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What are Lazarus taxa?

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The many definitions and interpretations associated with the 'Lazarus effect' have considerably confused this notion. While several authors regard the Lazarus effect as the temporary disappearance of taxa from the fossil record in any given time interval, many others consider the Lazarus effect as a pattern restricted to mass extinction episodes. The adequacy of the fossil record is the key for interpreting the Lazarus pattern: either Lazarus taxa reflect the incompleteness of the fossil record (the 'stratigraphic alternative'), or they illustrate genuine extinction-linked phenomena (the 'biological alternative'). The latter option includes two traditional hypotheses implying existence of refugia and post-extinction low population diversity. Differences between these two biological explanations seem to be more rhetorical than substantiated. In addition, the sampling intensity is an external factor commonly linked with both the stratigraphic and the biological alternatives. Interpreting the Lazarus effect is an asymmetrical procedure because the biological alternative is only favoured when the stratigraphic one cannot be documented. Consequently, analytical techniques assessing the completeness of the fossil record are critical to understand the meaning of Lazarus taxa. In particular, gap distributions are better compared with extinction and origination rates rather than with total diversity estimates. Finally, the Lazarus effect should be defined broadly to include range gaps from any given time interval.

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1. INTRODUCTION

Palaeontologists acknowledge that the fossil record is incomplete, but most of them hope that it is adequate to document major evolutionary patterns. Whereas the existence of mass extinctions in the fossil record was known to the earliest authors (Cuvier 1817), the timing, causes and aftermath of biotic crises are still debated today. Following the heuristic key-paper of Alvarez *et al.* (1980), the past two decades have seen a huge amount of work done about patterns of mass extinctions and their recovery (see Hallam and Wignall (1997) for a review). In this context the term 'Lazarus effect' was coined (Flessa and Jablonski 1983; further developed in Jablonski 1986), after the biblical character who miraculously rose from the dead. The Lazarus effect designates the 'disappearance and apparent extinction of taxa that later reappear unscathed' in the fossil record (Jablonski 1986). Despite the non-occurrence of these Lazarus taxa in a given time interval (also known as their 'outage'), their existence can be deduced from their occurrences in both older and younger time intervals.

Jablonski (1986) originally defined the Lazarus effect for any 'given time interval', but he illustrated and discussed the concept for the Cretaceous/Tertiary (K/T) mass extinction (Jablonski 1986, Figure 6). The Lazarus effect is indeed well-documented for many groups at various bioevents (e.g. Birkelund and Hakansson 1982; Surlyk and Johansen 1984; Jablonski 1986; Harries and Kauffman 1990; Erwin 1996; Casier and Lethiers 1997), and Jablonski's (1986) term has subsequently entered the mass extinction terminology. However, an overview of

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the recent literature demonstrates that there is confusion surrounding the Lazarus concept, with a variety of definitions and interpretations hiding behind this important notion.

The presence of gaps within the stratigraphic ranges of taxa is not a recent discovery, but their quantitative study on a large scale and the first attempts at interpreting them can, at the least, be attributed to the pioneering works of Batten (1973), Nakazawa and Runnegar (1973), and Waterhouse and Bonham-Carter (1976). For these authors, gaps merely illustrated the distortion suffered by the fossil record, which Paul (1980, 1982) and Holman (1985) later formalized as gap-analyses for assessing the completeness of the fossil record. Paul (1982) gave the following definition: 'a gap occurs when a taxon is known from below and above, but not actually within, a given stratigraphic interval'. Clearly, during a gap, 'at least one species must have existed to carry on the line but has not been preserved or is yet to be discovered' (Paul 1982). The later definition of the Lazarus effect by Jablonski (1986) is not different, but the *context* in which it was defined directly related to mass extinctions. Here lies the first dichotomy in the subsequent understanding of the Lazarus effect. On the one hand, some authors synonymized 'gappiness' and the Lazarus effect as a measure of fossil record quality, whether at times of mass extinction or not (Benton 1987; Patterson and Smith 1989; Hecht 1992; Bardet 1995; Markwick 1998; Fara and Benton 2000). On the other hand, some authors restricted the Lazarus effect to the temporary disappearance of taxa exclusively at times of mass extinctions. For example, Harries *et al.* (1996) regarded Lazarus taxa as 'species that survive the extinction event(s) but disappear from the record for an interval of time spanning a portion or the entire mass extinction event'. In the same way, according to Lethiers and Casier (1999), the Lazarus effect 'designates the apparent extinction of a taxon that disappears during an event, and reappears afterwards unscathed' (translated). Whereas gaps in the fossil record are frequent at times other than mass extinctions, 'these are usually not described as a Lazarus effect' according to Erwin and Droser (1993; see also Mamay and Bateman 1991). Kauffman and Erwin (1995) and Kauffman and Harries (1996) further restricted the definition of Lazarus taxa as 'immigrant survivors', representing both short- and long-term refugia species during biotic events. The literature further contains some additional definitions of Lazarus taxa, which correspond to what would later be described as ghost lineages (Smith 1988), or which are simply defined as taxa with significant gaps in their fossil record (Smith 1994; Markwick 1998).

