Incompleteness of the Permian–Triassic fossil record: a consequence of productivity decline?

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Analysis of published data shows that, for most animal groups, the fossil record in the immediate aftermath of the end-Permian biotic crisis is less complete than during the Late Permian or Middle Triassic. Completeness is measured by the Simple Completeness Metric. The interval of poor quality fossil record spans the entire Lower Triassic and may have serious consequences for our perception of the magnitude of the end-Permian event. A model is presented which seeks to explain this phenomenon. There is abundant evidence that levels of primary productivity were severely reduced in the very latest Permian. In response to this, animal biomass must also have been reduced. The biomass of a particular taxon is the product of the size of individual organisms multiplied by the number of individuals. Those taxa that reduced population size, but maintained original body size, would tend not to be preserved (apparent extinction) and would also be more prone to 'real' extinction. Those taxa that retained large population sizes, but reduced body size, would resist extinction and would also maintain their presence in the fossil record. One testable prediction is that taxa present in the fossil record in the immediate aftermath of the end-Permian crisis will have smaller body size than their pre-event relatives, regardless of their initial size. Anecdotal evidence supports this prediction. Such a biomass reduction model may also be applicable to other mass extinction events. Copyright © 2001 John Wiley & Sons, Ltd.

1. INTRODUCTION

Most palaeontologists would concur with the view that during the Phanerozoic there were five major episodes of mass extinction, of which the end-Permian event was by far the largest. However, proving when an organism became extinct is difficult, if not impossible. Typically, a taxon will appear in the fossil record, and then disappear for any number of years, only to reappear again, apparently unchanged, in younger strata. A taxon that has temporarily disappeared from the fossil record is termed a Lazarus taxon (Flessa and Jablonski 1983). Originally, this term was coined for taxa that disappear during mass extinction events, although it has been applied to taxa at intervening times as well. For example, the proportion of Lazarus taxa present in a particular stratigraphic interval has been used as a measure of completeness of the fossil record of that interval. This is the Simple Completeness Metric (SCM) of Benton (1987): the more Lazarus taxa that are present in a particular interval, the less complete is the fossil record.

Thus, disappearance from the fossil record does not always imply extinction. Crucially, this applies even if the taxon in question never reappears in younger strata. There are numerous examples of extant taxa that last appeared in the fossil record many millions of years ago and which were once thought to be long extinct. Famous examples include the extant coelacanth family Latimeriidae, which was last recorded in the Campanian (Benton 1993, p. 661). Coope (1995 and references therein) lists a large number of Quaternary beetle species that were thought to be extinct on the basis of their fossil record, prior to the discovery of living populations.

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While it is clear that the vast majority of fossil taxa have indeed become extinct at some point in time, it may not have been at the moment when they disappeared from the fossil record. This has caused a number of authors to question whether mass extinction events really record periods of global diversity decline or whether they are merely the result of the vagaries of the fossil record.

Many such questions concerning the potential biases in the fossil record were raised in the 1970s (e.g. Raup 1972; Sheehan 1977; Signor 1978), but in recent years a general consensus has been reached that the diversity plots of Sepkoski (e.g. 1982) represent a realistic estimate of Phanerozoic diversity. The problem of equating last occurrence with extinction has not gone away, however, although the application of statistical methods for placing confidence limits on taxon durations (e.g. Marshall 1994) is one possible solution. Even when statistical methods are available, however, they are rarely applied objectively. One recent study of the end-Permian event noted that if 95% confidence limits were applied to taxon durations, the vast majority of taxa would not become extinct until maybe a million years after the traditional extinction horizon; a 50% confidence interval was therefore chosen by the authors for their subsequent analyses (Jin *et al*. 2000). Such statistical approaches assume that fossilization potential remains constant throughout the section studied. Other studies have shown that first and last appearances of marine taxa often cluster at specific horizons (e.g. transgressive surfaces) and are possibly linked to sea-level changes (Holland 1995).

In this study, I will show how the fossil record in the aftermath of the Permian–Triassic (P–Tr) event is less complete than the fossil record of the Late Permian or Middle Triassic. This may be the result of the mass extinction event, as has recently been claimed (Wignall and Benton 1999), or it may have some other cause. Variations in completeness of the fossil record are potentially very worrying as they can affect our perception of the magnitude of extinction events. I will go on to describe a model which may explain these, and other, observations of the P–Tr fossil record and show that similarities exist with other extinction events.

2. COMPLETENESS OF THE P–TR FOSSIL RECORD

There is growing evidence that the end-Permian event, the 'mother of mass extinctions' (Erwin 1993), was also followed by a 'fossilization low' for most marine animal groups (e.g. Twitchett 2000b).

Following the work of Batten (1973), this phenomenon was documented recently by Doug Erwin, who showed that the Permian–Triassic gastropod fossil record is strongly affected by preservation (Erwin and Pan 1996; Erwin 1996). The data (Figure 1) clearly show an increase in the numbers of Lazarus taxa through the Lower Triassic, which is attributed, in part, to the complete absence of silicified faunas during this interval. Some of the Lazarus taxa are known solely from silicified faunas, while others are difficult to identify without well-preserved (i.e. silicified) specimens (Erwin 1996). In addition, the Late Permian gastropod record has been significantly enhanced by data from well-studied, silicified assemblages of China (Pan and Erwin 1994). A mere 31% of genera known to be present in the Griesbachian are represented by actual fossils, compared with 67% in the latest Permian Changxingian Stage (Figure 1).

