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DICYNODONTS AND THE END PERMIAN EVENT

by

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ABSTRACT

Patterns of diversity changes in several groups of Late Permian South African terrestrial tetrapods are examined. Using data contained in Kitching (1977), histograms are presented which illustrate changes in a) total number of tetrapod genera per biostratigraphic zone; b) total number of therapsid genera per zone; c) total number of herbivore genera per zone; and d) total number of carnivore genera per zone. Herbivorous and carnivorous genera are categorized as comprising small, medium or large individuals and histograms which document changes in number of genera in each of these six categories per zone are presented. Potential sources of error inherent in the data are outlined. Broad changes in generic diversity are noted and possible explanations for these changes are presented. It is concluded that the present data do not provide overwhelming evidence for a rapid and catastrophic drop in terrestrial tetrapod diversity at the very end of the Permian, but do illustrate a gradual and continuing decrease from the middle of the Late Permian into the middle of the Triassic.

INTRODUCTION

In the past the fossil record has been held to provide evidence of macroevolutionary phenomena such as adaptive radiation, replacement and extinction, although often the interpretation of such evidence has been the subject of intense debate and controversy. Many examples of such studies could be cited, but those of Gould & Calloway (1980), Williamson (1981), Bonaparte (1982) and Benton (1983), as well as compilations such as Valentine (1985), give the flavour of the work involved.

Basically such studies involve a two-part process. First, the fossils are classified into taxa at whatever taxonomic level the study has chosen, and second, the number of such taxa during a stated stratigraphic interval is assessed. Assessment may be in terms of overall number of taxa present within the stratigraphic unit, of number of first-known appearances, or some other measure of diversity (as in Pitrat 1973). Patterns in the change of diversity through time may then be detected and it is usual to go on to propose some kind of process, or mechanism, for bringing about the pattern. Alleged changes in taxonomic diversity at the Cretaceous-Tertiary boundary have produced a plethora of ideas on explanatory processes, culminating in the proposal of several cyclic mechanisms which might account for large-scale changes in diversity at other times in earth history (Raup and Sepkoski 1984). Similarly, the Permian/Triassic boundary has also been seen as a time of dramatic change in taxonomic diversity, in which, by some estimates, up to 80% of all reptilian families became extinct (Albritton 1989: 98). The present study considers the fortunes of one group of organisms at and around this boundary, the terrestrial tetrapods from South African fossil localities (mainly mammal-like reptiles), in an attempt to clarify further the kinds of taxonomic change (if any) which were occurring at the boundary, and whether different ecotypes were affected differently by whatever event might have been occurring.

METHODS

If the patterns of diversity seen in the fossil record are to be interpreted in terms of causes or processes, then it is particularly important that the taxonomic category chosen in the study is a meaningful one.

Conventional attempts to plot changes in taxonomic diversity through time have mostly looked at some measure of diversity of supraspecific taxa, commonly orders or families (Newell 1982). Some recent studies, for example by Raup & Boyajian (1988), have attempted to investigate extinctions at the genus level. In addition, by applying techniques such as rarefaction (Raup 1979), it is possible to interpolate from generic or higher level diversity to species level diversity, but this does not actually record real number of species. On the whole, though, suprageneric categories have been used and as workers define orders and families in different ways, for example, by including different numbers of genera, say, within a family, it is hard to achieve comparative consistency using this level. Families often tend to be fairly flexible associations of genera. For example, the

Triassic members of the dicynodont mammal-like reptiles have been grouped into one subfamily (King 1988) or two (Keyser & Cruickshank 1979) or three (Cox & Li 1983) families, depending to a certain extent whether the authors are splitters or lumpers. If the number of Triassic families were to be compared with the number of Permian families, very different conclusions might be drawn concerning changes in diversity, depending on which classification were used.

The ideal categories to use for studies of changes in taxonomic diversity should be numbers of individuals of a species, and numbers of species (Benton 1983, Raup & Boyajian 1988). If we are trying to put forward explanations for changes in diversity, such as competition between groups of organisms, the ecologically important categories are the individual and the species, not genus, family or order. The former entities have ecological and evolutionary reality, whereas the latter are human constructs. Therefore, it is changes in the diversity of the former entities which should be studied. It is felt by some workers that supraspecific categories such as genera or families track species diversity and may therefore be used as proxies for species (Sepkoski *et al.*, 1981). However, using these supraspecific categories will dampen the extinction signal since a genus cannot be recorded as becoming extinct until all of its constituent species have done so. Until this happens, those species of the genus which do become extinct are effectively ignored in the analysis. There is really no ideal substitute for using number of species or number of individuals in diversity analysis.

