Enkeberg Event was named by House (1985) but, as correctly re-interpreted by Becker (1993b), is now applied to the sharp extinction event shown by ammonoids at the top of the UD II-E level.

5.3.7. *Annulata Event*

The German development has been documented by Becker (1992a, 1993a) who has emphasised that there are Lower and Upper Annulata Shales in the *annulata* Zone (UD IV-A). The event (Walliser, 1984a) may be a small-scale extinction event but rather a discrete sedimentary dysoxic perturbation which can be recognised in many areas of the world (House, 1985).

5.3.8. *Dasberg Event*

Defined by Becker (1993a) this event is characterised by the radiation of the Gonioclymeniina. This is thought to be associated with transgression recognised by Johnson et al. (1985).

5.3.9. *Hangenberg, D/C boundary event*

This marked dysoxic intercalation has long been recognised as a faunal break of great significance. The faunal break, then imprecisely known, was used to establish the D/C boundary in the 1830s in North Devon. The entry of *Gattendorfia*, in limestones above the event, was used to define the base of the Carboniferous from 1937 until the base of the conodont *sulcata* Zone was adopted by the IUGS (Paproth et al., 1991). This falls within a zone of perturbations documented at the GSSP by Feist et al. (2000). This event is complex with many phases (Becker, 1992b, 1996), particularly an intercalating arenite, the Hangenberg Sandstone (Bless et al., 1992), which represents a regression within it. Although described by some as global, evidence for it in Siberia, India and the Antarctic is absent (Becker, 1993b), but associated extinctions appear international. Most significant is the extinction of clymeniid, tornoceratid, and sporodoceratid ammonoids and for trilobites, of the phacopids. There is evidence of complex phasing for most groups, for example, *Cymaclymenia* ranges just above the main extinction event where, in Germany, the limestones end (Becker, 1993a). Korn (1986, 2000) and Kullmann (2000) have given detailed biostratigraphic analyses of ammonoid extinctions across the D/C boundary. Quite a new fauna enters above the event marking the distinctive radiation of the early Carboniferous. There have been important general reviews by Streel et al. (2000) and Caplan and Bustin (1999).

6. Setting of mid-Palaeozoic extinction events

The protracted Caledonian Orogeny controls much of early Devonian palaeogeography, with widespread regimes of clastic detritus dominating many areas. Carbonates are in pelagic areas or areas distance from such clastic floods. The succession is, however, punctuated by transgression/regression rhythmicity (House, 1983; Johnson et al., 1985, 1986). It is in this setting that the Lower Devonian 'events' occur which are discussed above. By the early mid-Devonian carbonates begin to be more widespread presumably as a result of widespread earlier planation of shelf areas and the development of very extensive carbonate ramps.

The Givetian appears to represent the major period of carbonate production in the Phanerozoic (Kiessling et al., 2000), excluding the Cretaceous chalks. Widespread carbonate platforms are documented. The main collapse of these carbonate platforms occurred with the transgressive Taghanic Onlap, the associate of the Taghanic Event, which is documented in so many areas that it appears global. By the early Frasnian reef complexes are more limited (Scrutton, 1997, 1998) and in the later Frasnian much less extensive than in the Givetian with reef knolls, pinnacles and atolls in certain belts and on restricted ramps. Areas, such as Western Canada, the Canning Basin (Becker et al., 1993), Europe (Bultynck, 2000a,b) and northern Russia (House et al., 2000a), show a reduction of reefs through the late Frasnian. If the reefs are established by transgressions, then the decline is punctuated by regressions. Often, after reefs are lost, they develop again later, either on the same site (good examples in the Ardennes), by retrogradation and backstepping (examples in the Canning Basin), or by progradation (examples in northern Russia). Even in eastern North America, where reefs are limited to a small occurrence in the Tully Limestone, the succession is punctuated by transgressive pulses (House, 1983; Johnson et al., 1985, 1986; House and Kirchgasser, 1993). The progressive reduction of late Frasnian coral/stromatoporoid reefs leads to termination by the close of the Frasnian. Microbialites enter within the Frasnian (Becker and House, 1997) and dominate as reef builders in the Famennian. The extinction of Frasnian coral reef complexes shows as major family taxon extinctions, especially of reef-associated organisms. The coral extinctions at the family level (Fig. 2) show that those of the Givetian were greater than at the end Frasnian and occur with the main international carbonate complex collapse. Even pelagic groups show a complex history which can be related to the transgressive pulses (Fig. 3).

7. Causes of mid-Palaeozoic extinction events

Of the 20 or so Devonian 'events' which have been discussed briefly, most of the Middle and

Upper Devonian events share many features in common. They are short-term, they usually are clearly defined events, they usually comprise dark to black dysoxic or anoxic sediments, they show a general or absence of benthos, the usually rich fauna is comprised of plankton or nekton thought to be pelagic, there is evidence that they are transgressive, and they are often limited by regressive phases. Many are associated with faunal extinction, sometimes with the entry of dysoxic events, sometimes with its close, often both. The richness of the death assemblages bears witness to massive mortality, but whether this indicates 'killing horizons' (McLaren, 1982, 1983, 1988) or normal mortality of rich faunas is not clear. The primary cause of the dysoxia or anoxia is debated, but it had a clear short-term effect on the contemporary sea floor. The history in many events showing a complex phasing from the entry of changed oxic conditions to its close (House, 1985; Schindler, 1990). It appears to the writer that, whilst certain events may show more extinctions than others, they follow a common pattern and probably have a common cause, and that 'all Devonian events must be taken into account when modelling the Kellwasser event' (House, 1989, p. 104).