Clearly, the Lazarus effect is confused by conflicting concepts of its either continuous or crisis-related nature. But this is no surprise. Indeed, some of the factors responsible for the Lazarus effect act in all time intervals, mass extinctions included. They are 'stratigraphic factors' that cause gaps in the stratigraphic ranges of taxa. Other suspected origins for the Lazarus effect are more specific to major extinction events, and they might illustrate migration of taxa to refugia or post-extinction low population diversities. These are 'biological factors'.

The few literal quotations listed above illustrate a second major source of confusion: the lack of distinction between pattern (the outage of taxa) and process (cause of the outage). While *interpretations* of the Lazarus effect by potential processes may be varied (Waterhouse and Bonham-Carter 1976; Erwin and Droser 1993; Benton 1994; Smith 1994; Harries *et al.* 1996; Wignall and Benton 1999; Conway Morris 1999), the *definition* must remain unique and relate to the single observed pattern.

The present contribution critically reviews the various meanings traditionally assigned to the Lazarus effect, namely, quality of the fossil record, migration to refugia, and depauperate post-extinction biotas. It also explores some analytical techniques designed to measure and to interpret the Lazarus effect better.

2. LAZARUS EFFECT AND FOSSIL RECORD INCOMPLETENESS

First, the generic term 'gap' must be used cautiously. A stratigraphic gap means the absence of a volume of sedimentary rocks and, in turn, the non-representation of a certain amount of time by sediments (hiatus). A gap in the stratigraphic range of a taxon (range gap) is the absence of this taxon in a particular set of strata within its range. Stratigraphic gaps are paramount over range gaps simply because a taxon cannot be recorded in non-existing rocks. In a given section, a range gap may also occur in any stratigraphic level even if the latter is well developed. This distinction may seem trivial, but it should prove helpful in avoiding potential misunderstandings in the interpretation of 'gaps', especially for local sections.

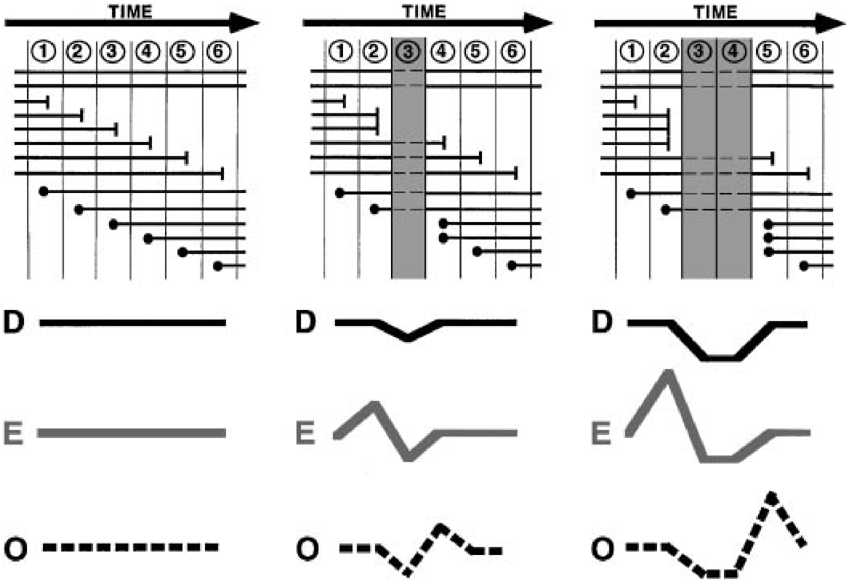

Figure 1. The effect of poorly-documented intervals on estimates of diversity (D), extinctions (E) and originations (O). The original distribution of stratigraphic ranges (left diagram) is characterized by constant values of D, E and O through a series of six time intervals (1–6). If a dramatic gap occurs in interval 3, estimates of D, E and O are affected (middle diagram). This distortion increases as the gap spans successive time intervals (right diagram).

The idea that range gaps may illustrate the imperfection of the fossil record appeared in the literature along with the first detailed gap analyses. These pioneering works dealt either with long time intervals (Waterhouse and Bonham-Carter 1976; Paul 1982), or were focused on major extinction events (Batten 1973; Nakazawa and Runnegar 1973; Jablonski 1986). In all cases, the absence of a taxon in a particular time interval was regarded as a result of the incompleteness of the fossil record. This interpretation can be termed the 'stratigraphic alternative'. As shown in Figure 1, a very poorly documented interval increases the number of Lazarus taxa, but it also modifies observed extinction and origination patterns. The longer the gap, the more dramatic the effect on diversity change estimates. Gappiness can push observed last occurrences backwards in time (Signor and Lipps 1982), as it can also push observed first occurrences forwards in time. Either observed extinction and origination patterns are totally artificial, or their magnitude and timing are exaggerated by the incompleteness of the fossil record. Consequently, the temporary disappearance of taxa in the fossil record at times of major extinctions has attracted particular attention, especially in the gradual versus catastrophic extinctions debate, and this context originally stimulated the definition of the Lazarus effect (Flessa and Jablonski 1983; Jablonski 1986).