Data from *The Fossil Record 2* (Rigby *et al*. 1993) show that a similar pattern is seen in the fossil record of the Porifera (Figure 2). Here, only 10% of those families that must have been present in the Early Triassic are known from actual fossil specimens: 90% are Lazarus taxa. In contrast, 46% of Changxingian taxa have a fossil record, and by the time we get back to the Capitanian this has increased to 66%. Similar figures are found in the Middle and Late Triassic stages (Figure 2).

The lack of 'intervening' data for the family ranges of other groups in Benton (1993) makes compilations such as Figure 2 more difficult for other groups. However, if we turn to the bivalves, according to the data of Skelton and Benton (1993) some 38 families must have been present in the Early Triassic. Personal observations (work in progress) show that only nine families (24%) have a Griesbachian fossil record. This figure rises to 36% by the Spathian. In contrast, at least 50% of Late Permian and Middle–Late Triassic families have a fossil record.
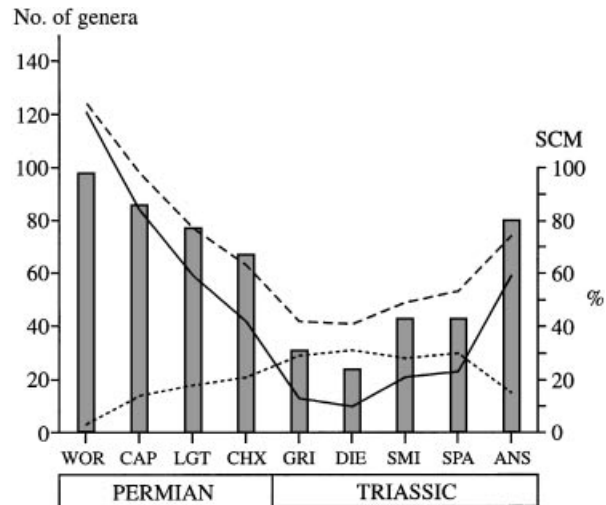
Figure 1. The changing diversity of gastropod genera through the Permian–Triassic interval. Solid line shows number of taxa present as fossils; dotted line shows number of Lazarus taxa; dashed line shows total diversity (sum of other two lines). Shaded bars show the Simple Completeness Metric of Benton (1987) calculated for each stage. Stage abbreviations from Benton (1993). Data from Erwin (1996).
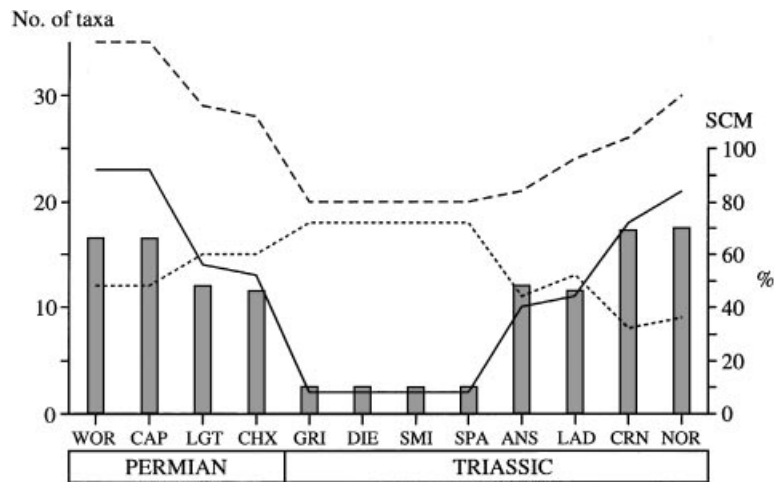

Figure 2. The familial diversity of the Porifera through the Permian–Triassic interval. Key as in Figure 1. Data from Rigby *et al.* (1993).

3. MASS EXTINCTIONS AND THE LAZARUS EFFECT

It has been demonstrated above that relatively more Lazarus taxa are known from Lower Triassic strata than from the Middle–Upper Permian or Middle–Upper Triassic deposits. Other studies have also shown that this effect is not uniform throughout geological time, but varies from stage to stage and group to group (e.g. Benton *et al.* 2000 and references therein). Can simple variations in the quality of the fossil record affect our perception of extinction events?