However, measuring all individuals of a particular species present at any one time presents huge practical difficulties. It would be necessary to estimate the proportion of individuals fossilized, the proportion of those fossilized which might be discovered, the proportion of those discovered which have been identified, and so on, in order to arrive at an error factor which could be applied to the actual number of individuals counted in order to be able to estimate the true number likely to have lived. Only one such attempt has been made which includes mammal-like reptile groups (Benton 1983) and not all authorities would agree with some of the estimates of numbers of individuals contained therein.

On the other hand, estimating the number of species which might have lived at any particular time is also fraught with difficulty. Because of the tendency in the last century to call every new fossil discovered by a different name, and the tendency to err on the side of variety rather than conservatism, the number of species recognised has been greatly overestimated. Since we do not have very much idea of the level of intraspecific variation in fossil forms, we tend to assume that it is low, and therefore every new fossil discovered that is just slightly different from its contemporaries is taken to indicate a new species. Such species are again, by and large, human constructs, relying heavily on a morphological definition of what constitutes a species, rather than depending on any underlying biological reality. Within the Dicynodontia, such classificatory techniques led to there being, at one stage, over one hundred species of the genus *Dicynodon*. However, recently, valiant attempts have been made to redress the balance (see Keyser 1975, Cluver and Hotton 1981, Cluver and King 1983) and to break up genera into what could be more ecologically valid collections of species, and the time may not be far off when it may be possible to look at diversity changes in dicynodonts, at least, at the specific level. However, at the present time (and certainly for the rest of the therapsids) we must use another level. Another potential problem in carrying out studies of diversity changes at the species level is that members of one species may be known from only one fossil locality, presumably being absent from others because the ecological conditions in the various localities differ slightly. Many species may therefore be left out of the analysis because they lived in conditions not as conducive to fossilization as did others. Higher taxonomic categories are more likely to be found from more than one locality and so the effect is not so marked at supra-specific levels. This is the sampling problem referred to by Newell (1982).

Pitrat (1973) puts forward a positive reason for using supra-specific (indeed supra-generic) taxa. He suggests that carrying out diversity studies at the genus level might be inappropriate because vertebrate genera are so short lived anyway that the impression would automatically be gained that many forms became extinct at the end of every stage. As far as the dicynodonts are concerned, there is evidence that certain genera (*Diictodon*, *Oudenodon*) cross the boundaries of the time zones of the Late Permian. It is possible, therefore, that the apparent observation that vertebrate genera become extinct within stratigraphic stages may be the result of inadequate (or over-enthusiastic) taxonomy, rather than their being short-lived.

Olson (1982) feels that the family is the lowest practical taxonomic unit for investigation of diversity changes of Permo-Trassic non-marine vertebrates at present because of the problems of establishing a reliable database at the generic level.

As far as dicynodonts are concerned we cannot yet approach the ideal of counting numbers of individuals or species, because of the problems outlined above. However, we can look at changes in the diversity of genera with time with some confidence, because of the taxonomic work that has been done, but also because we are dealing with organisms from a fairly short span of time (the Late Permian to Early Triassic), and within a discrete geographical area (South Africa).

The methodology of the study involves counting all genera of tetrapods recorded from the Late Permian and Early Triassic localities of South Africa. These have been listed, locality by locality, in a work by James Kitching, published in 1977.

The Late Permian to Early-Middle Triassic in South

Africa may be divided (as Kitching 1977 did) into five stratigraphic units: *Tapinocephalus* Zone, *Cistecephalus* Zone, *Daptocephalus* Zone, *Lystrosaurus* Zone and *Cynognathus* Zone (Anderson and Cruickshank 1978). Alternative units have been proposed by other workers (see, for example, Keyser and Smith 1979) but the system used by Kitching will be followed here. Exactly where boundaries between zones are drawn is somewhat irrelevant to the present study. Ideally what is needed is continuous sampling of the record. Since this is not possible, it does not matter so much when the samples are taken, as long as they can be dated relatively. The fact that some dicynodont genera cross zone boundaries underlines the arbitrariness of the boundaries, as far as measuring changes in taxonomic diversity is concerned. Anderson and Cruickshank (1978) estimate the duration of the time Zones as approximately two million years. All five Zones span a period of time of approximately 256-243 MY (dates from Harland *et al.* 1982), i.e. 13 MY, which indicates that either gaps must exist between some of the zones, or their actual duration is different from that proposed by Anderson and Cruickshank. At the moment it is difficult to decide which is the case.