Recognition of a pronounced Lazarus effect following major bioevents has led many authors to regard observed extinction intensity cautiously (Nakazawa and Runnegar 1973; Paul 1982, 1990; Jablonski 1986; Erwin 1996; Suter and Erwin 1996; Paul and Donovan 1998; Kozur 1998). Whether at times of mass extinction or not, what stratigraphic factors can lead to the outage of taxa? Clearly, Lazarus taxa will be abundant when facies in which those taxa are usually found are missing from the stratigraphic column. The probability of finding fossils of pelagic sharks is low where continental, upland deposits dominate a stratigraphic interval. As an example, Paul and Donovan (1998) showed that the end-Ordovician extinction of cystoids is certainly accentuated by a facies change in Llandovery (early Silurian) deposits. Facies-dependence is even more important for taxa with demanding preservation requirements. Erwin and Pan (1996) and Erwin (1996) documented this case with numerous Lazarus gastropod genera in the Capitanian (Middle Permian) in relation to a reduction in the number of silicified assemblages. Note that preservational factors should not be confused with sampling failure, which will be discussed later.

3. REFUGIA

Besides considerations of the Lazarus effect as an indicator of fossil record quality, Jablonski (1986) acknowledged that it also suggests the existence of refugia during mass extinctions. Refugia are usually regarded as sanctuaries sheltering Lazarus taxa during environmental crises before they reinvade their former territories and reappear in the fossil record (Jablonski 1986; Donovan 1989; Kauffman and Erwin 1995; Erwin 1996; Kauffman and Harries 1996; Kozur 1998; Lethiers and Casier 1999). Refugia are commonly viewed as small areas where taxa migrated, and, because these locations are restricted in their geographical extent, taxa will only rarely be found and will display the Lazarus effect. Consequently, Kauffman and Erwin (1995) have considered the frequency of Lazarus taxa as a measure of the importance of refugia during environmental crises, and Kauffman and Harries (1996) further restricted Lazarus taxa as ‘short-term’ and ‘long-term’ refugium survivors. The argument is linked to sampling theory principles and it suggests that further investigation of the fossil record should reveal some of these relict taxa in the critical intervals. For studies made on a global scale, note that the Lazarus effect should arise because of the small geographical extent of refugia, not because of the migration of taxa to these places. The refugium archetype is the oceanic island, where shallow-water taxa can flee from continental shelves at times of environmental crisis. However, Vermeij (1986) warned that the role of oceanic islands as refugia is not supported by strong evidence, and many failures to discover Lazarus taxa in such locations seem to confirm his views (Kamada 1979; Tamura 1981, 1982; Vermeij 1986; Sano and Nakashima 1997). *Phacelostylophyllum* and *Neoguadalupia* are exceptions. This Mesozoic coral and sponge are the only taxa demonstrated to be refuge genera after they were respectively found in Early Jurassic and Late Triassic terranes corresponding to ancient oceanic islands (Stanley and Beauvais 1994; Senowbari-Daryan and Stanley 1998). Similarly, a single example of an extant insular ‘refugee’ is provided by the balanomorph *Tesseropora* (Newman and Ross 1977). Clearly, oceanic islands do not provide abundant evidence of refugia taxa, and this classic example is mainly restricted to shallow-water invertebrates.

But many questions arise from the refugium hypothesis. If refugia differ from the primary habitats of Lazarus taxa, why should the latter display such a wide array of specialized ecological features (Erwin 1996; Harries *et al.* 1996)? Also, as pointed out by Hallam and Wignall (1997), how can such emigrants compete successfully in other environments with resident taxa?

4. POST-EXTINCTION DIVERSITIES

Recognition of the Lazarus effect is a taxonomy-based procedure. Once a taxonomic level is chosen (or more often dictated by the available data), a simple counting of Lazarus taxa is made for a succession of time slices. However, all other factors being equal, representation of these often-supraspecific taxonomic entities in the fossil record will depend on their respective number of species. Jablonski (1986) demonstrated that Lazarus taxa tend to be paucispecific. But the same argument can be extended to individuals by virtue of similar probabilistic principles: a taxon has more chance to enter the fossil record if the number of its individual representatives is high. In the distinction between taxonomic and population diversities lies the third traditional explanation for the Lazarus effect. Because mass extinctions might drastically reduce population diversities, the non-occurrence of Lazarus taxa can reflect the actual *in situ* low abundance of individuals that is below the detection limit of the fossil record. This hypothesis finds its roots in the works of Waterhouse and Bonham-Carter (1976) and Paul (1982), and it has been developed and debated in the literature recently (Hallam and Wignall 1997; Wignall and Benton 1999, 2000; Twitchett 2000). So interpreted, the Lazarus effect is even regarded as an extinction metric in itself (Hallam and Wignall 1997). Assessing the intensity of a mass extinction with Lazarus taxa includes two aspects: either the outage measures the duration of the stressful physical conditions following the bioevent (Hallam 1991; Wignall and Benton 1999), and/or it measures the ecological kinetic of the recovery of the biota (Schubert and Bottjer 1995). Other sources of evidence (sedimentology and geochemistry) are required to distinguish between those two options, with data from both extinction and post-extinction intervals. In any case, the interpretation of the Lazarus effect as a result of a post-event depauperate biota carries an important message: survival of Lazarus taxa is not equivalent to an absolute immunity from extinctions. Distinction between taxic and population diversity thus prevents any interpolated conclusion regarding a group's resistance to extinctions.