If we imagine a hypothetical set of taxa with hypothetical ranges then we can measure the diversity and calculate the number of taxa going extinct in each time unit (Figure 3a). This assumes that we have 100% fossilization throughout our 'fossil record'. If we now imagine that for some part of this record there is a period where none of the taxa are fossilized and recalculate the extinction rate, we see that a peak in extinction rate is present where
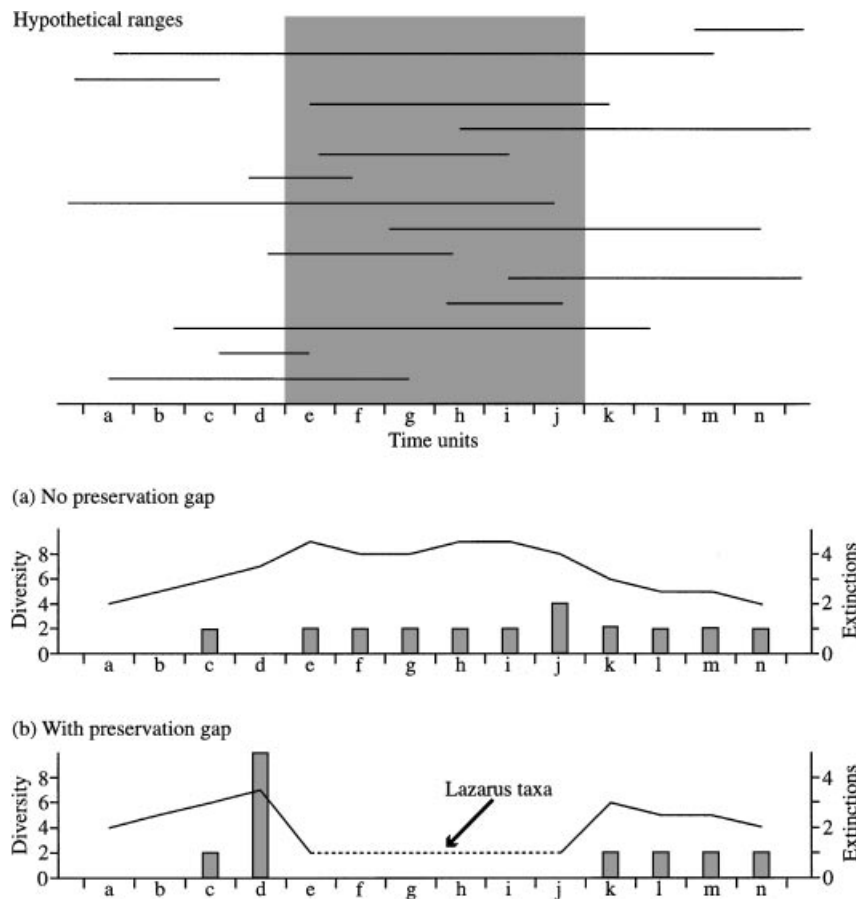
Hypothetical ranges

Figure 3. Thought experiment showing how the apparent diversity and number of extinctions of hypothetical taxa through time interval a–n varies when a gap in preservation occurs (shown by the shaded area). Solid lines show number of taxa apparently present; shaded bars show number of taxa apparently becoming extinct in each time unit.

none existed before (Figure 3b). An apparent extinction event has been created. It is possible to demonstrate that there is a 'fossilization low' because a number of Lazarus taxa are present where none existed before. The same thought experiment could be repeated for fossilization gaps where only 50% or 25% of taxa were fossilized and the results would be similar.

It is clear that as the duration of our 'fossilization low' increases, so does the extinction rate. Assume a fossilization gap where no taxa are preserved. Relatively short gaps (e.g. one time unit in Figure 3) would be characterized by large numbers of Lazarus taxa but little or no increase in extinction rate. However, as the width of the gap and the number of extinctions increase, the number of Lazarus taxa will tend to remain the same or even decrease. This is because to qualify for Lazarus status, the taxon in question must have a range that spans the fossilization gap. Thus, the most severe 'apparent extinction' events should be followed by relatively few Lazarus taxa (those of above-average duration) spanning a very long Lazarus interval.

4. THE END-PERMIAN EXTINCTION EVENT: REAL OR APPARENT?

The data so far presented show that changes in the quality of the fossil record have certainly occurred during the Permian–Triassic interval. For most fossil groups, the entire Early Triassic is a period of time characterized
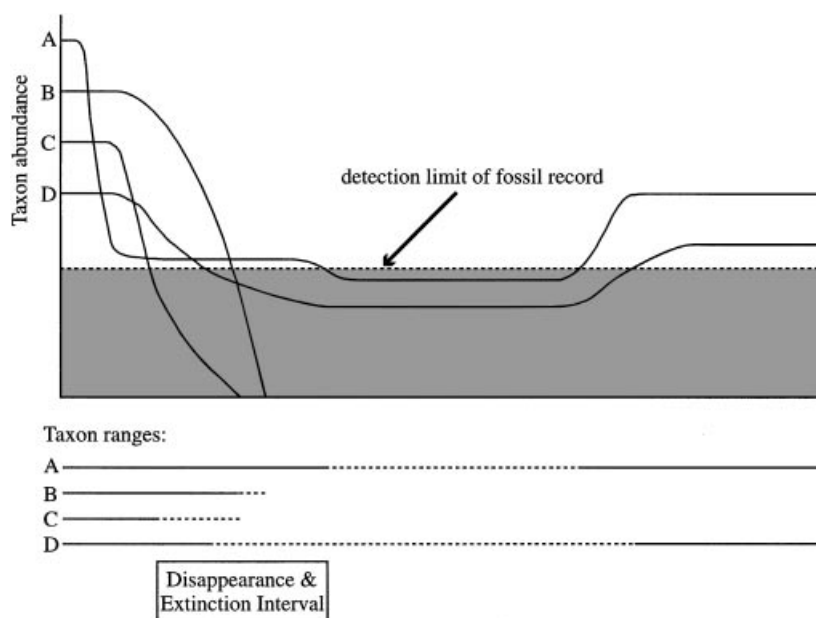
Figure 4. The Wignall–Benton model showing how taxon abundance may change during an extinction event. Redrawn from Wignall and Benton (1999), reproduced by permission of the Geological Society.

by increased numbers of Lazarus taxa and therefore a less complete fossil record. This is despite a huge increase in our knowledge of the P–Tr interval over the last ten years, with many new localities being discovered and studied worldwide. Is it possible that this fossilization low is responsible for creating an apparent extinction event? Or have these changes in completeness of the fossil record been caused by the extinction itself?

