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ANALYSIS OF MID-PALAEOZOIC EXTINCTIONS

by

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ABSTRACT

There is a correlation through time of diversity plots of invertebrate taxa with onlap/offlap and eustatic sea-level curves. Major extinctions occur at periods of regressions. For the Devonian the conjunction of the ammonoid and conodont zonation provides a time scale for the analyses of evolutionary events. Some ways in which this precision can be used are outlined. There often appear to be specific tectonic causes of 'events'. Despite its acclaim, the Frasnian/Famennian boundary extinctions are similar in style, if not degree, to others in the mid-Palaeozoic and common exlanations are required. Analyses of 'events' suggest models for innovation in evolution.

ZUSAMMENFASSUNG

Zeitliche Fluktuationen der Diversität von Invertebraten korrespondieren mit Zeiten von Meeresvorstössen und -rückzügen bzw. eustatischen Meerespiegelschwankungen. Wichtige Aussterbephasen finden zur Zeit von Regressionen statt. Im Devon stellt die Verbindung von Ammonoideen- und Conodonten-Zonierung eine extrem detaillierte Zeitskala zur Analyse evolutionärer Ereignisse dar. Einige Beispiele werden ausgeführt, wie diese Präzision angewandt werden kann. Oft scheinen besondere tektonische Ereignisse der Grund für "Events" zu sein. Trotz ihrer Besonderheiten sind Aussterbeereignisse an der Frasnian/Famennium-Grenze wenn nicht im Ausmass, so doch in ihrer Art ähnlich zu anderen des mittleren Palaeozoikums. Dies erfordert eine einheitliche Erklärung. Untersuchungen an "Events" erlauben die Erstellung von Modellen für das Auftreten innovativer Neuerungen in der Evolution.

KEY WORDS

Extinctions, evolution, Frasnian/Famennian, events, Devonian/Carboniferous, Kellwasser.

SCHLÜSSELWORTER

Aussterbeweignisse, Evolution, Frasnium/Famennium, Event, Devon/Karbon, Kellwasser.

1. INTRODUCTION

Meaningful analysis of evolution in time is difficult. Incomplete collection and identification the fossils themselves, vagaries of preservation and representation of the fossil record, problems in quantifying criteria of abundance, distribution and ecological role, unequal knowledge and available expertise among fossil groups and other factors combine to provide less than satisfactory data bases. Nevertheless, for many years, but especially since reviews by Newell (1952, 1982) and others (Harland *et al.*, 1967), working palaeontologists have recognised the major role which palaeogeographic and palaeoenvironmental change has had on the course of evolution. Furthermore, the nature of operation of these changes has been long recognised. This relationship may be illustrated for the 330 millions years of goniatite and ammonite (ammonoid) diversity record (Figure 1). Diversity of this group may be regarded as an indication of contemporary success in either specialisation or relative freedom from selection pressures and has been documented in detail elsewhere (House & Senior (eds), 1981 ; House, 1986, 1989).

2. THE SPECIES/AREA EFFECT

The evolution data may be compared with data on palaeogeographic change as indicated by estimated onlap/offlap changes in sea level, such data being quite independantly derived. The correlation between the two is obvious (Figure 1). The existence of such a correlation has been doubted by some authors (Stanley, 1984 ; Wilde & Berry, 1984) but, for the Ammonoidea at least, it is a reality.

Comparisons of this sort were made by Kennedy (1977) and Wiedman (1988). The compilation presented here is based on reviews by Johnson *et al.* (1985, 1986), House (1983), Ramsbottom (1979), Sanders *et al.*(1979), Ross & Ross (1985),

