S P E C I A L

Lazarus taxa and fossil abundance at times of biotic crisis

P. B. WIGNALL[1] & M. J. BENTON[2]

[1]*Department of Earth Sciences, University of Leeds LS2 9JT, UK (e-mail: p.wignall@earth.leeds.ac.uk)*
[2]*Department of Earth Sciences, University of Bristol BS8 1RJ, UK*

Mass extinctions are often followed by intervals in which taxa disappear from the fossil record only to reappear again later. This 'Lazarus effect' is often attributed to a poor-quality fossil record or migration to refuges. Testing these alternatives, with examples from the end Permian and late Triassic extinctions, reveals that there is no link with the abundance of fossiliferous sites and the proportion of Lazarus taxa nor are missing taxa encountered in potential refuges. Therefore, the abundance of Lazarus taxa in the aftermath of these extinctions is probably a reflection of the extreme rarity of organisms at this time.

Keywords: Triassic, Lazarus taxa, refugia, extinction events.

At times of biotic crisis many taxa go extinct, but others only temporarily disappear from the fossil record, often for intervals measured in millions of years, before reappearing unchanged (Batten 1973; Waterhouse & Bonham-Carter 1976; Paul 1982; Jablonski 1986*b*). This has been termed the Lazarus effect, after the biblical character who returned from the dead (Flessa & Jablonski 1983; Jablonski 1986*a*), and Lazarus taxa have subsequently entered the literature as an important concept in the discussion of mass extinctions. What happens to Lazarus taxa during their absence from the fossil record, known as their outage, has been the subject of a debate which is crucial to understanding the enigmatic and often prolonged lag phase that follows some mass extinctions. It is argued here that one of the principal causes, and therefore the significance of the Lazarus effect, has been overlooked.

The abundance of Lazarus taxa may reflect the variable quality of the fossil record either in terms of preservation or abundance of fossiliferous strata (Waterhouse & Bonham-Carter 1976; Jablonski 1986*a*). For example, the prolonged outage of many gastropod taxa during the Late Permian to Early Triassic interval may reflect the loss of well-preserved, silicified fossil assemblages at this time (Erwin 1996). In this view, high proportions of Lazarus taxa are deemed to reflect a poor-quality fossil record, thus rendering the accurate assessment of diversity changes difficult. Additionally, or alternatively, it has been argued that the Lazarus effect is related to the importance of refugia at times of crisis (Jablonski 1986*b*; Vermeij 1986; Kauffman & Harries 1996). Many types of refugia have been discussed (cf. Vermeij 1986), but for crisis intervals in particular they are considered to be areas of

sanctuary to which species flee at times of environmental stress in their normal habitat (Jablonski & Flessa 1986; Kauffman & Harries 1996; Erwin 1996). Such refuges are of small area, thus limiting the chances of discovering the 'refugees'. Only when conditions ameliorate in the original habitat can the Lazarus taxa reinvade their former territory and reappear in the fossil record. For benthic marine invertebrates, oceanic islands provide a theoretical refuge from crises on continental shelves (Jablonski 1986*b*), and they are commonly invoked (Erwin 1996). Unfortunately, it is the fate of most oceanic islands to be intensely deformed and metamorphosed at destructive plate margins, thereby severely reducing their chance of discovery. One of the few known examples comes from a Lower Jurassic displaced terrane in British Columbia where a small reef yields a single species of scleractinian coral that elsewhere went extinct during the end-Triassic mass extinction (Stanley & Beauvais 1994). The rarity of such examples may also be explained by the study of modern oceanic islands which have shown that they are not significant repositories of relict taxa (Vermeij 1986). Perhaps refuges are much less important at times of crisis than has generally been assumed.