This latter view was recently argued by Wignall and Benton (1999) who proposed that the enhanced Lazarus effect after mass extinction events is due to a reduction in population sizes in the wake of the extinction crisis. This alternative explanation of the Lazarus effect was deemed necessary after the authors argued that it could not be explained by a lack of fossiliferous sites or fossil-bearing formations.

Wignall and Benton (1999) propose that a particular taxon will only enter the fossil record if its population size is above a certain threshold level (Figure 4). Presumably, this threshold will vary between taxa and different environments. Their model implies that taxa either become extinct or become Lazarus taxa as a result of population crash during an extinction event. While this is a very plausible scenario, it is equally possible that a non-lethal reduction in population size could create an apparent extinction event (Twitchett 2000a). This would happen if (i) the minimum viable population size is well below the threshold required for appearance in the fossil record, and (ii) if the period of low population size were long enough to allow for background processes to cause significant real losses (Figure 5). In this scenario, the 'disappearance interval' and 'extinction interval' are not the same. Unfortunately, Wignall and Benton (1999) provide no testable predictions for their idea, and no mechanism by which population size may be reduced during mass extinction events. It is thus impossible to directly test between the two alternative interpretations of the Wignall–Benton model (Figures 4 and 5).

5. POPULATION SIZE AND PRODUCTIVITY COLLAPSE

Assessing population size of fossil species is not possible. However, is there any evidence for a mechanism at work during the P–Tr interval that could, potentially, have led to a population crash? In general, animal population sizes
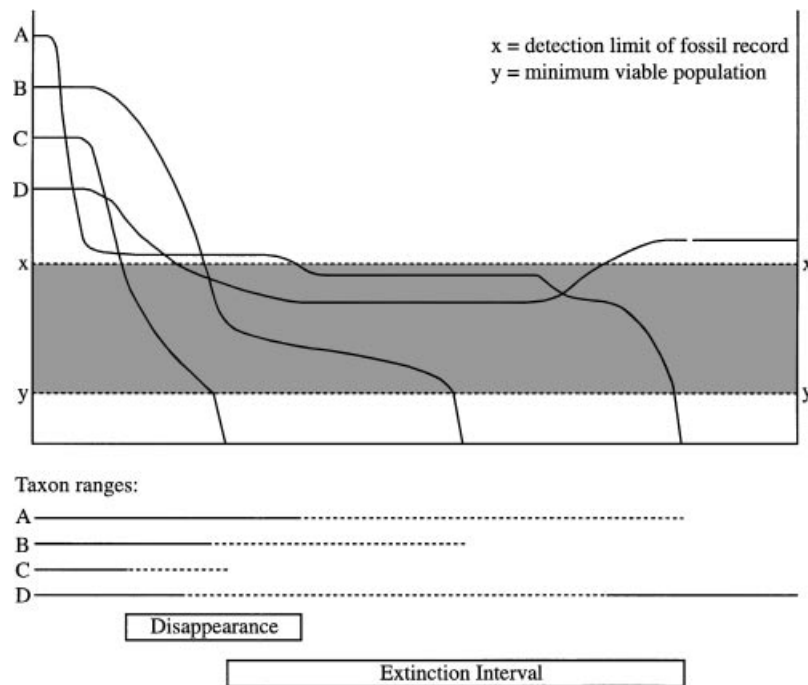
Figure 5. Alternative interpretation of the Wignall–Benton hypothesis. Taxa that disappear may not necessarily become extinct at the same time, but may persist below their fossilization threshold for an extended interval (cf. Figure 4).

fluctuate in response to pressures from predation, disease, habitat loss, environmental change or changes in food supply. There is no evidence that increased predation or disease occurred during the P–Tr interval. Likewise, the apparent extinction occurred during a time of sea-level rise (e.g. Hallam and Wignall 1997; but see Holland 1995), so the area of shallow marine shelf was probably increasing, not decreasing. There is, however, abundant evidence for environmental changes such as increased volcanism, global warming, marine dysoxia etc. (e.g. Erwin 1993; Hallam and Wignall 1997). Unfortunately, it is impossible to know precisely what effects these events would have had on population size.

On the other hand, there *is* ample evidence for decreased primary productivity (i.e. food supply) during the Early Triassic. Firstly, in every shallow marine section so far studied, the Lower Triassic marine sediments contain very little organic matter. This is despite the fact that for the most part these Lower Triassic sediments were deposited under low oxygen conditions (e.g. Wignall and Twitchett 1996) which would tend to promote the preservation of organic matter. Thus, if productivity levels remained constant, shallow marine Lower Triassic sediments would be expected to contain more, not less, organic matter than their Late Permian equivalents. For example, in East Greenland, oxygen-restricted Upper Permian sediments contain 3.0% total organic carbon (TOC), well-bioturbated (i.e. oxygenated) Upper Permian sediments contain 0.6% TOC, whereas oxygen-restricted Lower Triassic strata only contain 0.4% TOC (Surlyk *et al.* 1986, Table 1).

In addition, there is a negative excursion in $\delta^{13}C$ curve that may (at least in part) be a record of primary productivity collapse (e.g. Wang *et al.* 1994). This negative excursion has been found in all P–Tr sections so far studied (e.g. Baud *et al.* 1989; Erwin 1993; Hallam and Wignall 1997). Usually, the negative shift is of *c.* 2–3 ppm and spans at least the majority of the Griesbachian (e.g. Magaritz and Holser 1991). None of the sections so far studied shows a return to Late Permian levels before the end of the Lower Triassic (Baud *et al.* 1989). In some sections, the magnitude of the shift appears to be too great to be explained by productivity change alone, leading some authors to propose that gas hydrates may also have contributed to the excursion (e.g. Erwin 1993). However, larger-magnitude shifts are still consistent with models of Strangelove ocean dynamics (Kump 1991).