However, this hypothesis for the Lazarus effect has its own weaknesses. On the one hand, for any time interval, it is valid only if the preservation potential of a particular group can be shown to be constant. Indeed, it is usually assumed that the lower detection limit of the fossil record, under which taxa with low population diversity are not preserved, stands at a constant theoretical threshold (see for example Figure 1 in Wignall and Benton 1999). The demonstration of changing facies and taphonomic parameters through time, as discussed earlier, can invalidate such an assumption. On the other hand, the post-extinction depauperate biota hypothesis for the Lazarus effect is purely speculative. It is a sensible and seductive interpretation, but, like the refugia hypothesis, it can only be supported by the lack of evidence to support the stratigraphic alternative.

5. HOW MANY ALTERNATIVES?

Whereas the Lazarus effect is usually discussed with regard to the three potential explanations presented above (e.g. Hallam and Wignall 1997; Conway Morris 1999; Wignall and Benton 1999), distinction between the refugia and low abundance hypotheses is ultimately far from straightforward. In fact, the critical point lies in the definition of refugia. In its restricted meaning, a refugium corresponds to an unusual habitat for taxa surviving an environmental crisis *away* from their original territory (Kauffman and Harries 1996). With this definition, and for studies made on a local or regional scale, the refugium hypothesis is sound. However, for global studies, it is difficult to see why migration and a shift in habitat would systematically prevent the occurrence of taxa in the fossil record. Without pure speculation about the preservation potential of the new habitats within refugia, these factors become irrelevant to the Lazarus effect issue. The key point is that refugia must be *small* in their ecological and geographical extent if they are to play an evolutionary role in the outage of taxa. In turn, this leads to the broader definition of refugia by Vermeij (1986), for whom the characteristic feature of refugia stands in the *distributional contraction* of taxa, regardless of their original distribution (see also Jablonski and Flessa 1986). Many empirical studies have illustrated that reduction in habitat implies reduction in both taxonomic and population diversity (see Boecklen and Simberloff (1986) for references). Reciprocally, it seems extremely dubious to consider population size and ecological–geographical distribution as independent variables. Because restriction in distribution of taxa is the only obvious biological factor acting on the Lazarus effect, the distinction between the refugia and low abundance hypotheses appears to be more rhetorical than substantiated. Consequently, these two hypotheses are here gathered into the single denomination of 'biological alternative'. The latter differs from its stratigraphic counterpart in that it usually explains the Lazarus effect on a large scale for major extinction episodes only, and it supposes the idea that Lazarus taxa illustrate true biological phenomena rather than the artificial incompleteness of the fossil record.

Also, any species can suffer a life crisis and exhibit the Lazarus effect for biological reasons at times of background extinctions. However, this possibility is rarely discussed because the small sample of taxa becoming extinct or displaying the Lazarus effect makes the biological alternative even more speculative than for mass extinction episodes (see question marks for the biological alternative in Figure 2).

Finally, Lazarus taxa are implicitly regarded either as taxa that did not enter the fossil record, or as rare but preserved taxa yet to be discovered. These are two different things, though rarely distinguished, because both may arise from the two alternatives previously discussed (Figure 2). For example, one might argue that refugia do not need to be small areas, and that they may simply correspond to unsampled zones. However, the sampling intensity is a modern, human-based, artificial factor, whereas refugia are expected to illustrate specific evolutionary episodes. Conflating the two notions is dubious because it defines an important evolutionary concept based on negative evidence.

In the case of sampling failure, one hopes that an increase in the labour of palaeontologists, in the number of fossil sites and their accessibility could fill in part of the present range gaps. Problems in sampling stress the fundamental difference between a poor fossil record and a poor knowledge of a representative fossil record (Paul 1998).

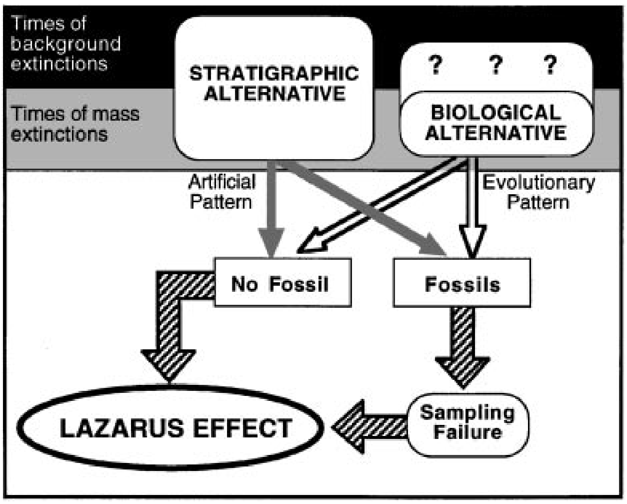

Figure 2. The origins of the Lazarus effect. Whereas the stratigraphic alternative can act at any time, the biological alternative is mainly invoked for mass extinction episodes (see text). Both alternatives either prevent the preservation of taxa, or they restrict the number of preserved taxa that remain undiscovered through a sampling failure.

Together with assessment of sampling biases, interpretation of the Lazarus effect must rely on objective lines of evidence. This is the purpose of the next section.