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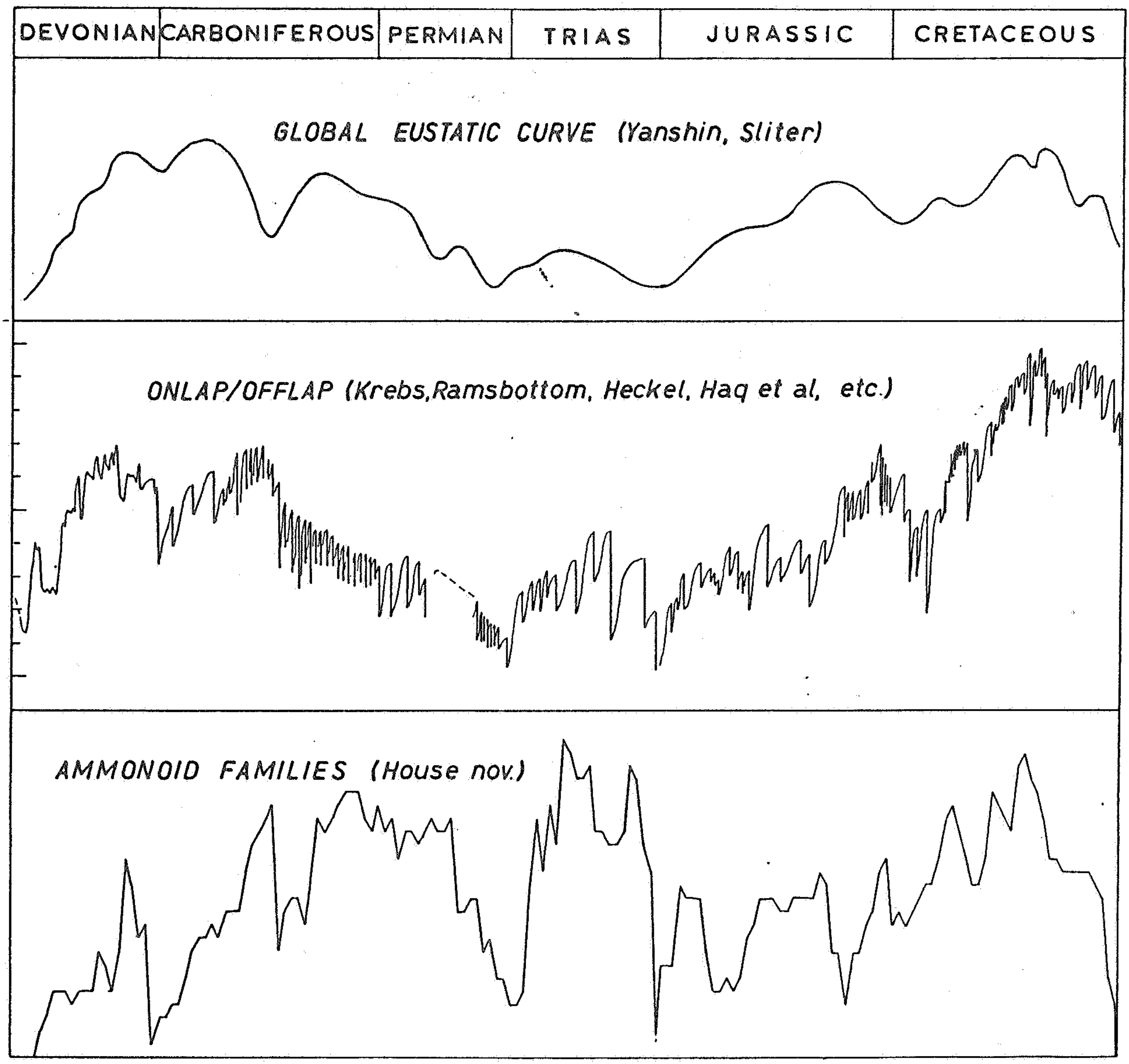

Figure 1. Totals of ammonoid families through time compared with estimates of the extent of sea level.: A, Total of ammonoid families (data from House & Senior, 1981 ; House, in press) plotted against two million year units (based on Snelling, 1985). B, Sea level onlap/offlap fluctuations (based on Johnson *et al.*, 1985, 1986 ; House, 1983 ; Ramsbottom, 1979 ; Saunders *et al.*, 1979, Ross & Ross, 1985 ; Holzer & Magaritz, 1987 ; Haq *et al.*, 1987). Based on more detailed presentation in House, 1989.

Holser & Magaritz (1987) and for the Trias to end Cretaceous, Haq *et al.* (1987). This compilation really supercedes earlier analyses but the whole subject is weakened by the poor radiometric data and the lack of detailed palaeogeogeographical maps through geological time to enable onlap/offlap to be rigorously quantified and, of course, the problems inherent in using taxonomic data in this way.