Where possible and necessary, obvious synonymies (after Cluver and King 1983 and King 1988) have been eliminated. The following histograms have been drawn for comparative purposes (figures 1 and 2): Total number of tetrapod genera per zone; Total number of therapsid genera per zone; Total number of therapsid genera as a percentage of total number of tetrapod genera per zone; Total number of herbivore genera (therapsid and non-therapsid) per zone; Total number of carnivore genera (therapsid and non-therapsid) per zone. In addition each genus has been placed within a size group based on the skull size of its constituent members: small (where skull length of members of the genus is <100 mm), medium (skull length 101-350 mm) and large (skull length >351 mm). This gives six different categories of genera: (small-, medium- and large-sized herbivores: small-, medium- and large-sized carnivores). The total numbers of genera in each of these six categories per zone are expressed as histograms in Figure 2A-F. Whenever terminology such as "medium-sized carnivore genera" is used below, the size descriptor refers to skull size of the individuals within that genus, not to any other attribute, such as number of species within the genus.

It must be remembered that each total number of genera per zone given is the total for a whole zone, not for any particular point in time within it. The total number of genera recorded from any one zone did not necessarily all live at the same time: some may have succeeded others in time. This aspect of diversity change cannot be investigated until smaller stratigraphic units, and the fossils which they contain, can be recognised consistently.

POTENTIAL SOURCES OF ERROR

If the pattern of diversity changes seen in the fossil record is to be taken as a reflection of the real diversity changes which were happening when the animals in question lived, then certain potential errors must be recognised and, if possible, taken into account, as discussed by Newell (1982) and Raup & Boyajian (1988), *inter alia*.

First, there may be biases in fossil preservation. Large animals may not be so liable to fossilize as small forms, or *vice versa*. Those living in burrows or along the edges of water courses may fossilize more easily than upland forms. For example, the Late Permian dicynodonts *Diictodon* and *Cistecephalus* are both very common. *Cistecephalus* has been interpreted as a digging form (Cluver 1978) and *Diictodon* is implicated in building burrows (Smith 1987) and these habits might therefore account for the abundance of numbers of individuals of these genera. Similar reasoning could be applied if it emerged that there were also large numbers of species of these two genera, or large numbers of genera which were fossorial.

Secondly, there may be collector biases. If specimens from museum collections are being investigated it must be borne in mind that collectors in the past may have looked more diligently for fossils from a certain taxon or from a certain time zone.

Thirdly, it is possible that different time zones may be exposed to greater extents than others and may therefore yield more fossils, in turn increasing the possibility of more taxa being recorded. We can make some elementary kind of correction for this by estimating the total area of exposure of each zone, and if they are very different, then perhaps expressing diversity per 100 square km, or a similar unit. Rarefaction analysis, which is designed to answer the ecological question of how many species would have been recorded if fewer specimens had been collected (Raup 1979), might also be applicable here.

In the context of stratigraphy there is also the more general problem of accurate stratigraphic correlation of different localities which is obviously crucial.

Fourthly, the taxonomy of the forms under investigation may present problems. In this particular study the genus level taxonomy of the tetrapods in question, particularly the non-dicynodont forms, is inadequate in parts. For example, there seems to be a preponderance of carnivore groups, probably due to the overclassification (splitting) of gorgonopsian and therocephalian mammal-like reptiles. This kind of effect could be due to active research interest in the group: one would expect that the more intensively a group has been worked on, the more new specimens that might be found, and the more new taxa erected. The apparent diversity of a group may simply be a reflection of the fact that it has been well-studied. However, Raup & Boyajian (1988) note that although such bursts of activity affect the number of taxa described, they do not affect the overall shape of the diversity curve, at least for the brachiopod genera used as a test case by Grant (1980).