6. ANALYTICAL CONCEPTS

As noted by Paul (1982), studies on the Lazarus effect are hampered by the difficulty in gathering the appropriate data. The literature is full of stratigraphic ranges with first and last occurrences, but intervening occurrences are seldom given. When background levels of extinction prevail, the stratigraphic alternative best explains the outage of taxa. The meaning of the Lazarus effect becomes a challenge in time intervals following major extinction events. A good example is given by Palaeozoic echinoderm families, for which the highest numbers of Lazarus taxa almost exclusively occur in post-extinction intervals (Figure 3). Paul and Donovan (1998) preferred the stratigraphic alternative that casts doubt upon the actual intensity–or even reality–of the bioevents concerned, although the biological alternative may also have a role. The tests that could be applied to enlighten this issue are those traditionally used to assess the quality of the fossil record.

A simple test is to estimate the available volume of fossiliferous rocks. Wignall and Benton (1999) applied this rough method by counting fossiliferous formations and localities through the end-Permian–Early Triassic and Late Triassic–Early Jurassic intervals to dismiss the stratigraphic alternatives suggested by Erwin (1996) and Olsen and Sues (1986), respectively. Although of interest, this approach is far too coarse to draw any firm conclusion about the cause of the Lazarus effect. As pointed out by Twitchett (2000), equivalence in definition, preservation potential, geographical and temporal extent of fossiliferous formations or localities has to be demonstrated before these units are used as proxies to assess fossil record quality.

When occurrences of taxa are available throughout their entire ranges, a ‘simple completeness metric’ (SCM) can be calculated (Paul 1980, 1982; Benton 1987). It corresponds to the proportion of taxa actually recorded relative to the overall diversity in each time interval (Figure 4). This metric suffers from the following limitations. (1) Since the Lazarus effect is common at times of diversity drops, the uncertainty associated with its measure becomes larger because of the reduced taxonomic sample in such intervals. Both numbers of the ratio must be provided to allow discussion of this problem. The level of uncertainty can be tested statistically using binomial error bars calculated according to Raup’s (1991) method. This probabilistic approach provides arguments towards

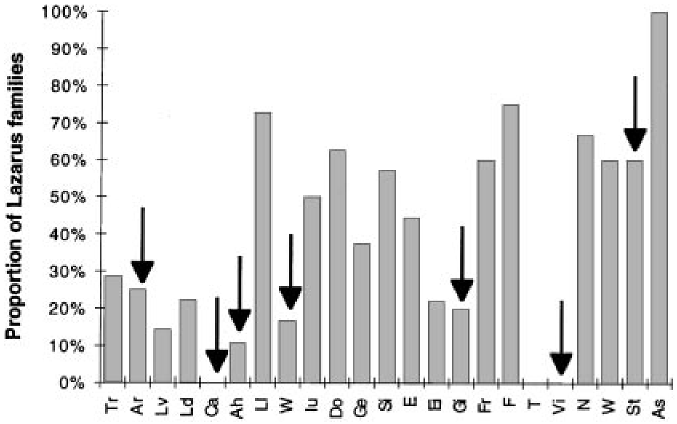

Figure 3. The proportion of Lazarus families among Palaeozoic echinoderms. The black arrows represent the major extinction peaks identified by Sepkoski (1986) in the Tremadocian (Tr)–Asselian (As) interval (Latest Cambrian–Earliest Permian). Except for the Upper Arenigian (Ar) crisis, all extinction episodes are immediately followed by high numbers of Lazarus families (modified from Paul and Donovan 1998, reproduced by permission of John Wiley & Sons limited).

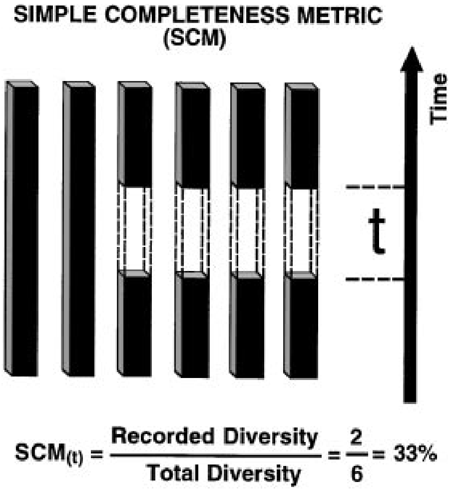

Figure 4. Simple completeness metric (SCM). In a given time interval t, some taxa are known from fossils (solid bars), whereas others display the Lazarus effect (dotted bars). The SCM for that time interval is the ratio of its recorded diversity to its total (Lazarus + recorded) diversity.

the significance of time intervals characterized by high proportions of Lazarus taxa. In turn, the binomial procedure recommended here should avoid subjective statements about the intensity of the Lazarus effect. (2) As pointed out by Benton (1987), SCM values may be overestimated when a long succession of gaps occurs, simply because fewer taxa can span wide time intervals. (3) The SCM does not account for potential truncations at both end-points of stratigraphic ranges. A solution to the last bias may lie in the confidence intervals method (Strauss and Sadler 1989; Marshall 1990, 1998). Importantly, the SCM index can be used as a relative measure of completeness only if the Lazarus effect is entirely due to stratigraphic factors.