A new element, of refreshing precision, has been added with the work of Crick and Ellwood in their studies of magnetosusceptibility (MSEC). A number of their studies across 'events' have appeared (Crick et al., 1997, 2000; Ellwood et al., 1999). Their recognition of MSEC anomalies relates to changes in the original rate of supply of iron-bearing materials into the marine system. These changes they consider may be due to land-based climate-induced erosion cycles, or eustatic or epeirogenic sea-level changes which are non-cyclic. The fine order microcyclicity appears related to orbitally forced climatic change which, hopefully, will 1 day provide a Milankovitch timescale. Meanwhile it seems clear evidence of a climatic drive as one major cause. In 1985, the writer speculated on an orbitally forced, climatically driven primary cause for many Devonian events, but shelved the idea for lack of evidence. A similar model arriving from MSEC evidence raises this hypothesis for serious consideration.

As is known from the Quaternary record, the interpenetration of orbitally forced factors (precession, tilt, eccentricity) gives complex changes in the solar energy reaching the Earth's surface, and complex means by which that may modify surface temperatures, climate and environments. The 404-ka-long eccentricity cycle, for example, gave often Quaternary sea-level changes in excess of 100 m, more than adequate for the patterns required. The discovery of longer-term cycles, up to 1.75 Ma (Olsen and Kent, 1999), some perhaps of chaotic origin, may also be important. The rapid fluctuations of extreme cold and hot, and heterodynes when several cycles combine, can give marked signatures. Relevant also is the curious Devonian palaeogeography, with restricted continental cratons on one hemisphere only, and extensive shallow waters in tropical areas. These factors may also help to explain the complex, and sometimes conflicting, geochemical evidence on events since those will be more controlled by the differing locations of sedimentation. Such explanations have been applied in the Silurian, for example, by Jeppsson (1998). The author prefers an interpretation in which the transgressions, and associated dysoxic or anoxic spreads, correspond to warming events (Becker and House, 1994b). Such conditions would also produce MSEC anomalies.

The Taghanic Event, with its association with major transgression, may prove to be controlled more by tectonic causes, and especially rates of ocean ridge separation. Such effects as local igneous activity, tectonic events throughout the Devonian, may mask an orbitally forced pattern which might exist.

8. Conclusions

A new analysis of the extinction of marine invertebrate families for each stage of the Devonian shows that the highest family extinction is, in decreasing order, in the Famennian, Givetian and Frasnian. When converted, using recent radiometric data, to rate of family extinction per million years, stage by stage, the figures give, in decreasing order of rate, Givetian (14.2 families extinct/

Ma), Frasnian (11.2), Eifelian (6.8). Such data are dependent on changing taxon data and radiometric dates but suggest statements that the end Frasnian extinctions are the greatest of the mid-Palaeozoic, are not supportable and that it may be the Taghanic that is the greatest.

In terms of definition it seems best to restrict the term 'mass extinction' to cases where at least 10% of contemporary families become extinct, but a timescale would need defining: perhaps this might be within the time range of the eccentricity cycles (0.1–0.4 Ma). Another figure might be appropriate for generic extinctions.

An analysis of the recognised 20 'events' in the Devonian shows that there may be several such events within a stage. Since the duration of a specific 'event' is currently unknown (although Schindler (1990) suggested 100 ka – the short eccentricity cycle – for the Upper Kellwasser Event) the true extinction rate at a particular event will be higher than the stage average, perhaps very significantly higher. Attention is drawn to the fact that the 'events' may have a complex history and are phased.

The evidence indicates that most events described are associated with a transgression phase and with a later regression, but the phases may be complex. Associated palaeontological extinction events are often world wide, but the sedimentary perturbations may not be matched internationally. Attention is drawn to the recent magnetosusceptibility evidence which has now documented many events in detail and provided a more quantitative means for their definition. This evidence suggests that the high signatures are associated with land pluvial periods and high sea-stands suggestive of high temperatures. If climatic fluctuations due to orbital forcing are an important cause, then eccentricity and tilt interpenetration of climatic heterodynes could lead to short-term fluctuations between climatic extremes.

There is no consistent evidence of volcanicity or tectonism as a general cause of the events although, for the Taghanic Event, international onlap might suggest an association with ocean ridge volcanism. The Hangenberg Event matches in time the volcanism and mineralisation of Rio Tinto age. There is, however, considerable igneous activity on continental areas which is insufficiently well dated so that this may be an important factor. Consistent and matching evidence for bolide impact and contemporary ejectamenta has proved quite elusive.

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