But in general, we must ask whether the taxonomy

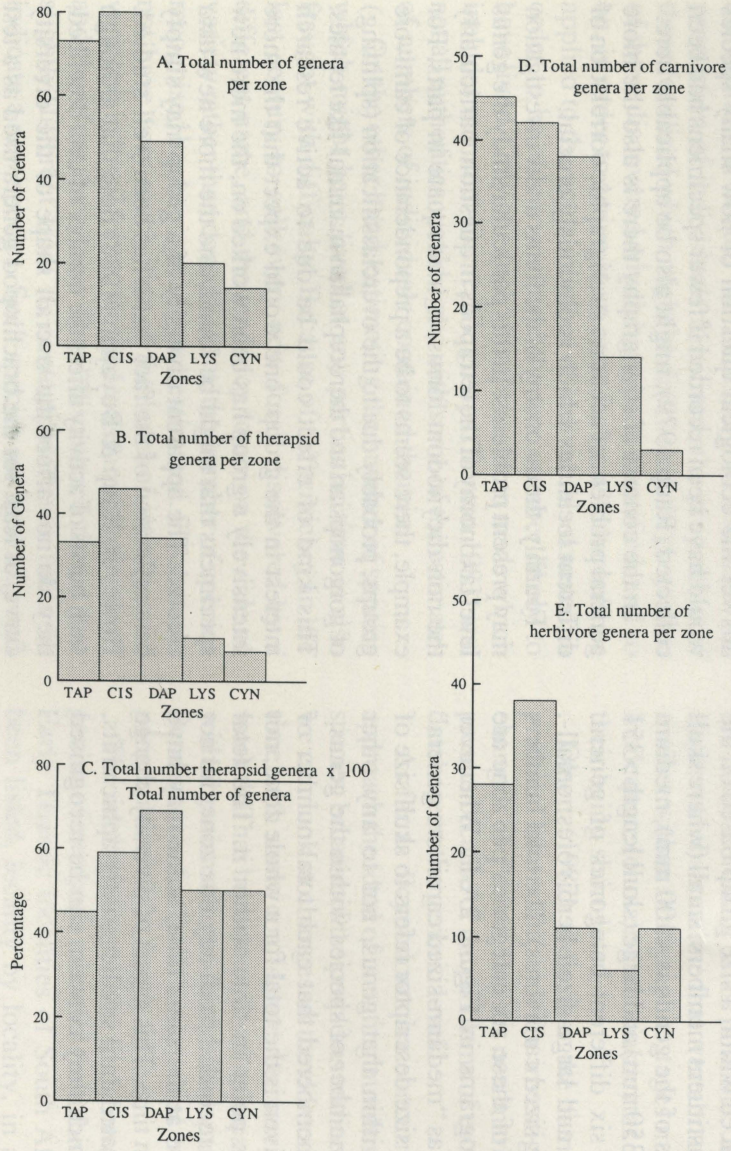


Figure 1: Histograms showing the total number of genera per biostratigraphic zone for various tetrapod groups. TAP=*Tapinocephalus* zone, CIS=*Cistecephalus* zone, DAP =*Daptocephalus* zone, LYS=*Lystrosaurus* zone, CYN=*Cynognathus* zone

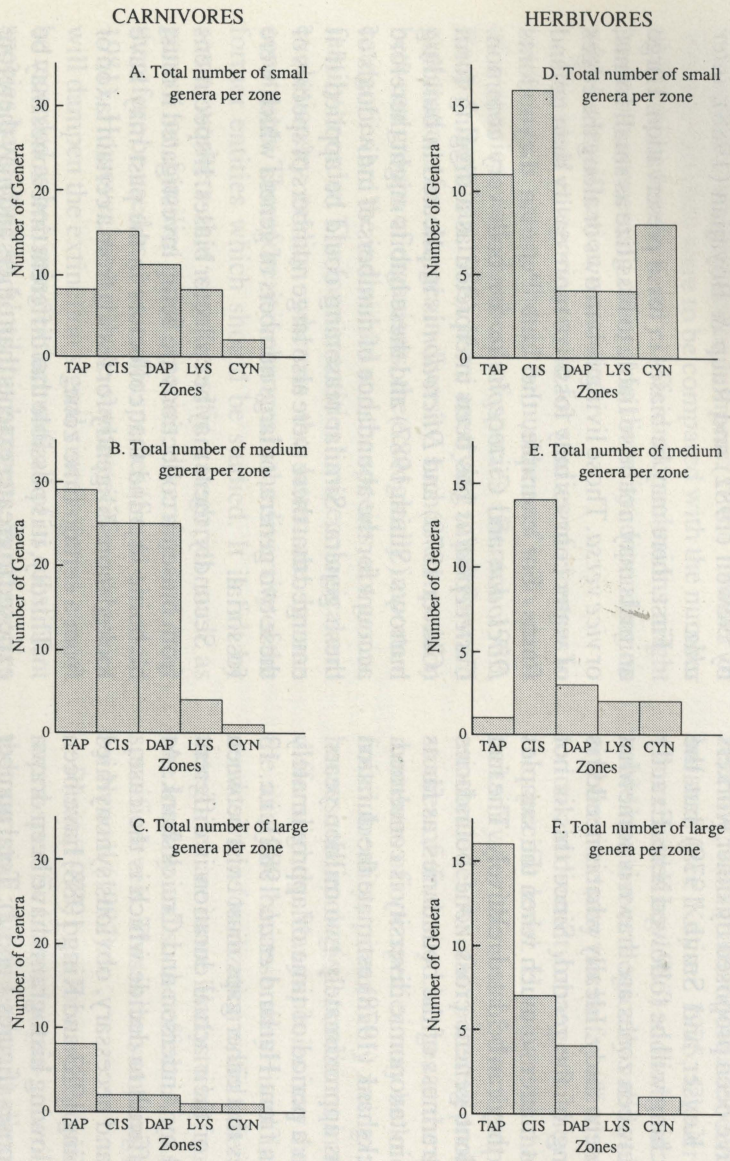


Figure 2: Histograms showing the total number of genera per zone for certain size ranges of carnivorous and herbivorous tetrapods Abbreviations as in Figure 1.

employed for various groups is reliable. If one taxon appears to become extinct at the end of one Zone, can we be sure that it has not simply been misidentified as something else in the succeeding zone, giving a false record of extinction at the end of the earlier zone? Raup & Boyajian (1988) make the point that palaeontologists are loth to carry taxa over boundaries, preferring instead to erect a new name. For this psychological reason also stratigraphic boundaries therefore become points of apparent extinctions.