Extinction and fossil abundance. Rather than denoting the quality of the fossil record or the importance of refugia, the Lazarus effect may directly record the severity of a mass extinction. Species extinction is caused by a reduction in numbers of the constituent populations until the final individual dies. In the fossil record it is exceedingly unlikely that this individual will be found and so, inevitably, the last recorded appearance of a species is to some extent 'back-smeared' from the true extinction point (cf. Springer 1990; Fig. 1). The abundance level at which a species will disappear from the fossil record is impossible to quantify, although it is likely to be lower in environments which favour fossilisation, such as deep shelf settings. However, even for marine species, a population reduced to a few thousand individuals distributed over a large shelf area is unlikely to be discovered: they are, in effect, below the detection level of the fossil record (Fig. 1): herein lies a potential cause of the Lazarus effect. During mass extinctions the population density of numerous species declines drastically and they disappear from the fossil record. For many species the decline in abundance is terminal and they become truly extinct, but some species may survive in much reduced numbers, above their minimum viable population size, but beneath the detection level of the fossil record. Only in the aftermath of the crisis, as population levels increase, do such Lazarus taxa reappear (Fig. 1). Such 'disappearances' need not, therefore, record migration of taxa away from their usual geographic range, but rather they could record a drastic *in situ* decrease in abundance.

Testing the alternatives. With our new addition, there are now three alternative explanations for the Lazarus effect:
 (i)   it reflects the quality of the fossil record;
 (ii) it records the migration of taxa to refugia;
 (iii) it records the true abundance of taxa at times of crisis.

The first alternative can be tested by comparing the amount of strata available for sampling with variations in the abundance of Lazarus taxa. This has been done for two extinction intervals, the Permo-Triassic marine record and the terrestrial record across the Triassic–Jurassic boundary. Compiling the stage-by-stage variation in the numbers of shallow marine formations that have yielded age-diagnostic fossils in the
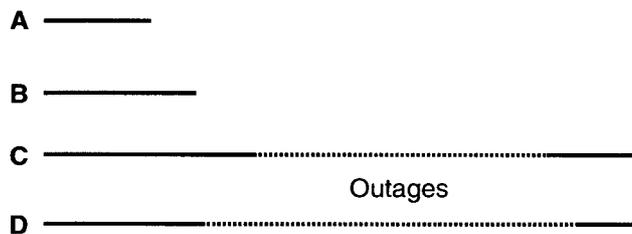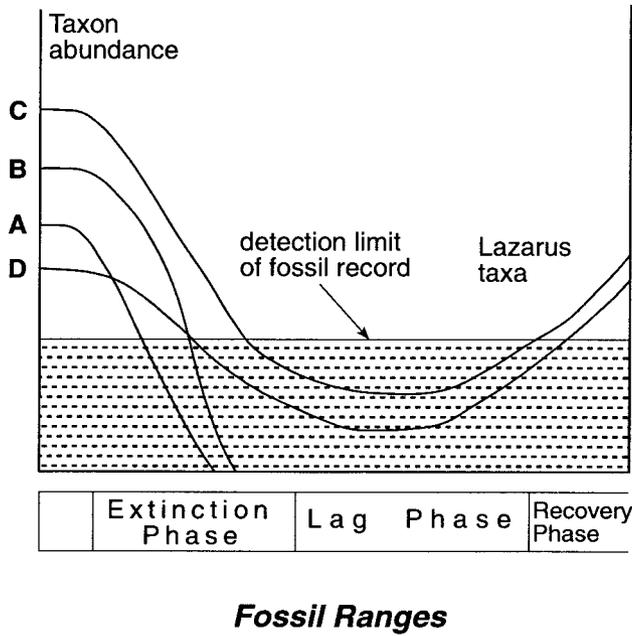
Fossil Ranges

Fig. 1. Changes in population abundance during an extinction crisis for four hypothetical taxa A–D: A and B decline rapidly in abundance and ultimately go extinct whereas taxa C and D become very rare (and are therefore unlikely to be collected as fossils), but they remain extant. Only with the improvement in environmental conditions do C and D become sufficiently abundant to cross the detection limit threshold and thus 'reappear' in the fossil record. Note that, in this explanation of the Lazarus effect, the lag phase is considered to be a prolongation of the stressful conditions associated with the extinction crisis and not part of the biotic recovery.