This broad correlation between evolution and palaeogeographic changes, particulary at well-known extinction levels, is the reason why experienced palaeontologists have not been impressed by theories which claim bolide impact or periodic extraterrestrial control as the major cause of evolutionary interruptions. A detailed statement of the views of such palaeontologists is given in a broad review of most fossil groups (Larwood (ed.), 1988). None would deny that meteorites and extra-terrestrial factors may have a role ; but they are not considered to be major evolutionary controls. Further, even if periodicity can be proven, global endogenic causes of such periodicity would more easily match the correlation with offlap/onlap and eustatic sea-level curve data than would extra-terrestrial immediate causations. In short, the author prefers causes such as those outlined by Johnson (1988). The purpose of this paper, however, is to comment on ways in which detailed documentation of organic fluctuations may be assembled and how the factual background for analysis and speculation may be improved.

3. MID-PALAEOZOIC EVENTS

In recent years there has been much interest in the recognition that particular times within the

Devonian were periods of significant extinction and evolutionary radiation (House, 1963 ; Harland *et al.*, 1967). Following the Calgary Devonian Symposium in 1967 and its collative publications (Oswald (ed), 1968) attempts were made to relate facies movements with evolutionary changes (House, 1975a, b) and this was followed by a compilation of faunal and floral records against time for Devonian groups (House *et al.*, 1979). An attempt was made to specify major international eustatic events (House, 1983) using a lettering system which has not found favor. Walliser (1984, 1985) attempted to name certain events and Johnson *et al.* (1985, 1986) gave a terminology of depophases for the Devonian eustatic curve. This has developed into the understanding that evolutionary changes are linked with environmental changes (House, 1975b, 1985 ; Walliser, 1984 ; Walliser (ed), 1987 ; Chlupàc & Kukal, 1987) or, on some views, may be interpreted as specific bolide or chemical events (McLaren, 1970, 1982). The times at which these changes occurred are now quite well documented and they are summarised, for the Devonian in Figure 2.

	STAGE	ZONE	"EVENTS"	FAUNAL GUIDES	TRANS./REGR.
		SU		*Gattendorfia*	IIf
DEVONIAN	FAMENNIAN	PR	HANGENBERG	*Acutimltoceras*	
		EX			
		PO	ANNULATA	*annulata*	IIe
		TR			
		MA	ENKEBERG	*(clymeniids)*	
		RH			
		CR	NEHDEN	*Cheiloceras*	
		TR			
	FRASNIAN	GI	KELLWASSER	*Crickites*	IId
		TR			IIc
		AS	FRASNES	*Manticoceras*	IIb
	GIVETIAN	DIS			IIa
		H/C			
		V	TAGHANIC	*Pharciceras pumilio*$^{+}$	
		EN			Ie
	EIFELIAN	KO	KAČÁK	*rouvillei, otomaria*$^{++}$	
		AU			Id
		CO			
		PA	CHOTEČ	*jugleri*	Ic
	EMSIAN	PAT			
		SE			
		LAT	DALEJE	*elegans*$^{++}$	Ib
		GR			
		DE	ZLICHOV	*Anetoceras*	
	PRAGIAN	KIN			
		SU			
		PE	L. PRAGIAN		
	LOCHKOVIAN	DE			
		EU			
		HE		*uniformis*$^{+++}$	

Figure 2. : **Table showing stages of the Devonian showing the evolutionary 'events' recognised (House, 1985 ; Chlupac & Kukal, 1986), faunal guides (partly from Walliser, 1984, 1985), and transgression/regression depophases (Johnson *et al.*, 1985, 1986).** The faunal guides are ammonoids unless marked with one asterisk (brachiopod), two asterisks (dacryoconarid) or three asterisks (graptolites).

The term 'event' is fashionable but misleading. Some of the changes considered are short term, others long term, and we have as yet no means of expressing numerically the gradations which occur. The terminology has essentially been copied from Cretaceous workers where it has served a useful purpose in detailed correlation. Furthermore it attracts attention to the sedimentary perturbations to which evolutionary changes are related and in that way has sharpened very considerably the precision with which these events have been examined. The concept has been a catalyst to produce more refined thinking.

For the Devonian, however, two parallel terminologies have been developed. The first (Figure 2), and historically the oldest, is based on local lithostratigraphic sedimentary perturbations : these were recognised long before 'event' ideas gained interest, and the Kellwasser Kalk, Annulata Schiefer and Hangenberg Schiefer, for example, were well known as distinctive long before they gave rise to the Kellwasser (Lower and Upper), Annulata and Hangenberg 'events'. This scheme is essentially linked to a type section where the sedimentary perturbations are thought to be well shown. The names have local use and this can be extended internationally if the evidence warrants this or discarded if it does not.