Another taxonomy-induced error will arise from the inclusion of paraphyletic groups in the diversity analysis, i.e. those taxa which do not include all the descendants of their ancestor. For example, if a diversity analysis were being carried out at a fairly high taxonomic level and involving the taxon Therapsida, it would be misleading to consider the therapsids as having become extinct at the end of the Jurassic, since they would actually have evolved into mammals. This problem is probably much less important when dealing with lower taxonomic categories, such as the genus, but Patterson and Smith (1987) give a clear account of the difference which the inclusion of paraphyletic and polyphyletic families makes in the analysis of extinction.

Fifthly, there is the problem that some groups of organisms seem to have inherently higher or lower rates of extinction than others. If these formed a large proportion of the diversity sample from any one time, this would obviously distort the picture obtained. This error becomes more severe the more taxonomically wide-ranging the collection of organisms is that is used in the analysis, since physiological and genetic differences, which may influence rate of extinction, are liable to be so much more different between taxonomically diverse collections of organisms. In the present study the majority of organisms are amniotes of a reptilian grade of organization, and it might be expected that the individual intrinsic rates of extinction of the taxa would not vary too much.

Apart from these more general problems which arise with diversity analyses, there are also some problems which are specific to the particular project outlined here.

First, the identification of forms as herbivores and carnivores in this study is very tentative, often based only on tooth morphology. In many cases too little functional information is available to permit a reliable categorization. But in any case the broad division into herbivores and carnivores is itself very crude. It neglects forms which are omnivorous or which might change strategy depending on season.

Secondly, the skull size of many forms can only be estimated, as adequately preserved and prepared material is not available.

Thirdly, some of the ecological categories used, such as large herbivores, may contain very few genera, and it is therefore difficult to know how significant trends in these groups actually are.

Lastly, the present study may be too dependent on Kitching (1977), which may no longer be a totally comprehensive list of Karoo forms. This is, perhaps, one of the more easily corrected errors.

INTERPRETATION

Figure 1 shows changes in generic diversity in various tetrapod groupings. Several points are noteworthy: 1. All groups apart from carnivores (Figure 1D) experience an increase in generic diversity in the *Cistecephalus* Zone compared to their levels in the *Tapinocephalus* Zone. 2. Between the *Daptocephalus* and *Lystrosaurus* zones (crossing the Permo-Triassic border) all groups experience a drop in diversity - in some cases a dramatic drop, as in the carnivore groups (Figure 1D). 3. However, in all cases this is a continuation of a decrease in diversity which is apparent between the *Cistecephalus* and *Daptocephalus* Zones. It is interesting that therapsids would appear to constitute a greater percentage of tetrapod genera at this point. In other words, other tetrapods must have experienced a greater decrease in diversity. 4. Furthermore, the decrease in diversity continues into the Triassic, as witnessed by the difference in number of genera recorded for the *Lystrosaurus* Zone and those for the *Cynognathus* Zone. This applies to all groups apart from the herbivores (Figure 1E).

In order to establish which of these trends might approximate to reality, and which are the results of the errors mentioned above, it is necessary to take a close look at the kinds of organisms involved. One way of doing this is to break up the herbivore and carnivore genera into size ranges of individuals, as noted earlier. This will enable us to assess taxonomic and preservational biases to a certain extent, and will also permit an attempt at explaining the trends which might be left.

Figure 2 shows changes in diversity in different size groups of herbivores and carnivores.

Figure 2A shows that small-sized carnivore genera follow the general trend seen for all tetrapods (Figure 1A) which is an initial increase in genera, followed by a sustained decrease into the *Cynognathus* Zone. No obvious taxonomic corrections suggest themselves for this histogram. This is not the case for Figure 2A, which illustrates the total number of medium-sized carnivore genera. It is almost certain that the numbers for the first three zones are much too high, reflecting the prepoderance of over-classified therocephalians and gorgonopsians in these zones (gorgonopsians are extinct by the *Lystrosaurus* Zone, and therocephalians much rarer). The dramatic drop between *Daptocephalus* and *Lystrosaurus* zones for this category may therefore be an artefact. There was no doubt a drop in diversity, but it was probably not as significant as the histogram would suggest. A more accurate representation obviously awaits further taxonomic revision of the forms involved. As far as Figure 2C is concerned no taxonomic corrections suggest themselves, but obviously large carnivores are rare in the environment so the significance of the details of the trend seen in this histogram is hard to judge, because of small sample sizes. The same would apply to large

herbivores (Figure 2F).