Within each time slice, the total diversity (D) can be dissected into several additive components (Figure 5): Lazarus taxa (L), taxa crossing the interval and known from fossils (C), taxa having their first occurrence (O) and those having their last occurrence (E) in the interval. If H denotes the taxa restricted to the time interval (single occurrence counted in both E and O), one can write:

$$D = L + C + E + O - H \tag{1}$$

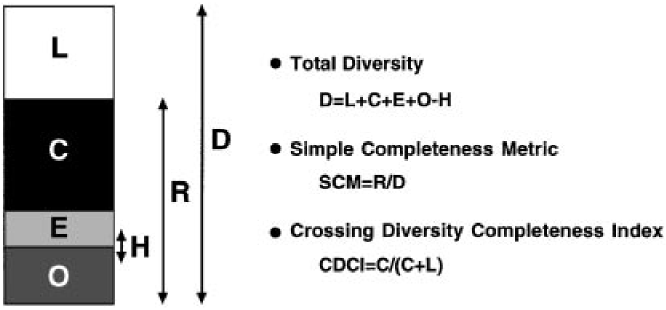

Figure 5. Diagram showing how, in a given time interval, the total diversity (D) can be dissected into Lazarus taxa (L), recorded taxa crossing the interval (C), taxa having their first occurrence (O) and those having their last occurrence (E). The taxa restricted to the time interval are denoted H, and the total recorded diversity is denoted R.

With the recorded diversity R being given by $R = C + E + O - H$, the SCM index is equivalent to the ratio R/D. Another useful ratio, named here the 'crossing diversity completeness index' (CDCI), corresponds to the quantity $C/(C + L)$. This measure is not modified by the variations of E and O, and it therefore provides a more homogeneous estimate than the SCM does. In any case, $SCM \geq CDCI$, equality of the two terms only occurring in cases when there are no Lazarus taxa or when the quantity $(E + O)$ is nil. Also, given any two successive time intervals i and $i + 1$, the taxic diversity in $i + 1$ is:

$$D_{i+1} = D_i - E_i + O_{i+1} \tag{2}$$

(Sepkoski and Koch 1996).

This may seem a trivial reminder but it has important implications in the study of the Lazarus effect and diversity estimates. For example, Wignall and Benton (1999) discussed the Carnian–Norian (Late Triassic) extinction event by comparing the variations in SCM, total diversity, and number of localities for continental tetrapod families. These authors rejected the stratigraphic alternative as a cause of the Late Carnian event and the Early Norian Lazarus taxa because they did not find any marked correlation between the three indices. This is hardly surprising. Indeed, variations in diversity through time are only due to the net difference between E_i and O_{i+1} (as dictated by Equation 2), and the relation between this quantity and the SCM values, or the number of localities, is consequently much more complex than usually assumed. In this context, it is obviously more informative to analyse origination and extinction rate estimates separately (O/D and E/D respectively) than total diversity alone. The data used by Wignall and Benton (1999) actually yield significant correlations (Figure 6a) both between SCM values and origination rate (Spearman rank-order correlation coefficient $rs = 0.582$, $p < 0.05$, one-tailed test), and SCM values and extinction rate ($rs = 0.594$, $p < 0.025$, one-tailed test). Similar correlations were found by Fara and Benton (2000) with Late Jurassic–Early Paleogene tetrapod families (Figure 6b). Interestingly, the latter case showed that the correlation between extinction and origination rates vanishes when the influence of the SCM is removed statistically (Fara and Benton 2000). In turn, this casts doubt on the rejection of the stratigraphic alternative because an artificial component linked to the incompleteness of the fossil record is suggested (Lazarus taxa seem to result from stratigraphic factors in this example). It also demonstrates how the paramount influence of the fossil record over observed diversity patterns may be overlooked by using diversity curves only.

Holman (1985) proposed two other analytical approaches to study gaps in stratigraphic ranges, but unfortunately they were not taken up in the subsequent literature. Because they are of interest in the study of the Lazarus effect, these procedures are recalled here. The first one consists in plotting the CDCI values (that is, the proportion of recorded taxa among those strictly crossing a time interval), conditional upon whether the taxa were recorded or Lazarus in the previous interval. Under a random sampling model, these two proportions should not differ. If they do, it implies that the occurrence of taxa in a given time interval is more probably an intrinsic taxonomic property than an independent consequence of fossil record quality. The second approach explores the following