The alternative scheme emphasises palaeontological criteria which are held to be important. Terms such as *Otomaria, Rouvillei, Crickites* or *Annulata* 'events', used in this sense, refer to some aspect of the taxon concerned, often its abundance in the 'event', or its extinction, or its appearance, for usages vary. The implication of universality of the palaeontological event is something which usually has not been proven, so this type of terminology is misleading. Furthermore, the terminology suffers from the usual trouble of fossil names, a lack of permanence. For example, *Cabrieroceras crispiforme* and *C. plebeiforme* are generally considered to synonyms of *C. rouvillei.* Of these names, *C. crispiforme* has priority. Should the *Rouvillei* 'event' therefore be renamed ? Is it not wise to use lithostratigraphic terms which can be precisely specified rather than faunal terms which can at best be only generalised ?

4. METHODS OF ANALYSIS

In order to commence the task of elucidating detailed study of evolutionary perturbations, much more critical assembly of data is needed. The detailed conodont biostratigraphy assembled over the past twenty years (Klapper & Ziegler, 1979) coupled with the goniatite zonation (House, 1979) gives about fifty five divisions of the Devonian. This is rather more divisions than Raup & Sepkovski (1984) used for the whole Mesozoic and Tertiary in their analysis for periodicity at stage level. But for the Devonian only certain groups are known in detail and an overall synthesis is not yet possible. Nevertheless a good deal of data does exist and some of this is used here ot illustrate how more numerically based analysis should be possible in the future. Emphasis is therefore placed here on techniques which may be applied rather than on solutions.

4.1. Global unselected taxon tots

This has been the most frequently used technique and is assembled by totting up taxa against time units. The problems of the technique have often been set out, the inadequacy of taxon definition and comparability, the dependence on assumptions of even monographic treatment, the different meaning at different taxon levels, the dependance on the actual as opposed to the real record or the preservability and collectability of the group, the evolutionary meaning of diversity as a guide to 'success', and so on. Nevertheless, on the broad scale, it is a way in which the current state of knowledge may be summarised and it gives a picture which is often confirmed by other methods. Thus the maxima and extinctions of late Devonian ammonoid genera (Figure 3N, based on Korn, 1987) match 'events' very closely, but some of the 'events' were recognised by the pattern (House, 1985).

4.2. *Global distribution-selected taxon tots*

In this technique some particular attribute is favoured over total raw data. For example, the review of global cosmopolitan conodont species (Figure 3A) given by Klapper & Johnson (1980) is of this type and favours more universally distributed taxa. The peaks of cosmopolitan species roughly correlate with transgressive events. Such methods can be definable cut-off points for the taxa included and hence be reasonably objective. However much one has misgivings about any quantitative value taxon divisions may have there is some preference for data in which selection is clearly definable.

A contrasting approach is that adopted by Ziegler & Lane (1987) (Figure 3C) in which subspecies and species data for pectiniform conodonts are given in a more generalised way, and in this case not very precisely related to a time scale. This curve shows through the early to late Devonian peaks of diversity of increasing magnitude and, in particular, the late Frasnian and late Famennian extinctions are shown. This cruder and subjective approach rather blurs the clarity with which faunal changes are often shown by other more meticulous methods.

4.3. *Global facies-selected tots*

The extinction process is usually related to particular facies which, for some reason, have become unsuitable, thus causing extinction. Therefore analyses of particular facies-related groups are helpful.