Some interesting trends are seen in the herbivorous groups (figs 2D-F). The total number of small-sized herbivorous genera per zone (Figure 2D) requires a small correction to the numbers in the *Cistecephalus* zone. These genera are nearly all dicynodonts, some of whose taxonomy has not been rigorously reassessed. However, the correction required should be fairly small, not of the same proportions as that of the medium-sized carnivore genera. The general trend in small herbivores, an initial decrease then a reasonable drop followed by a modest recovery, is probably quite accurate.

Another correction is probably required for the medium-sized herbivore genera in the *Cistecephalus* Zone (fig. 2E). Again it would be a modest correction, necessary because the medium-sized dicynodont genera of this zone also require some taxonomic refinement. Similarly, large-sized herbivore genera (fig. 2F) of the *Tapinocephalus* Zone are probably over-estimated. The main component of this group is the dinocephalians, and the taxonomy here leaves something to be desired. The overall trend in large herbivores, a sustained decrease, may be fairly accurate, although the previous caveat concerning small sample size must be borne in mind.

With these provisos in mind, what, if anything, do the observed trends noted above tell us about overall changes in diversity at the end of the Permian?

The general consensus of opinion is that the mass extinction at the end of the Permian is the most far-reaching of all such events. However, despite a detailed treatment of the marine invertebrate fossil record, very little analysis has been carried out on terrestrial tetrapods at the end of the Permian. Exceptions are papers by Pitrat (1973) and Olson (1982, 1989).

Pitrat (1973) analysed diversity at the family level and suggested that the effects of the end-Permian event were confined mainly to marine organisms, those on land or in fresh water suffering less. He makes the point that one of the enigmas of this event is that a large number of mammal-like reptiles suddenly appear and disappear at the end of the Permian in Africa. Pitrat suggests that this is due to local factors. He says (quoting Parrington 1948 and Cox 1967), for example, that the end Permian faunas contain a sizeable upland component which is missing from the first Triassic faunas, suggesting therefore that organisms are preserved abnormally well at the end of the Permian. It would be interesting to see if this were also true for contemporaneous faunas from other parts of the world. It also begs the question of how upland faunas are recognized and why they were preserved (if indeed they were) at the end of the Permian. Was it because such environments were much more common or is it simply a random effect?

Pitrat also draws attention to the fact that the very large number of recorded first appearances for reptiles at the end of the Permian is in great contrast to that for marine organisms which was at an all time low during that stage.

The figures presented here suggest amendments to these views in several ways: Reptile diversity begins to decrease earlier than the last stage of the Permian. Decrease in the number of genera is apparent between the *Cistecephalus* and *Daptocephalus* zones as well as between the *Daptocephalus* and *Lystrosaurus* zones. If there is evidence of organisms preserving abnormally well it actually comes from zones earlier in the Late Permian.

Pitrat comments on the abnormally high rates of first-known and last-known appearances of reptiles at the end of the Late Permian, while the figures presented here are for the total number of genera per zone. However, if the total first-known and last-known appearances are investigated, while it is true that the former is high within the *Cistecephalus* Zone and drops within the *Daptocephalus* Zone, the number of last-known appearances decreases during the *Cistecephalus* Zone. The trend is not a simple one (these data will be presented elsewhere).

Olson (1982) looks at changes in family level diversity of non-marine tetrapods during the Permo-Triassic transition. He gives only two data points for the time span with which we are concerned here, the Late Permian (or Upper Permian in his terminology), which amalgamates all records for 245-235 MYBP; and the Lower Triassic, which amalgamates all records for 235-218 MYBP (Olson's dates, from Waterhouse 1978). His data derive largely from Romer (1966), with some modifications to take into account subsequent work. He presents histograms which show that the number of reptile families increases from the Middle to the Upper Permian, and then decreases again in the Lower Triassic. Family diversity of therapsids increases from the Middle Permian to the Upper Permian, then decreases sharply from the Upper Permian to Lower Triassic, and a continuing decrease is shown through the Middle and Upper Triassic.

Since the generic analysis of the present paper contains three points rather than one used by Olson for the Late Permian, it can be seen that decline of therapsids during this period of time does not follow a simple trend (Figure 1B). The number of therapsid genera first rises (*Tapinocephalus* to *Cistecephalus* zones), then decreases (*Cistecephalus* to *Daptocephalus* zones). This decrease is sustained into the *Lystrosaurus* and *Cynognathus* zones.