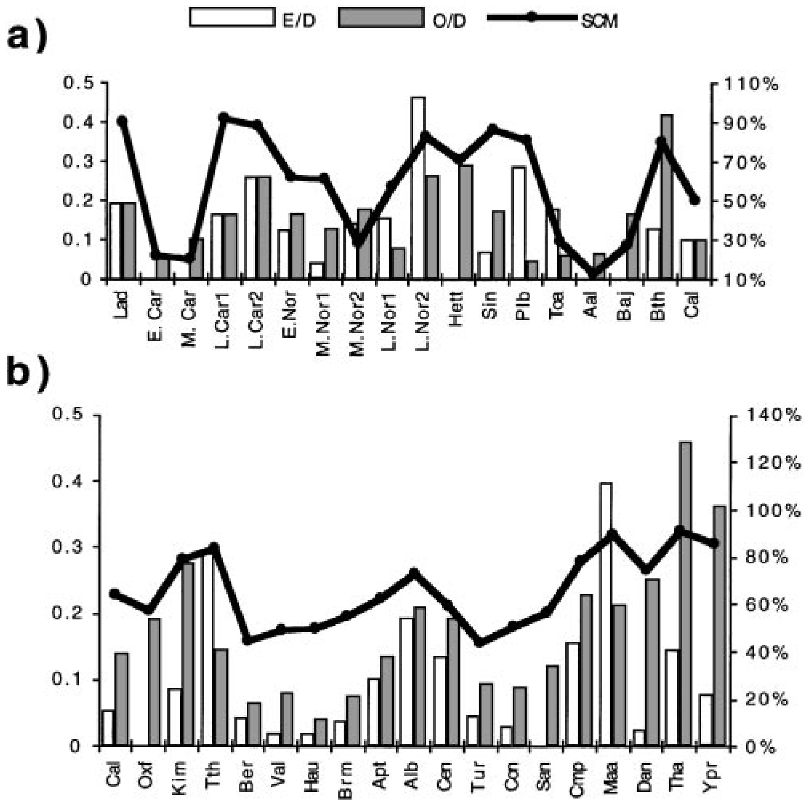

Figure 6. Correlation of proportional extinction and origination rates (E/D and O/D respectively, left-hand scale) with simple completeness metric (SCM) values (right-hand scale). Abbreviations as in Figure 5. (a) Middle Triassic–Middle Jurassic tetrapod families (data from Benton 1994); (b) Middle Jurassic–early Eocene tetrapod families.

statements: if the disappearance of a taxon in a given stratigraphic interval is due to its actual extinction, this taxon will never reappear in some later interval, whereas if the disappearance is due to incompleteness, the taxon may eventually reappear in the record. Starting from all the taxa that disappear in a given interval, the proportions of those taxa that are still missing from the record at the beginning of each later interval are plotted. Cohorts of ‘absent taxa’ are thus produced, estimating the degree of incompleteness relative to the extinction rate. The higher the proportion of absent taxa, the more complete the record or the higher the extinction rate.

A critical test assessing whether gaps represent a preservation failure or a sampling problem stands in historical studies. If Lazarus taxa merely resulted from a poor knowledge of the fossil record, palaeontological labour should gradually fill the gaps through time. Two examples of such history-based comparisons illustrate this point. After Erwin (1996) refined his database on gastropod genera crossing the Permian–Triassic boundary, the number of Lazarus taxa he found was the same as that found in Batten’s (1973) work made two decades before. Despite numerous taxonomic, stratigraphic and geographical revisions made between these two studies, the absolute number of Lazarus taxa remained stable, whereas the total diversity increased. This observation suggests the actual absence of Lazarus taxa from the fossil record rather than a mere sampling problem. Similarly, Fara and Benton (2000) used the increase in SCM values since the compilation of Benton (1987) to show the growing knowledge about the fossil record of Cretaceous continental tetrapod families. In fact, historical studies should only focus on already-known gaps. The latter must be distinguished from gaps newly created by recent discoveries and taxonomic revisions that greatly complicate the problem.

In addition, Smith (1990) and Benton (1994) summarized a set of key questions when a preservation failure is to be tested. How does diversity vary according to the distribution of rich fossiliferous horizons? During the outage of taxa, is there any indication of poorer taphonomic conditions (articulated versus disarticulated specimens, complete versus fragmentary material, etc.)? Do different indicators (palynomorphs, trace fossils, micro- or macrofossils) vary in parallel?

Even if taxa can be recorded in different types of facies, their expected ecology and typical preservation facies provide further evidence for distinguishing between genuine evolutionary patterns and preservational artefacts. For example, if the Lazarus effect of an ecologically well-defined group of taxa occurs when their typical preservation facies is not represented, that argues for a preservation failure (Gilliland 1992; Erwin 1996). Alternatively, if the Lazarus effect occurs in facies deemed to be suitable for the corresponding ecological group to be fossilized, then the biological alternative may be favoured. For example, Kozur (1998) illustrated this case with the absence of scolecodonts and holothurian sclerites in Scythian deposits, despite 'suitable facies for occurrence and preservation' in this interval. Similarly, Bryan and Jones (1989) favoured a biological alternative to explain the pronounced Lazarus effect observed in the Maastrichtian–Danian molluscan faunas at Braggs (Alabama) because of 'the good time resolution, the comparable preservation and lithologies throughout the section, and the consistently low Cretaceous and Tertiary diversities'. Generally, the distinction between the two alternatives is much more subtle. For instance, the Maastrichtian–Danian sections studied by Jeffery (1997) in Kazakhstan display local extinction patterns in between the opposite expectations from biological and stratigraphical factors.

Finally, computer-based models integrating sedimentological, taxonomic, ecological and taphonomic parameters may prove useful in exploring quantitatively the incompleteness of the fossil record. Holland and Patzkowsky (1999) have shown how computerized simulations could be used to dissect incompleteness by estimating the relative roles of sampling, facies and depositional biases. This approach has great potential in the Lazarus effect debate, because it provides quantitative values under the model's assumptions.