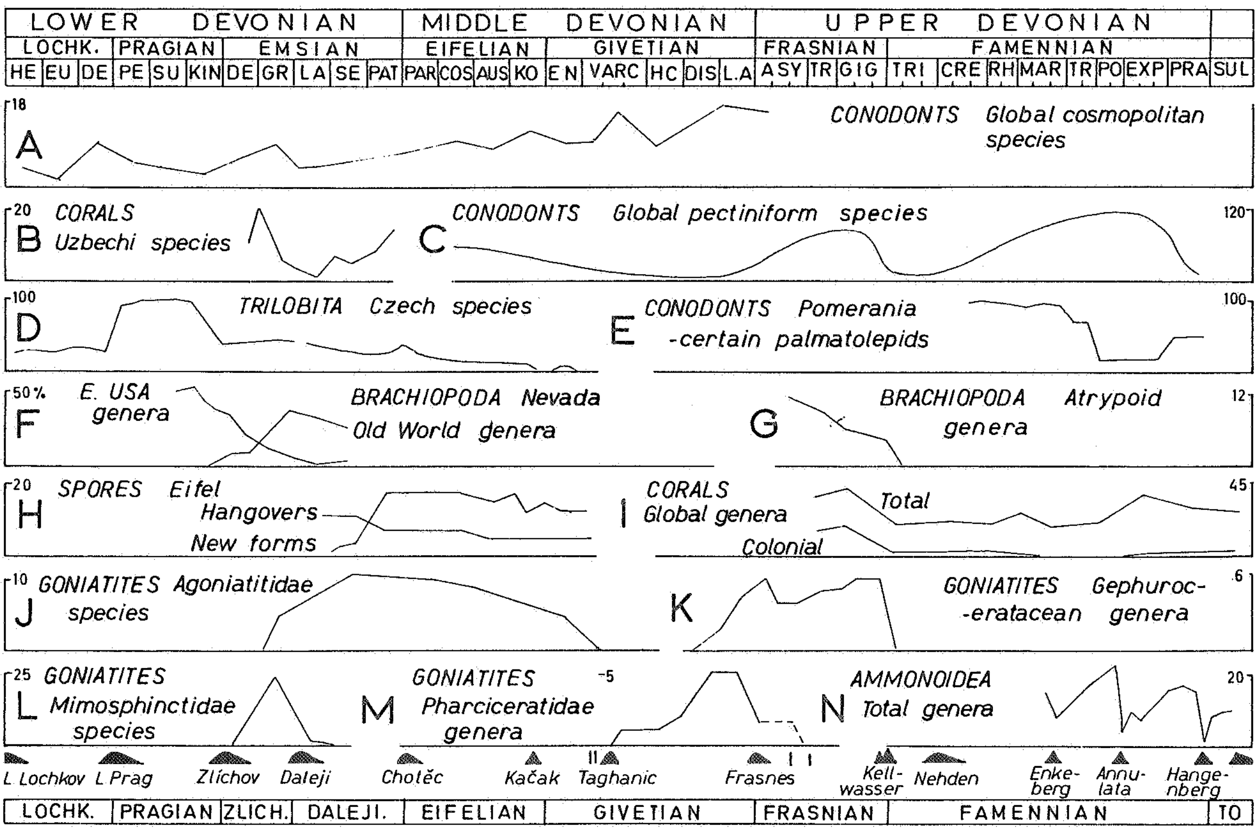

Figure 3. **Diagrams illustrating several ways in which Devonian faunal changes have been analysed:** Plotted against series, stages and conodont zones and indicating along the base the main periods of evolutionary change or 'events'. A, Global abundance of cosmopolitan conodont species (data from Klapper & Johnson, 1980). B, coral record in the Khodza Khurgan section of Uzbechistan (Kim *et al.*, 1978). C, showing broad cyclicity in abundance of conodont pectiniform species according to Ziegler & Lane (1987). D, Diversity of trilobite species in Bohemia (Chlupac & Kukal, 1986). E, local record of palmatolepid conodonts in Pomerania (Matya, 1986). F, proportions of Old World and eastern USA endemic brachiopod genera in Nevada (Johnson, 1986). G, the decline and extinction of atrypoid brachiopod genera (Copper, 1977). H, spore record of the Eifel area showing the entry of new forms (Riegel, 1973). I, global genera of corals with colonial corals separately indicated (from Scrutton, 1988). J-N, Ammonoidea. J, agoniatitid species. K, gephuroceratacean genera (Becker, 1986). L, mimosphinctid species. M, pharciceratid genera. N, total ammonoid genera (Korn, 1986). Significant extinction events shown at the foot of the diagram.

The tots shown here for corals (Figure 3I), based on Scrutton (1988) and others, shows how colonial corals become virtually extinct at the Frasnian/Famennian boundary whilst solitary corals continue with little change (Pedder, 1982), the difference in shallow as opposed to deeper biotic changes is thus illustrated in a way which global total tots would obscure.