Midian (Late Guadalupian) to Anisian interval provides an approximate measure of the amount of fossil record that has been sampled. This reveals an initial gradual increase in fossiliferous formations until a peak is reached in the Changxingian and Griesbachian Stages, followed by a fall in the Dienerian and Smithian (Fig. 2). Comparing these fluctuations with Erwin's (1996) gastropod dataset reveals that there is no correspondence with variations in the size of the Lazarus effect, which was at its most severe in the Griesbachian and Dienerian. Indeed, the number of formations halves from the Griesbachian to the Dienerian, but the number of fossilized genera remain constant. The dramatic drop in apparent diversity took place between the Changxingian and the Griesbachian stages with equal numbers of fossiliferous units. Waterhouse & Bonham-Carter (1976) similarly showed that for brachiopods the Lazarus effect was greatest in the Changxingian and Griesbachian, an interval when fossiliferous shallow marine formations were at their peak of abundance. It therefore appears unlikely that the Permo-Triassic Lazarus effect was due to a poor quality fossil record.
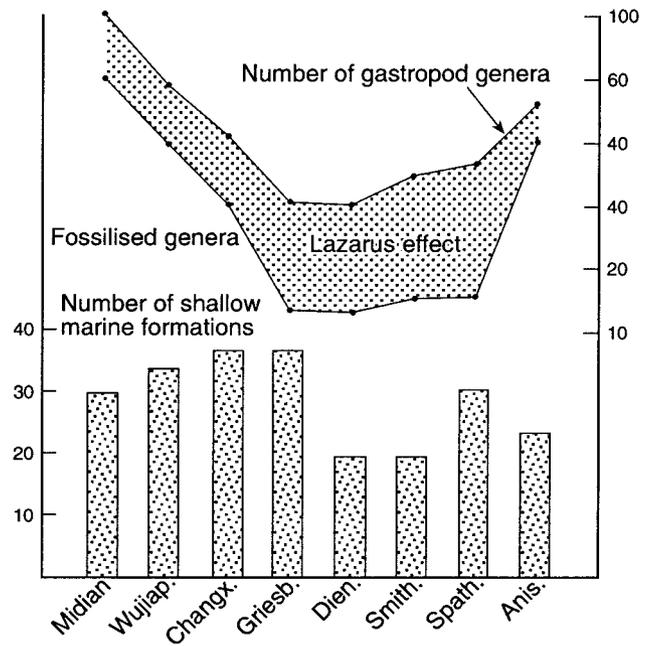

Fig. 2. Diversity changes of gastropod genera through the end Permian mass extinction (from Erwin 1996), where the lower line shows the recorded number of taxa and upper line includes Lazarus taxa, compared with fluctuations in the number of shallow marine formations yielding benthic fossils in the Midian to Anisian interval. The importance of the Lazarus effect (depicted as the space between recorded and total number of genera) shows no correlation with the abundance of fossiliferous strata. Stage abbreviations are, in order, Wujiapingian, Changxingian, Griesbachian, Dienerian, Smithian, Spathian, Anisian. The Permian–Triassic boundary occurs between the Changxingian and Griesbachian Stages.

A second test of the first alternative has been outlined by Benton (1994). It concerns a postulated extinction event among terrestrial vertebrates in the Late Carnian (Late Triassic). Benton (1983, 1986) proposed that such an event had occurred, based on the disappearance of major groups of medium to large herbivores, the rhynchosaurs, dicynodonts, and chiniquodontids, as well as the mastodonsaurid and trematosauid amphibians, and the carnivorous proterochamp-sids. The net drop in diversity from the latest Carnian to the early Norian (Fig. 3a) is modest, since the loss of seven families in the latest Carnian is partially concealed by the origin of four new families in the early Norian. Olsen & Sues (1986) challenged the reality of the postulated extinction event, asserting (p. 343) that 'early Norian vertebrate assemblages are very poorly known, and, therefore, it is difficult to place much faith in the peak of Carnian extinctions'. Thus, there are two alternative explanations for the end Carnian extinction: firstly, it is a true extinction followed by a recovery interval charac-terised by a rare fauna and secondly, it is a 'pseudo-extinction' caused by the decline in quality of the fossil record in the early Norian. The nature of the early Norian fossil record is the crux of this dichotomy.