In his interpretation of the trends seen in his data, Olson makes the point (re-iterated in Olson 1989) that many of the early therapsids were large, and that these forms, including the dinocephalians, anomodonts, gorgonopsians and primitive therocephalians, dominated the middle and upper Permian faunas. He suggests that large size was a factor in the severe losses of these forms in the Upper Permian, since large size tends to increase vulnerability to changes in the environment. We shall return to this contention below. For the time being it is necessary to see whether Olson's observations that large

therapsids dominated the upper Permian faunas hold for the data obtained from South African Late Permian tetrapods. Figure 2 shows that there is no fossil evidence to substantiate this claim as far as carnivores as concerned (fig. 2A-C): there are many more genera of small- and medium-sized genera in the Late Permian. As far as herbivores are concerned, Figure 2D-F shows that there was a preponderance of large forms in the *Tapinocephalus* Zone. This is due to the presence of the herbivorous dinocephalians, and has already been commented on. However, in succeeding zones, small- and medium-sized herbivore genera outnumber large forms. It is hard to substantiate Olson's contention that Late Permian faunas were dominated by large forms.

The main conclusions from the present study are that there is no overwhelming evidence for a dramatic extinction event at the end of the Permian. Decrease in diversity occurred, but this trend had actually started much earlier than the latest Permian – perhaps as much as eight million years before the conventional placing of the Permian boundary. Large reptiles (both herbivores and carnivores) start to decline from the *Tapinocephalus* Zone, and the same is largely true for medium carnivores. Small carnivores show a gradual decline which continues through the Permian boundary and the same is true for small and medium herbivores, except that their decrease in diversity between the *Cistecephalus* and *Daptocephalus* zones is probably more marked.

EXPLANATIONS

Is it possible to offer any explanation for the decrease in diversity of mammal-like reptiles, and more specifically, dicynodonts, at the end of the Permian? Apart from stochastic events, three broad kinds of explanation are possible: 1. Dicynodonts were badly adapted in some way. This explanation would include ideas that the group was racially senescent, inferior to competitors because they were over-specialized, and so on. Such explanations tend to be dismissed nowadays. The concept of an organism's becoming too badly adapted to survive, becoming over specialized, goes against our understanding of the mechanism of neo-Darwinistic evolution. We may argue that changes in the environment might have made adaptations inappropriate, but not that dicynodonts were "over specialized". 2. Changes in the environment, either caused by interactions with other organisms, or from physical environmental change, affected the fitness of dicynodonts. Implicit in the concept that organisms interact has been the suggestion that one group might outcompete another group whose environment it shared. This suggestion is thought to be dubious, as Benton (1983) has shown, relying as it does on an unsound understanding of ecological competition. However, even if the concept were sound, there is no direct evidence of another group of herbivores arising in the Late Permian and outcompeting dicynodonts. At the points at which dicynodonts suffer their largest decreases in diversity there are no obvious herbivorous competitors taking over dicynodont niches. Rather, herbivores such as cynodonts and rhynchosaurs arise later and occupy niches either left vacant by dicynodonts, or more realistically, created by the environmental changes which led to the decrease of dicynodonts. 3. Changes in the physical environment are therefore left as the most reasonable explanation of dicynodont decrease in diversity. Certainly during the later part of the Permian there were obvious changes in climate, flora and so on which would have had an impact on the fate not only of dicynodonts, but also other Late Permian terrestrial organisms. The coalescing of Pangaea at the end of the Permian must have had far-reaching effects on the physical environment, affecting climate, topography, and the organisms present. In this sense, continental movements could be seen as the ultimate cause of change in diversity of dicynodonts, but this is still a long way from being an explanation which is able to sort out individual causes of extinction for individual groups or communities of organisms. We may be able to gain a greater understanding of such processes by looking at the fates of the different ecotypes identified earlier.

At the present stage of study it is only worth offering some general suggestions. If it is possible to deal with some of the errors mentioned above, then it may be possible to refine the suggestions and present more detailed explanations. Let us assume that some widespread and irreversible change in the physical environment, for example some climatic change, was occurring during the period from the Late Permian to the end of the Early Triassic. Dicynodonts (and, of course, other organisms) could respond in three kinds of ways to this change.

First, they might possess the ability to switch their behaviour to make use of the changed conditions. In other words, the habitat changes, but the organism is generalized enough to cope more or less unchanged. An example of such a response is provided by the urbanization of foxes or gulls, which capitalize on new sources of food without much modification.