7. DISCUSSION

Gaps in the stratigraphic ranges of taxa occur in virtually all time intervals throughout the Phanerozoic. The frequency of these temporary disappearances monitors the quality of the fossil record. This first assumption, the stratigraphic alternative, is possible in all time slices, including episodes of mass extinction. Even if real, the latter can have their magnitude and timing highly biased by a coeval poor fossil record quality. The biological alternative, stipulating that the Lazarus effect represents a genuine extinction-related phenomenon, can be made subsidiary to the stratigraphic alternative. In fact, interpretation of the Lazarus effect stands on an asymmetrical line of reasoning: the biological alternative is favoured only when the stratigraphic alternative cannot be documented. Attempts to support the former without consideration for the latter are purely speculative. This is a characteristic feature of interpretations that are based on negative evidence (i.e. non-occurrence), and such conclusions are 'procedurally dangerous but not always imprudent' (McKenna and Bell 1997, p. 7). For global studies, the distribution of Lazarus taxa outside mass extinction intervals provides a 'background' frequency of the Lazarus effect. This background level of range gaps is essential when mass extinction levels are to be analysed. Consequently, it seems logical to define the Lazarus effect as the temporary disappearance of taxa from the fossil record *in any* time interval. This does not preclude the use of this concept in mass extinction terminology, but definition must be kept separated from interpretation.

In cases where the stratigraphic alternative can be reasonably dismissed at times of biotic crisis, Lazarus taxa illustrate an equilibrium, a sort of evolutionary compromise. On the one hand, these taxa survived the bioevent, and as such, their ecological parameters provide evidence for survival mechanisms. On the other hand, they must stand below the detection limit of the fossil record because of their few representatives and their limited distribution. They were sufficiently affected not to enter the fossil record as currently sampled, but not enough to be driven to extinction. In fact, when the Lazarus effect is studied as an extinction-related phenomenon, a common mistake is made by amalgamating the parameters responsible for the survival of taxa and the Lazarus effect. For example, Jablonski's (1986) original statement that Lazarus taxa tend to be widespread actually arose from a confusion between Lazarus taxa and survivors at the K/T boundary (see Figure 10 in Jablonski 1986). While Lazarus taxa are obviously survivors, all survivors are not Lazarus taxa. Consequently, the Lazarus effect must be analysed with regard to features that are characteristic of Lazarus taxa *among* survivors in order to avoid such misinterpretations.

Additionally, duration of the Lazarus effect has an important bearing for taxonomy and studies of evolutionary rates. First, long outages of taxa may point towards probable taxonomic problems (Paul, 1990). The influence of taxonomic practices on Lazarus effect estimates has long been recognized. Batten (1973) already suspected that the magnitude of the Lazarus effect in the earliest Triassic may result from inconsistent taxonomies produced by specialists on either Mesozoic or Palaeozoic faunas. Erwin and Droser (1993) have also stressed the importance of accurate taxonomic assignments in order to distinguish among true Lazarus taxa and unrelated morphologically convergent forms, the so-called ‘Elvis taxa’.

Alternatively, when the taxonomic framework is robust, the outage of Lazarus species suggests morphological stasis during the critical interval. This is a peculiarity of the species level because the minimum amount of diagnosable morphological features is maintained unchanged through the interval. Higher taxonomic units also represent the temporary disappearance of natural entities, but they can acquire new morphological features in addition to the synapomorphies defining the group. However, using Lazarus taxa as proxies for morphological rates of evolution is a delicate task because the taxonomic properties of the Lazarus effect are still unknown.

8. CONCLUSIONS

Even if the Lazarus effect can be interpreted in various ways (different processes), its definition must remain unique (a single pattern). The pattern has been originally defined for any ‘given time interval’ (Jablonski 1986) and, as such, should not be restricted to mass extinction episodes. To determine the actual meaning of Lazarus taxa unequivocally at times following extinction episodes is not an easy task. The challenge is that artificial incompleteness of the fossil record may yield similar patterns to those expected to arise from true evolutionary phenomena. It is argued here that the latter are better gathered into a single ‘biological alternative’, by opposition to the completeness-related ‘stratigraphic alternative’. This distinction is more obvious when global-scale studies are undertaken. However, it would be incorrect to believe that such a clear dichotomy exists between the quality of the fossil record and genuine historical events. This is especially true for studies made on local or regional scale. It is well-known that transgression–regression cycles can simultaneously provoke extinctions and gaps in the fossil record. In the same way, the Lazarus effect of gastropod genera in the earliest Triassic may be a preservational artefact linked to the actual extinction of silicified micro-organisms (Erwin 1996; Erwin and Pan 1996; Kozur 1998). Interestingly, the only Lower Triassic silicified fossils known so far (ammonoids) come from the Lower Wordie Creek Formation of East Greenland, a locality that also yielded the only record of common Lower Triassic sponge spicules (Twitchett, personal communication). This suggests complex relations between observed evolutionary patterns and quality of the fossil record. As the Lazarus effect stands as a large interface between these two poles, its relevance for studies of palaeodiversifications is fundamental as it has a lot to reveal about the adequacy of the fossil record. In particular, the Lazarus effect could provide an independent test of the recent claim of a standard recovery delay following mass extinctions, regardless of their magnitude (Kirchner and Weil 2000). It seems paradoxical that the Lazarus notion, so commonly found in the literature, is still virtually unknown in terms of its taxonomic properties, its spatio-temporal scale-dependence, and its phylogenetic distribution. These are obvious topics for future works. Finally, because many data are required to document the proximal causes of the Lazarus effect, the advent of computer-based relational databases, together with the analytical techniques discussed here, may considerably enlighten this pattern in the coming years.

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