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Mass extinctions and data bases: changes in the interpretations of tetrapod mass extinction in the past 20 years.

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Introduction

The fossil record has potential to be strongly biased. Sampling errors resulting from variations in sediment area, sediment volume, and Palaeontologist Interest Units (the number of taxonomists working on a given period fauna) must be allowed for to obtain an accurate record of taxon diversity through time (Raup 1972, Signor 1985). Corrections for possible errors show that the record is essentially acceptable (Sepkoski et al 1981). The important question is; can we improve our knowledge of it?

Continual refinement of our knowledge of the present record should reveal whether mass extinctions conform to the fashionable catastrophist theory or the gradualist theory. Gradualists might expect that increased and improved collecting would reveal rare, late survivors, thus extending the range of families beyond an "event" (Fig. 1a). Catastrophists would expect that improved collecting and dating would shorten the time span, resulting in a short term event confined to one small part of a stratigraphic sub-stage (Fig. 1b). A comparison of the two most recent data bases for fossil tetrapods shows that our knowledge and interpretation of the fossil record is changing rapidly, and the results are presented here. The changes over the past twenty years may indicate future trends.

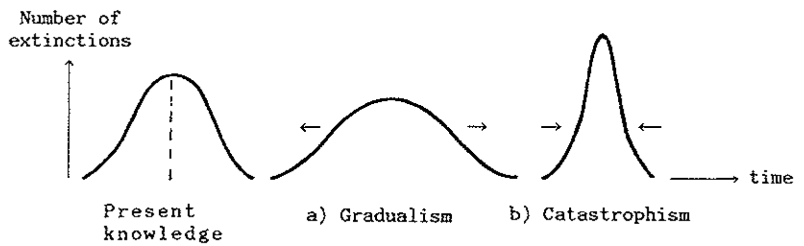

Fig.1. Two possible scenarios for mass extinctions, one of which may be favoured by refinment of our knowledge of the fossil record.

Comparison of a 1966 and a 1986 data base

When Raup and Sepkoski proposed in 1984 that mass extinctions occur with great regularity, their observations were based on an analysis of a data base compiled from various sources. Colin Patterson and Andrew Smith (in press) have suggested that Sepkoski's 1982 data for fish and echinoderms is approximately 76% incorrect due to the inclusion of monogeneric, monospecific, paraphyletic and polyphyletic families. An examination of Sepkoski's tetrapod data by Benton (1985a,b) revealed similar inaccuracies which have since been corrected. Most authors so far have used Romer's classic 1966 text as a source of data on fossil vertebrate distributions. The present study shows that Romer's data is no longer a reliable source, and outlines how and why it differs so markedly from our current knowledge of the tetrapod fossil record.

To compare the tetrapod fossil record of today and that of 20 years ago, ranges of tetrapod families in geological time were resolved to epoch level (and sub-epoch level in the Palaeogene). As Romer utilises the mid Permian, mid Palaeocene, mid Cretaceous,and mid Oligocene in his list of stratigraphic ranges, divisions of the geological timescale which are not recognised today in the Palmer (1983) timescale, some discrepancies arise when comparing the graphs. Only the mid Permian and mid Cretaceous anomalies are particularly relevant to this study but they do not affect the comparison of data for the late Permian or late Cretaceous events. All monogeneric or monospecific families present in the 1986 data were omitted from the analysis.

Plots of family diversity against time for both data sets (Fig. 2a,b) show the same general pattern with the total number of families not exceeding 65 until late Cretaceous times, after which numbers rise to 270 (1966) and 282 (1986) in the Pleistocene. The 1986 plot reveals a slightly greater diversity of families for any given period with the exception of the early Cretaceous and late Eocene. Overall the 1986 data records 751 originations and 491 extinctions from the late Devonian to the Pleistocene compared with 681 originations and 433 extinctions in the 1966 data. As may be expected from the observed increased family diversity, numbers of originations in the 1986 data exceed those in the 1966 data for most of geological time. Exceptions are noted for the mid Triassic (where Benton shows 6 originations less than Romer), early Cretaceous (11 originations less), and the late Eocene (25 less). Similarly, the number of extinctions recorded for any epoch in the 1986 data exceeds the corresponding number in the 1966 data. Again exceptions are noted for the early Triassic (where Benton shows 4 extinctions less than Romer), late Triassic (8 extinctions less), early Cretaceous (7 less), and the late Eocene (8 less).