The relative amount of gap in a fossil record may be represented by the simple completeness metric (SCM, Benton 1987). The SCM is the proportion of known to assumed taxa present during an interval. The 'known' taxa in a time unit are those actually represented by fossils, whereas the 'assumed' numbers also include the Lazarus taxa. The assumed total is a minimum estimate of actual diversity, since Lazarus taxa can
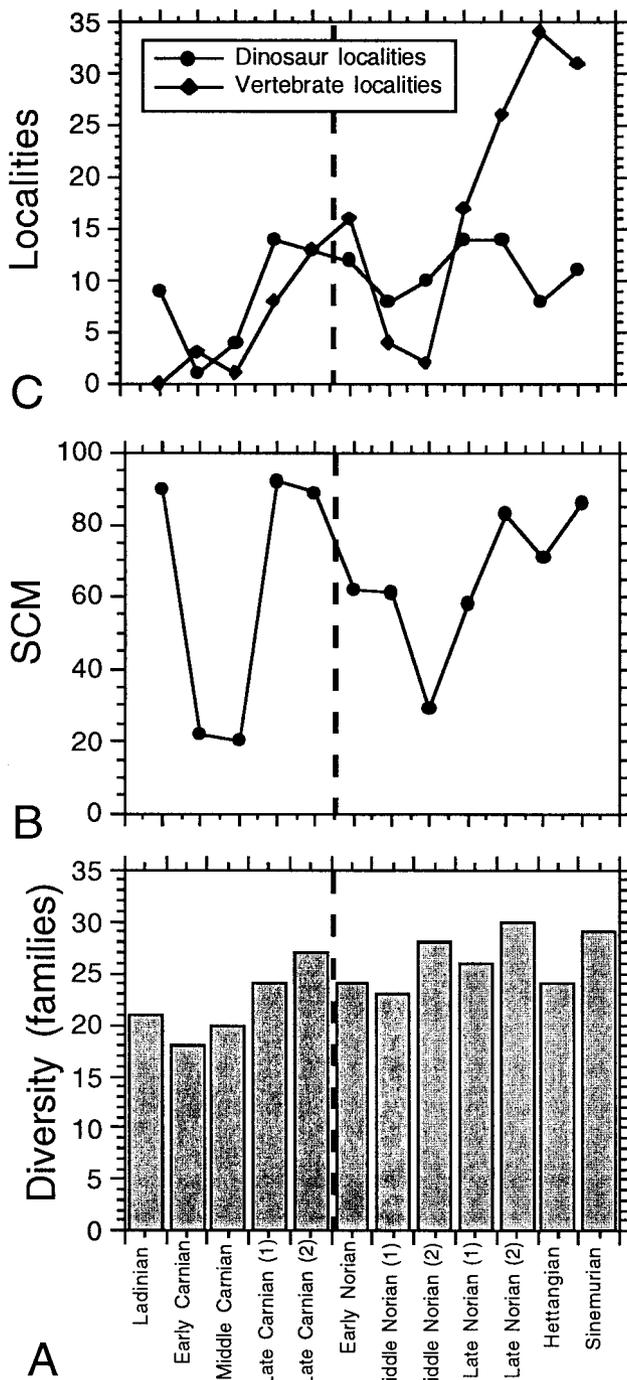
Fig. 3. Assessment of how the quality of the fossil record affects detection of a minor extinction event. (**a**) Histogram of familial diversity of continental tetrapods through the Late Triassic–Early Jurassic, showing an extinction event in the latest Carnian, marked with a dashed line. Time units are based on palynological zones (cf. Benton 1994). (**b**) The simple completeness metric (SCM) for the same part of the fossil record. High values indicate few Lazarus taxa, and low values many Lazarus taxa. (**c**) The availability of rocks containing continental tetrapods during the same interval as measured by the number of vertebrate localities (Benton 1994), and dinosaur localities (from Weishampel 1990).