The second response to an irreversible change is the ability of a collection of organisms to produce a variant of itself which can cope better with the changed circumstances. We usually envisage this culminating in the process of speciation. In this situation, the environment changes and the organisms also change.

The third response is that, faced with an environmental change, organisms are not generalized enough to switch to new food sources, etc., nor are they able to speciate, so they become extinct, either locally or globally.

Which kind of response did dicynodonts show? It is obvious from the data presented that, whatever the change that was taking place, large organisms coped less well with it; both large carnivore and herbivore genera show a gradual decrease in diversity, starting in the *Tapinocephalus* zone (Figure 2C,F). This indicates that some of these genera were becoming extinct without others replacing them. It could be argued that this was because as large specialists they could not exploit changing

niches so readily, not only because of their adaptations, but also because they had longer generation times and therefore did not produce variation at an appropriate rate to cope with changes. They would be unable to make either of the first or second responses to environmental change. Olson (1982: 509) sums this up by stating that large size tends to increase vulnerability to changes in the environment.

However, the evidence that organisms with longer generation times (which tends to be the larger forms) speciate less rapidly than those with higher generation turnover, is far from clear-cut (Vrba 1980: 76). Furthermore, Vrba quotes examples where specialist environmental adaptation is correlated positively with speciation rate, whereas flexibility is associated with a low speciation rate. On the other hand, Kochmer & Wagner (1988), quoting Van Valen (1973), suggest that taxa comprising small individuals do tend to have more species than taxa comprised of large organisms. They explain this by suggesting that the number of ways of life available to smaller organisms is greater. This would make the first response easier for such organisms, presumably, implying that larger organisms would respond less easily in this way. The question seems far from settled and it is possible that more refined fossil data would permit a better analysis of the situation.

For whatever reason the large forms became extinct, the environmental change causing that extinction opened up new niches into which small and medium sized forms radiated during the *Cistecephalus* Zone. However, as the changes continued, eventually even the small and medium forms could no longer adapt and some became extinct (figs 2A,B,D,E). However, it seems that smaller forms did not cope quite so badly with the environmental change as did larger ones. It is possible to envisage these forms being more opportunistic because of their small size, and also the environment offering more niches for smaller sized animals, as suggested by Kochmer & Wagner (1988) for passerine birds. In addition they may have been able to speciate more readily because they required smaller or less permanent barriers to reproduction.

Small herbivores increased most quickly after the environmental change (Figure 2D). Again this might be expected if they were more opportunistic and could speciate readily. It would also be expected that the small carnivores would follow suit. Here we see the obvious difficulty in interpreting these data in this way: the explanation for lack of small carnivore diversification could be that the general thesis is wrong and that smaller animals do not, in fact, always recover more quickly than large ones after an environmental change. But it could also be that the fossil record is less adequate here than for other forms, or that the small forms in question have been incorrectly categorized as herbivores and carnivores. Only further taphonomic and functional-anatomical data will permit us to distinguish between these alternatives.

CONCLUSIONS

The present study illustrates that the concept of a rapid and dramatic drop in diversity at the end of the Permian is difficult to sustain from the evidence presented by South African mammal-like reptiles, in particular, the dicynodonts. The changes in diversity were not simple and seemed to be occurring over a period of some millions of years before the end of the Permian. This view of the end Permian event corresponds with Newell's (1982) conclusions on mass extinctions. He notes that in general, mass extinctions were spread over millions of years and can be considered catastrophic only in the sense that the disappearance of the last members represents the final step in an accelerating downward trend in diversity.

However, Signor & Lipps (1982) argue that this appearance of gradual extinction could be an artefact of either sampling error or artificial range truncation of taxa, and that gradual extinction patterns prior to mass extinction need not necessarily rule out catastrophic hypotheses. Sampling error would be introduced if the exposure of fossil-bearing sediments diminished nearer the extinction event, yielding fewer fossil forms, and therefore fewer taxa. This could presumably be corrected for by estimating the area of sediments for different time zones. Artificial truncation of ranges of fossil forms is introduced because the last preservational occurrence of a fossil may antedate its last biotic occurrence. In other words the form may have lasted longer than the fossil record says it does. This error obviously becomes greater the poorer the fossil record is and will be particularly severe for forms which become extinct during a marine regression, since no deposits of marine sediments would be deposited on continental areas.

In order to resolve arguments of this kind, more detailed and reliable databases are necessary. The present study perhaps highlights more about what we do not know about the fossil record, rather than what we do know. If the fossil record is to be used to document trends in evolution, much better taxonomic, stratigraphic and functional studies are required before it will be possible to draw conclusions concerning the causes of changes in taxonomic diversity.

Despite this, the present study shows that the time is approaching when we might be able to document change more reliably at the specific level, and also to look at the different responses made by different ecotypes to environmental change.

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