The greatest difference in the number of families suffering extinction during any one event is observed for the late Triassic event (Table 1). Romer shows 33 families (80.5%) dying out compared with 25 (56.8%) in the present record.Further large differences are observed for the early Triassic event showing a difference of 4 families, and the early Cretaceous, 7 families. The other events outlined in Table 1 show little variation between data bases in the percentage of families becoming extinct despite a sometimes sizeable difference in the number of families. The early Permian event for example is shown by Romer to consist of 25 family extinctions corresponding to a 71.4% reduction in family numbers, while Benton lists 32 families becoming extinct which corresponds to a 74.5% reduction. This is most likely due to the more complete nature of the present record showing a greater diversity for the early Permian and an increased number of taxon extinctions.

	ROMER (1966)		BENTON (1986)	
Extinction event	No. of families suffering extinction	% of total families	No. of families suffering extinction	% of total families
U.Cret.- L.Pal.	47	51.7	55	49.6
L.Cret.- M.Cret.	16	27.6	9	17.3
U.Jur.- L.Cret.	19	32.2	20	30.8
U.Trias.- L.Jur.	33	80.5	25	56.8
L.Trias.- M.Trias.	18	56.3	14	41.2
U.Perm.- L.Trias.	41	78.9	43	76.8
L.Perm.- M.Perm.	25	71.4	--	--
L.Perm.- U.Perm.	--	--	32	74.5

Table 1. A comparison of tetrapod family extinction data for the main extinction events as revealed by examination of the two most recent data sets. Abbreviations: Perm.,Permian; Trias.,Triassic; Jur.,Jurassic; Cret.,Cretaceous; Pal.,Palaeocene.

Changes in our view of mass extinctions

In order to test the validity of Romer's data, two distinct and well established extinction events were considered. Lists of all the tetrapod families which Romer shows suffering extinction in the late Permian and late Cretaceous were examined and compared with present knowledge.

Romer does not define his stratigraphic ranges for families more accurately than epoch level. Benton however gives ranges to stratigraphic stage level, so in compiling the data for the above analysis, a certain amount of lumping of the 1986 data was required. Taking the early Jurassic for example, the numbers of families given by Benton for the Hettangian, Sinemurian, Pliensbachian and Toarcian were grouped together and taking the total originations and extinctions into account, a single figure for the number of families present in the early Jurassic was obtained. This problem of broad stratigraphic ranges is particularly relevant to the next part of the study. Taking one of the two events mentioned above as an example, the end Cretaceous event saw its greatest decline in family numbers during the latest Cretaceous (Maastrichtian). The number of families becoming extinct in the Maastrichtian cannot be determined from the 1966 data which merely shows 47 family extinctions for the late Cretaceous (consisting of the Maastrichtian, Campanian, Santonian, and Coniacian stages as Romer includes a mid Cretaceous epoch containing the Turonian, Cenomanian, Albian and Aptian). The 1986 data consisting of stratigraphic ranges resolved to stage level allows a list of all families suffering extinction in the Maastrichtian to be compiled, and it is with this list that all Romer's late Cretaceous family extinctions are compared.