only be identified if a taxon spans a time interval, leaving a gap in its known stratigraphic distribution. The assumed total does not include taxa that originated or went extinct during the gap. In Olsen & Sues's (1986) interpretation of Carnian–Norian diversity changes, a significant number of tetrapods are inferred to have gone extinct in the early Norian. For Late Triassic tetrapods, the SCM varies enormously, from 20% in the Mid-Carnian to 92% in the early late Carnian (Fig. 3b). For the critical interval, the SCM declines slightly, but the biggest drop, to 29% in the late mid-Norian, is associated with a rise in continental tetrapod familial diversity. Thus, the SCM hints at variations in the quality of the fossil record, but it fails to explain diversity trends. The slight drop in SCM in the early Norian may be best explained as an increase in fossil rarity in the aftermath of an extinction. This assertion is investigated below.

Measures that depend on assessing the relative numbers of Lazarus taxa, like the SCM, can indicate episodes of genuinely poor levels of preservation or they can reflect times when living organisms were rare. A rough method to distinguish between these two possibilities is to count up the number of fossiliferous localities within particular age ranges, and then to compare these figures with the SCM values. Benton (1983, 1986, 1994) enumerated all reported fossil sites for continental tetrapods in the Late Triassic world. When these fossiliferous localities are summarized into time divisions (Fig. 3c), it can be seen that there is a drop from 13 in the latest Carnian to 12 in the early Norian. Such a modest drop is surely insufficient to account for the drop in the global diversity of tetrapods. A parallel estimate, based on numbers of sites worldwide that have produced dinosaur skeletons or footprints (Benton 1994; data from Weishampel 1990) confirms this result (Fig. 3c). The number of dinosaur-bearing sites increases from 13 in the latest Carnian to 16 in the early Norian. In both cases, site numbers remain similar, while global diversity drops. Thus it is unlikely that the lower diversity of tetrapods results from a smaller number of finds, and reflects real reductions in the abundance and diversity in the aftermath of an extinction crisis.

It is inevitably more difficult to test for the importance of refugia, the second explanation for the Lazarus effect because, as noted above, they are intrinsically rare. Refugia have not been invoked for the Carnian–Norian tetrapod diversity trends, but they are considered to be of paramount importance during the Permo-Triassic extinction (Kauffman & Erwin 1995). Fragments of oceanic islands and seamounts are known from the Permo-Triassic interval, primarily in the accreted terranes of Japan and the Rockies of western North America. The Early Triassic fossil record of these terranes consists of the same low diversity fauna of bivalves (Tamura 1987; Sano & Nakashima 1997) that is encountered in all shallow marine sections of this age (Hallam & Wignall 1997). Significantly, no refugee taxa are known from any Lower Triassic terranes, although an Upper Triassic terrane in Oregon has yielded a single example; a sponge genus that elsewhere disappeared at the end of the Mid-Permian (Senowbari-Daryan & Stanley 1998). In summary, the importance of Lazarus effect in the aftermath of the end Permian extinction is best explained as a record of the rarity of organisms in this interval.

Conclusion

It is easy to assume that the non-recovery of fossils is a failure of the fossil record, but there is a risk that important data

about extinction events may be ignored. Low diversity may reflect the poor quantity of the fossil record, but it may also be a real, useful indicator of a genuinely low-abundance fauna in the aftermath of an extinction.

Rather than requiring the presence of chimerical refugia, the occurrence of Lazarus taxa during crisis intervals may be a record of the intensity of such events where many species go extinct and others are reduced in numbers below detection limits. Alternative explanations, such as the inadequacy of the fossil record after mass extinctions does not accord with the observation that the number of marine formations increases during the end Permian extinction events. It may therefore be implied that the duration of the outage of Lazarus taxa corresponds to the duration of the stressful factors that caused the crisis (cf. Hallam 1991). It is only with the alleviation of this stress that population densities can begin to climb. Thus, the considerable lag phase seen in the aftermath of several mass extinctions, most notably the end Permian and end Ordovician events (Hallam & Wignall 1997), may be viewed as a prolongation of the stressful conditions that caused the mass extinction and not as some intrinsic property of the recovering fauna.

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