Other evidence for disruption to the ocean surface ecosystem includes the acritarch fossil record. In East Greenland, there is an acritarch gap coincident with the negative decrease in $\delta^{13}C$ (Twitchett *et al.* in press). During the remainder of the Lower Triassic, acritarchs generally show peaks and troughs in abundance associated with bloom and dieback in an unstable ecosystem (C.V. Looy, personal communication). Extinctions amongst the Radiolaria (Kozur 1998) also show that there was severe disruption to the planktonic ecosystem. Finally, oceanic stratification and stagnation (Isozaki 1997) would have hindered upwelling and nutrient recycling from the deep ocean. A relative dearth of Early Triassic marine phosphorites (Trappe 1994) shows that the phosphorus cycle, necessary for planktonic production, was behaving abnormally compared to Late Permian times.

There is even some evidence of a decrease in terrestrial primary productivity. A sharp 'fungal spike' is observed at all sections so far studied, which has been interpreted as evidence for massive dieback of the standing biomass (e.g. Visscher *et al.* 1996). No coals, and hence no high-productivity coal swamp ecosystems, are known from any Lower Triassic units (e.g. Retallack *et al.* 1996). In fact, terrestrial vegetation of the Early Triassic was composed entirely of small, scattered, herbaceous shrubs and true forests did not return until the late Spathian (Looy *et al.* 1999).

Under such a dramatic reduction in primary productivity there must have been equally dramatic reductions in the biomass of the higher trophic levels. The biomass of a taxon is the product of the body size of individual organisms multiplied by the numbers of individuals present. There are therefore three ways in which the biomass of a particular taxon may be reduced in response to a decrease in its food supply: either body size remains the same, but numbers decrease (Figure 6b); or the numbers remain high but size decreases (Figure 6c); or a combination of both.

In real biological systems it is probably easier and quicker to reduce biomass through population decline than by changes in body size. Thus most taxa would be expected to undergo changes in population size in response to a dramatic decrease in food supply caused by a reduction of primary productivity. However, taxa that suffer such a reduction in population size will be less likely to enter the fossil record (Figures 4 and 5). In addition, they will be more prone to 'real' extinction from such proximate causes as inbreeding, genetic deterioration and random catastrophe (e.g. Simberloff 1986; Lawton 1995).

As an aside, extant species that have undergone population decline tend to retract their range to one (or a few) core areas (Lawton 1995) rather than be 'distributed over a large . . . area' (Wignall and Benton 1999). If such a species managed to escape extinction, and subsequently increase its range and population, these core areas would represent the 'refugium' of this taxon. Hence refugia are a key part of a taxon's pre-crisis range and not places to which they flee in times of trouble (cf. Harries *et al.* 1996).

On the other hand, those taxa which are able to reduce biomass by decreasing individual body size, and are therefore able to keep population numbers high, will tend to escape 'real' extinction and also maintain their presence in the fossil record (Figure 6c). Thus, one prediction of the model outlined above is that if such a mechanism operated during the P–Tr interval, those taxa that are present as fossils in the immediate extinction aftermath should have smaller body sizes than their pre-crisis relatives, regardless of initial size.

This prediction has yet to be adequately tested. However, anecdotal evidence suggests that this may indeed be the case. The size of the *Hindeodus* conodont lineage shows a reduction in element size of approximately 50% during the P–Tr interval (e.g. Kozur 1996). The smaller, Lower Triassic species *H. parvus* has maintained its abundance and is the proposed biostratigraphic marker of the base of the Triassic (e.g. Yin 1994, 1996). The size of burrowing infauna (estimated by burrow diameter) also decreases by an order of magnitude through the P–Tr interval in western Tethys (Twitchett 1999). Burrows of pre-crisis size do not reappear in the sedimentary record until the uppermost Lower Triassic (Spathian). The exceptionally well-preserved fossil fish from East Greenland also appear to be much smaller than their late Permian counterparts (personal observation). Finally, many Lower Triassic faunas around the world seem to contain an abundance of 'small' taxa that often reach rock-building densities, e.g. the microgastropod pack-grainstones of the Lower Triassic of western Tethys (Assereto and Rizzini (1975) and references therein).