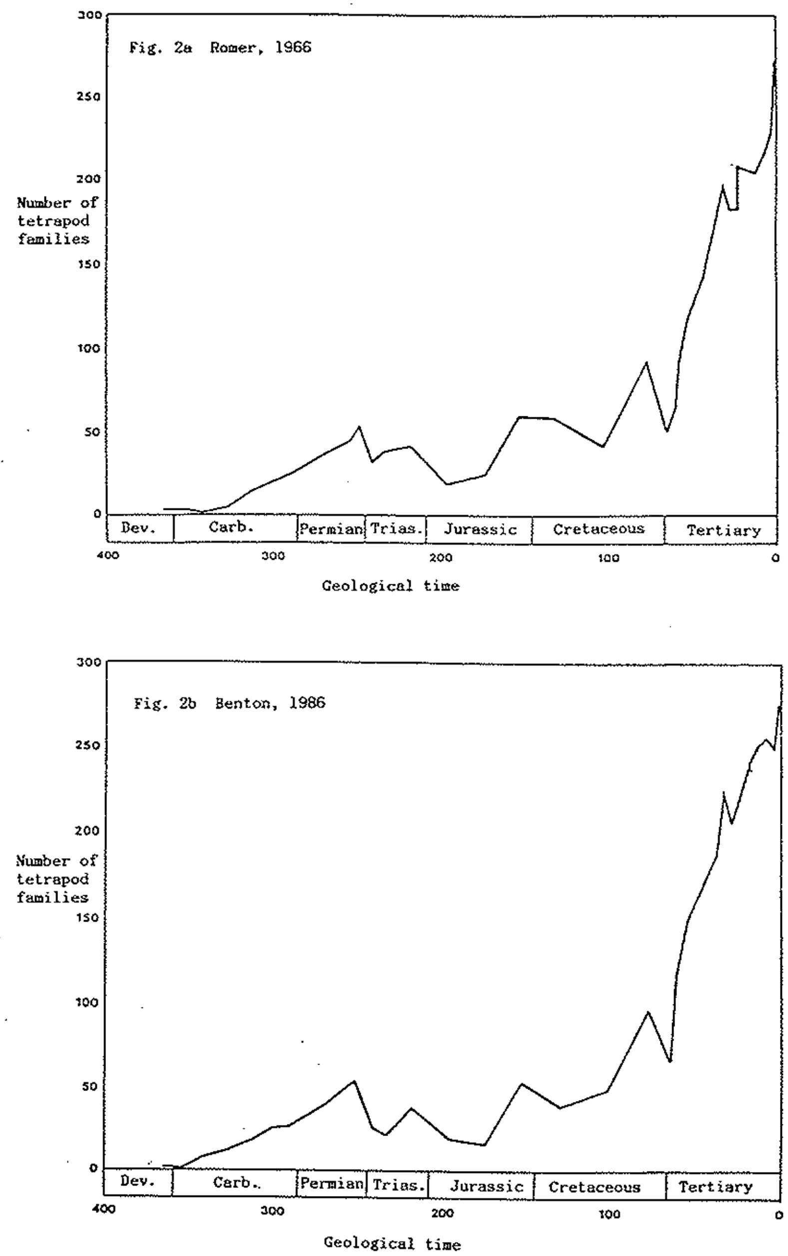

Fig.2. Plots of tetrapod family diversity through geological time, as given by a) Romer 1966, and b) Benton 1986.

The results of this comparison reveal that the change in the interpretation of the fossil record is not a systematic one. Of the families listed by Romer as suffering extinction during the end-Cretaceous event, 9% are monogeneric, 9% have been reassigned to other families, and 38% are incorrectly dated. Thus, increases in our knowledge of new specimens and stratigraphy accounts for 38% of the incorrect families, while 18% depends on taxonomic revisions.

Analysis of the end-Permian event reveals that 185 of Romers families are monogeneric, 37% have been reassigned, and 10% are incorrectly dated. In this case, the "new specimens" element of the erroris only 10%, while the remaining 55% element depends on taxonomic revision, particularly that of the mammal-like reptiles. A large number of families of mammal-like reptiles erected by Robert Broom and others, are now regarded as invalid because the specimens are too poor to determine their characteristics, there is only one species or genus in the family, or the specimens have been assigned to other families (Kenp 1982).

Conclusion

We can conclude that our knowledge and interpretation of the fossil record has improved considerably in recent times and it will continue to improve in a non-systematic fashion as a result of taxonomic revision, refinement of stratigraphic ranges, and the discovery of new fossils. The relative contribution of "new fossils", the perpetual cry of the palaeontologist, to improving our knowledge of the nature of mass extinctions is not always the key. A strict cladistic analysis, and reassessment of poorly defined taxa may be of just as much significance.

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