4.4. *Extinction tots*

Unless a group is known thoroughly, analysis solely based on where species or genera are thought to become extinct is useless. This is because changes of name occur where there are recognised evolutionary changes in an evolving lineage and this is not seperable from true extinction where the loss of a name refers to real extinction. Indeed an apparent 'extinction' may be indicated only where evolutionary diversification rates are high. A specialist can in many cases seperate these factors, but it appears to have been done for very few analyses.

4.5. *Local taxon tots*

Global analysis is only as good as the summation of the local data on which it is based. Local faunal or floral analyses are rarely complete or numerically based but their potential for contributing data for international comparison is considerable. Data such as the coral diversity data for local sections in Uzbechistan (Figure 3B), based on data in Kim *et al.* (1978), gives an illustration of the local effect of the Regularissimus Zone facies and its dating. Data for Pomeranian palmatolepids (Figure 3E) may indicate the effects of mid-Famennian regression (based on Matya, 1986). The analysis of local trilobite data for the Bohemian area (Figure 3D, based on Chlupac & Kukal, 1986) shows significant effects of the Zlichov and Kacak events. The advantage of such studies is that a commencement can be made to correlate lithofacies and biofacies criteria and approach bio-logs which can be digitalised for computer analysis and international comparisons. But much work has to be done before the stage is really reached. The importance lies in the fact that data are analysed at much finer time divisions than the zones which must form the only basis for global analysis.

4.6. *Local taxon replacement tots*

Two examples are given to illustrate the valuable role ratio analysis can play (Figure 3F, H). In an analysis of Nevada brachiopods, Johnson (1986) has documented with precision the changing proportions of Old World and Eastern USA (Appalachian) genera. Again the value lies in the way documentation can be done from bed to bed rather than being crudely summed on a zonal basis. This can be taken to illustrate the slowly developing effects of the Zlichov transgressional events witnessing that this is caused by a gradual change and not a sudden event. Somewhat similar is the well-known evidence regarding the sudden change in terrestrial floras for Germany (Figure 3H) resulting from the work of Riegel (1973, 1974), the actual change preceding the new definition of the Lower/Middle Devonian boundary. So little work of this quality has been done in other areas that it still has to be demonstrated how general this picture is, but it does demonstrate the potential of methods of this sort.

4.7. *Clone analysis*

In groups which are evolving rapidly, the recognition of short-term radiation events and discrete 'package' type evolution in which the clones have specific ranges is fairly well understood. This has been documented for Devonian ammonoids (House, 1985) and the correlation with specific sedimentary perturbations seems clear (Figure 3J-M). Multidisciplinary analysis of such changes related to other groups is desirable and has been attempted for several. Such studies have to be international to be exhaustive and trustworthy, but they can rarely be done except at a zonal level.

4.8. *Litho- and bio-facies analysis*

What has still to be attempted in any depth is the relation of local facies changes to global events. Suggestions on the international recognition of Frasnian sedimentary cycles by House (1983) was confirmed by Johnson *et al.* (1985) and has been extended by Hladil (1986). This may enable a far more precise documentation and understanding of faunal changes than has been attempted so far. It is of considerable importance in relation, for example, to the Frasnian/Famennian boundary extinctions, now more nearly at the actual boundary with the acceptance of the base of the Lower *Triangularis* Zone as defining the base of the Famennian.

Many groups show a gradual faunal decline in the late Frasnian (House, 1975) and this is illustrated also by some data summarised here, and particularly well by the recent analysis by Copper (1987) of atrypoid extinctions (Figure 3G). One is much more impressed by this carefully assembled evidence of specialists in individual groups than by the histrionic demands for catastrophic extinctions by the uninformed. However it is the potential for quite precise documentation of the actual events when lithofacies and biofacies evidence is combined which is critical for future work.

5. INTERPRETATIONS

The periods of greatest evolutionary change which have been elucidated in the Devonian are shown on Figure 1. The recognition of these, and the terminology for them, results from the writings of several authors. In recent years great emphasis has been placed on one of these, the Upper Kellwasser event, often named after the Frasnian/Famennian boundary which succeeds it. Also the extinctions at the end of the Devonian, the Hangenberg event have been commented upon, but less frequently. The main extinctions here again precede the stratigraphical boundary of the Devonian/Carboniferous, now defined at the base of the *Sulcata* Zone. The ammonoid data relating to this event has been documented (Price & House, 1984 ; Becker, 1988). The emphasis only on the first of these is misleading, since all show gradations of similar patterns : it has been argued that for most of these Devonian evolutionary events sedimentary perturbations can be correlated with them (House, 1985) and the evolutionary patterns associate with the ammonoid records shows a number of similar attributes, decline in diversity approaching a diversity low, often associated with the introduction of quite novel ammonoid stocks usually recognisable even in the earliest stages suggesting that aspects of larval strategy are critical to survivors (House, 1985). It is not suggested that all are identical, indeed such would be most unlikely, but they do have several attributes in common, suggesting a similar cause. The relation between certain events and sedimentary rhythms is important. Thus a deepening event above the Palliser near Medicine Lake (Geldsetzer *et al.*, 1987) has a pyritic level such as is often the case where sedimentary deepening is associated with lag events.