Could it be argued that small size in the Lower Triassic is a consequence of other environmental change rather than productivity collapse and food shortage? Given the widespread occurrence of dysoxic–anoxic facies in shallow marine Lower Triassic strata (e.g. Wignall and Twitchett 1996), an obvious candidate is oxygen stress.
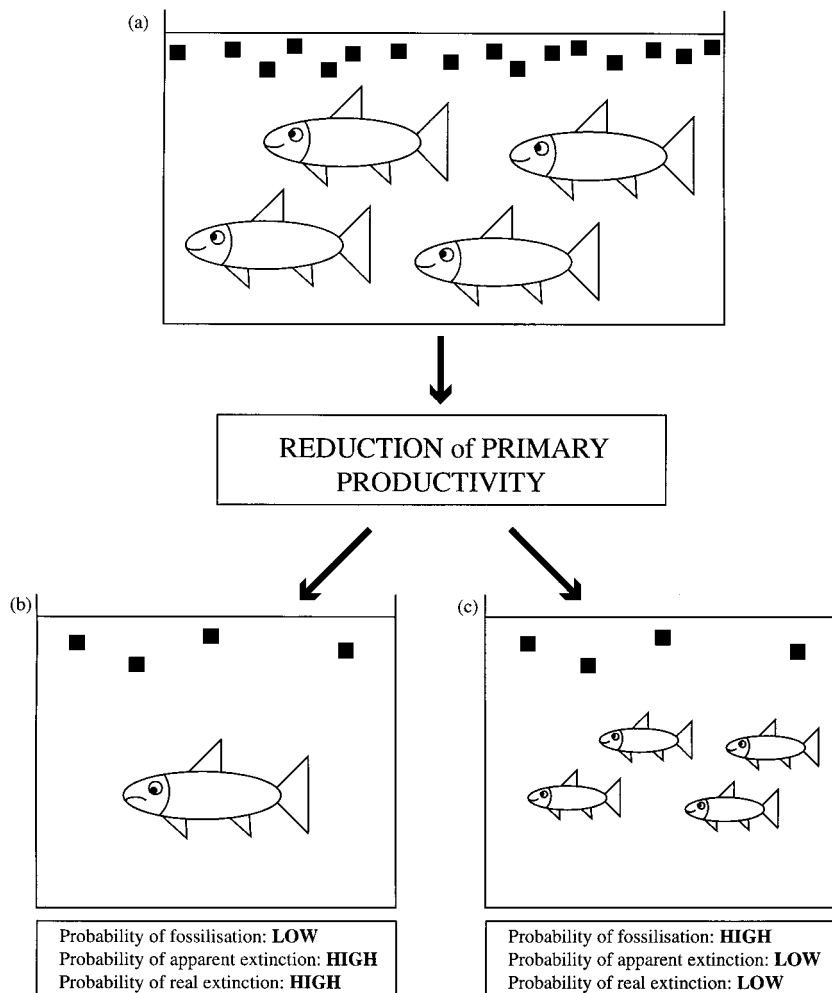
Figure 6. Biomass reduction in response to productivity collapse and subsequent effects on preservation potential. (**a**) Background conditions: high plankton productivity (black squares) supports large biomass of fish. Following productivity collapse, fish must reduce biomass either by reducing population size (**b**) or by reducing body size (**c**).

However, several lines of evidence suggest that low oxygen concentration is not the (sole) reason for body size reduction. Firstly, evidence for oxygen restriction is absent from post-Upper Griesbachian strata in shallow marine, Tethyan environments, such as the mixed carbonate–siliciclastic ramp settings of the Dolomites (e.g. Wignall and Twitchett 1996; Twitchett 1999). However, the trace fossil faunas do not begin to recover until the Spathian (Twitchett and Wignall 1996), and, despite a brief size increase in the Dienerian, burrow diameters do not reach pre-extinction levels until this time (Twitchett 1999). Taxa such as gastropods show no size increase until the Spathian (personal observation). Tiering of suspension feeders above the sediment surface does not increase until the Spathian (Twitchett 1999). Finally, benthic oxygen levels would not be expected to affect the pelagic fauna (fish and ammonoids), and if productivity levels were normal these taxa would show no size decrease. However, both groups of organisms appear to show similar size decrease through the P–Tr interval, with larger sizes only being reached after the Smithian–Spathian interval. Indeed, metre-sized fish (e.g. *Bobastrania*) are found in the Spathian–Anisian of Canada (J. P. Zonneveld, personal communication), in environments characterized by benthic oxygen restriction.

In summary, the P–Tr event is followed by a 'fossilization low' which spans the entire Early Triassic. There is also good evidence that primary productivity was severely reduced during this interval. The model described above (Figure 6) shows how the fauna would have responded to this crisis. Reduction in population size by some taxa would lead to increased risk of 'real' extinction as well as disappearance from the fossil record ('apparent extinction'). Evidence in support of this model is provided by (mostly) qualitative data that support one of the model's main predictions: that taxa present in the fossil record immediately after the end-Permian event should be smaller than their pre-crisis relatives. While it is probable that the end-Permian extinction event is the result of a mixture of real and apparent extinction, it is impossible to say which taxa really became extinct during the crisis and which became extinct at some subsequent point in time.

6. APPLICATION TO OTHER APPARENT EXTINCTION EVENTS

Available data show that all of the major extinction events, and most (all?) of the smaller ones, are followed by 'fossilization lows'. For example, Fara and Benton (2000, Figure 2) show that *every* extinction peak in the Callovian to Ypresian fossil record of tetrapods (including the end-Cretaceous peak) is followed by a 'fossilization low' as measured by an increasing proportion of Lazarus taxa. A similar pattern is seen in the tetrapod record for the Carnian–Norian and end-Triassic events (e.g. Wignall and Benton (1999) and references therein). Data compiled in Benton (1993) can be used to show that similar patterns of peaks in extinction followed by 'fossilization lows' occur in other groups as well. For example, data for the Porifera (Rigby *et al.* 1993) show that each mass extinction interval is followed by an extended period of poor preservation (Figure 7). Indeed, Lazarus taxa are so common after extinction events, that many workers have suggested that mysterious refugia must have been present which allowed safe havens for these organisms while the world collapsed around them (e.g. Vermeij 1986; Harries *et al.* 1996).

Currently, we have no way of knowing for certain whether or not these extinction peaks are 'real', or merely an artifact of the vagaries of the fossil record, or a combination of both. The biomass reduction model described above suggests a mechanism by which the Early Triassic marine 'fossilization low' may have been created. Could such a mechanism also operate during other so-called 'mass extinction' intervals?

The main predictions of the model are: (i) that fossil taxa in the immediate aftermath will be smaller than their pre-event ancestors; (ii) that the size of fossil taxa will increase as levels of primary productivity recover; (iii) that Lazarus taxa will reappear as primary productivity levels return to 'normal'. These predictions are equally applicable to terrestrial as well as marine ecosystems.

No published data exist to shed light on the latter two predictions, although data from Jackson (1995) strongly suggest that an *increase* in size amongst Late Tertiary Pacific molluscs follows an inferred *increase* in marine productivity. Regarding the first prediction: the observation that 'extinction events' are often followed by intervals dominated by fossil taxa of small size is fairly common. Indeed, so common is this phenomenon that it has been given a name: the 'Lilliput effect' (Urbanek 1993). It has been observed in Lower Silurian graptolites (Urbanek 1993) and corals (Kaljo 1996), the latter, especially, showing an association with dramatic changes in acritarch diversity and abundance (Kaljo 1996). A detailed study of several conodont genera through the late Devonian Kellwasser event shows that there is a marked reduction in size within surviving lineages (Girard and Renaud 1996). The authors of this latter study also suggest that food shortage following a decrease in primary productivity may have caused the observed size changes.

In summary, anecdotal evidence shows that the appearance of small body size is a fairly widespread phenomenon in the immediate aftermath of several so-called 'mass extinction' events. This suggests that all such events may be the result of primary productivity collapse causing changes to the body size and/or population size of the associated fauna. These changes will affect which taxa are fossilized in the aftermath of the event, and will lead to both 'real' and 'apparent' extinction. Therefore, in order to discover what ultimately caused a 'mass extinction' event, one should concentrate on possible causes of primary productivity collapse. Once the plants are taken care of, the animals will take care of themselves.
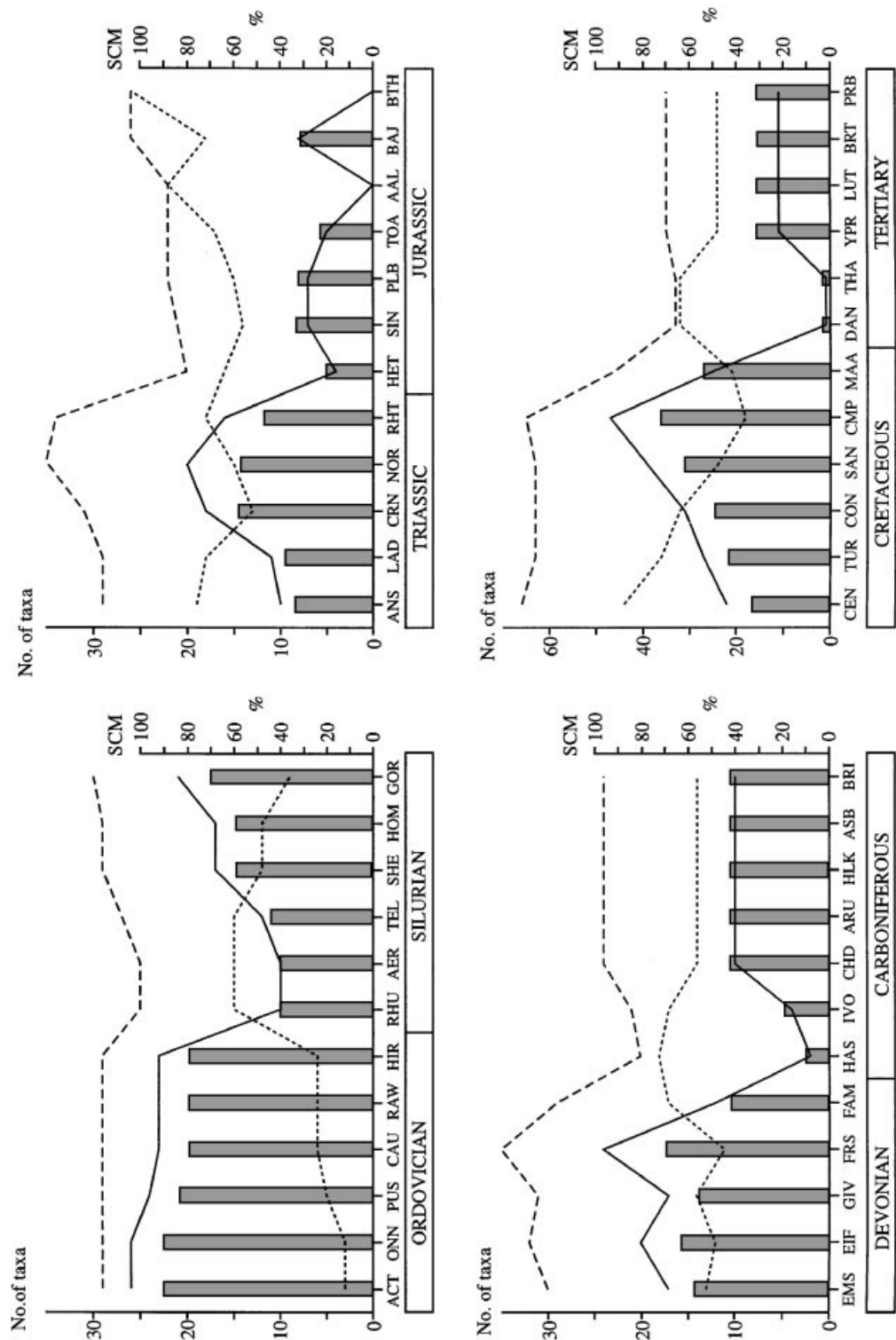
Figure 7. The familial diversity of the Porifera through the major Phanerozoic mass extinction events. Key as in Figure 1. Data from Rigby *et al.* (1993).