The great literature relating to the Kellwasser event extinctions polarises into three broad hypotheses, the first that it results from extraterrestrial causes, either due to a single impact event or bolide (McLaren, 1970, 1982 ; Geldsetzer *et al.*, 1987) or cosmic shower events. The second that it is due to climatic change (Copper, 1977, 1986 ; Stanley, 1986) particularly to cooling of the earth resulting from an extension of ice caps. The third that palaeogeographic changes are the immediate cause, operating through eustatic changes of sea level and resulting from tectonic effects rather than the other causes (House, 1983, 1985 ; Johnson *et al.*, 1986, Johnson, 1988). The possibility that the events represent a cyclicity has been suggested (House, 1985 ; Bayer & McGhee, 1986) and, although the time scale does not allow the testing of this hypothesis, this could operate under endogenic as well as extraterrestrial causations.

The best hypothesis in science is one that explains most of the facts. All Devonian events must therefore be taken into account when modelling the Kellwasser events. As the writer has been impressed by palaeogeographic causes for interruptions and irregularities in the evolution of the Ammonoidea as a whole (Figure 1) so he has been impressed by the relation between globally recognisable sedimentary perturbations and extinction and radiation events (Figure 3). The staged nature of the late Frasnian events and their relation to sedimentary cyclicity seems too major a factor to be set aside. The sedimentary cycles can be explained readily by eustatic changes as a result of this interplay of local epeirogenic and global eustatic effects of tectonic events. No such ready explanation is available to those that prefer bolides and cosmic showers. Climatic change can be important and has been invoked in relation to the survival of supposed cooler water forms of ammonoid through extinction events (House, 1985 ; Becker, 1986), but extension of cooler ocean waters with transgressions is to be expected. Thus endogenic hypotheses are preferred and a correlation recognised between evolution and sedimentary perturbations.

Now we seem to be approaching the stage where the sedimentary pulses themselves can be related to specific moutain building events in particular parts of the globe at particular times (Copper, 1986 ; Talent & Yolkin, 1987). Furthermore estimates can be made of the actual eustatic sea level changes themselves so that some quantification of plate movement and orogeny may be possible. Thus a considerable degree of scientific rigour could enter into palaeontological and sedimentological analysis.

The initial early Devonian regression following the main pulse of the Caledonian orogeny was estimated to have given a sea-level fall of 140 metres (House, 1975a) resultant upon mountain building a long a Laurentian/Eurropean suture alone, so this will be an underestimate. The Emsian regressional facies probably represent the last major clastic input into the seas of the Caledonian orogeny and when isostatic equilibrium starts to reassert itself the major global transgression of the early Eifelian is to be expected. The Acadian Orogeny initiates the facies movements culminating in the Taghanic event. The documentation of tensional activity in Morocco by Wendt (1965) around the Frasnian/Famennian boundary suggests a different type of tectonic cause for the Kellwasser events. In time there is a close correspondence of the *Annulata* event with the Antler orogeny. At the time of the Hangenberg event the Bretonic structural event has long been suggested.

6. THE FUTURE

It is the increasing time-resolution offered by the biostratigraphy of many groups but especially the conodonts, spores and ammonoids, which provides a tool for the detailed study of what actually happens in evolution and for the detailed study of stratigraphical changes and paleogeography. Detailed biostratigraphical analysis is the key to this. For the Palaeozoic such work is increasingly hampered by the lack of specialists for many fossil groups. Indeed, there is a very limited number of workers publishing details on actual sections. Speculation is less demanding. Much international cooperation is needed for programmes to assemble the actual data from individual groups to form the data base for numerical analysis of the evolutionary and stratigraphic record. Yet it is only on the basis of such studies that real progress will be made.

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