7. DISCUSSION

Body size affects virtually all aspects of an organism's physiology and ecology (Simberloff 1986). It is also an easy parameter to measure. These two factors mean that it is of major importance in palaeontological studies and a correspondingly sizeable literature has been produced (see Jablonski (1996) for a recent review).

One common claim is that (mass) extinction events are size selective; in particular, such events preferentially remove large-bodied taxa. Oft-cited examples include the end-Cretaceous extinction of the dinosaurs and the large rudist bivalves. How do these theories affect the model presented above?

In recent years several authors have shown that the issue is clouded by a lack of rigorous analyses (Raup 1995) and the fact that it is often difficult to factor out other important variables (e.g. geographic range) from such analyses (Jablonski 1996). Indeed, Jablonski and Raup (1995) have shown that because all rudists (even very small taxa) became extinct during the Cretaceous–Tertiary (K–T) event, the operation of clade-specific rather than size-specific mechanisms cannot be discounted. This same argument can be applied to the question of dinosaur extinction: all 'non-avian dinosaurs' became extinct at the K–T boundary, even those with very small body sizes (Jablonski 1996). Using a large, global database, Jablonski (1996) has shown that there is no statistical difference in the size of bivalve genera that survived the K–T event and those that became extinct. In addition, there is no statistical difference in the species longevity of large and small species of Cretaceous bivalves and gastropods (Jablonski 1996).

Thus, large taxa are *not* more prone to extinction than smaller ones. Yet, as we have seen above, taxa that are present in the immediate aftermath of apparent extinction events are all small (the Lilliput effect). The biomass reduction model outlined above explains these, apparently contradictory, observations because pre-crisis body size is irrelevant. All taxa that are present in the immediate aftermath of an apparent extinction event will be smaller than their pre-event relatives, *regardless of their original body size*. Taxa that show no apparent size change through an event will have a fossilization gap immediately after the extinction level.

Many studies have also shown that the abundance of marine invertebrates in modern communities is only very weakly correlated with body size, although each taxon exists at a specific biomass level that is dependent on factors such as food supply. Given the vagaries of preservation, it is impossible to assess the absolute (or even relative) abundance of any fossil taxon.

Crucially, testing the biomass-reduction model does not require assessments of absolute (or even relative) taxon abundance. In order to test the main prediction, within-lineage size change is the only variable that is required. For the other two predictions an assessment of relative changes in primary productivity is also needed. This is more problematic. Individually, all of the observations made above for the Lower Triassic interval (lack of coals, decreased TOC, negative δ^{13}C shift etc.) can be interpreted in other ways. It is only when taken together that they strongly suggest (though do not prove) changes in the levels of marine and terrestrial primary productivity. Thus, in common with many other hypotheses, predictions concerning size increase and the reappearance of Lazarus taxa 'will be difficult to test unequivocally until direct proxies for productivity are refined' (Kidwell and Brenchley 1996, p. 324).

8. CONCLUSIONS

1. Available data show that those intervals in the Phanerozoic that have higher-than-background extinction rates are always followed by 'fossilization lows' (i.e. stage(s) with higher-than-average numbers and/or proportions of Lazarus taxa). The fossil record is thus characterized by 'high extinction–low completeness' couplets. The corollary also appears to be true: intervals with above-average origination rates are *preceded* by 'fossilization lows'.
2. The widespread and statistically significant occurrence of these extinction–preservation couplets suggests a cause and effect relationship (see especially Fara and Benton 2000).
3. A biomass reduction model is presented as a possible explanation for the Early Triassic 'fossilization low'. The basic hypothesis is that the incomplete fossil record was caused by a sharp decrease in primary productivity in

the latest Permian. This drop in productivity would lead to a reduction in the biomass of each animal taxon, either through a decrease in abundance or a decrease in body size. Only those taxa that maintained high population size, by reducing body size, would become fossilized. Those with decreased population sizes would no longer be preserved (apparent extinction) and would also be in danger of becoming really extinct.

4. The end-Permian peak in extinction is therefore a combination of 'real' and 'apparent' extinction. It is currently impossible to identify those taxa that suffer real extinction during the crisis interval and those which only appear to go extinct. Lazarus taxa are those taxa which reduce population size during the productivity crisis and which also manage to 'weather the storm' without becoming really extinct.

5. Predictions of this model are: (i) that taxa present in the post-extinction interval will be smaller than their pre-crisis relatives regardless of initial size; (ii) that size will increase as primary productivity returns to pre-crisis levels; and (iii) that Lazarus taxa will reappear after primary productivity levels have returned to pre-crisis levels.

6. Anecdotal data (e.g. the commonly observed 'Lilliput effect') support the first prediction and suggest that this model may be applicable to other (so-called) mass extinction events, although more data are needed.

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