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The Lilliput effect in the aftermath of the end-Permian extinction event

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Abstract

Early Triassic animal body fossils and trace fossils are small relative to those in older and younger intervals. Size decreases sharply through the end-Permian extinction event and Permian/Triassic boundary, and the smallest sizes are encountered in the *parvus* and *isarcica* Zones of the earliest Induan. Animals appearing within these two zones are also exceedingly small, compared to younger congenerics and conspecifics. Temporary, dramatic size decrease of surviving taxa in the immediate aftermath of the extinction event is an example of the Lilliput effect (coined by [Urbanek, A., 1993. Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. Historical Biology 7, 29–50.]). Body size increases somewhat from the *carinata* Zone (mid-Induan) but remains depressed for the duration of the Early Triassic, and pre-extinction sizes are not commonly recorded until at least the Middle Triassic. Marine and terrestrial faunas appear to be similarly affected. The Lilliput effect and longer term size reduction could be the result of several factors. Environmental parameters such as marine anoxia, due to low atmospheric concentrations of oxygen at this time coupled with sluggish ocean circulation in a greenhouse world, and food shortage are the likely proximal causes for the Early Triassic Lilliput effect. No single cause can explain all the observations, and a combination of factors are likely to be involved.

Keywords: Permian; Triassic; Body size; Fossil; Trace fossil

1. Introduction

A widespread, and yet little unstudied, evolutionary phenomenon is the "Lilliput effect". This term, coined by Urbanek (1993), describes the pattern of size change through extinction events: in the immediate aftermath of such events fossil organisms are typically much smaller than during pre-extinction times. Body size is a key morphological variable, with implications for many aspects of an animal's biology, behaviour, and ecology (e.g. Barbault, 1988; Cotgreave, 1993). Understanding the Lilliput effect may therefore be crucial in understanding the nature of ecological, environmental, and biological change during past biotic crises, especially during the immediate post-event aftermath.

Urbanek's (1993) initial study documented a size decrease in several graptolite taxa in the wake of relatively small-scale biotic crises in the Late Silurian. The Lilliput effect comprised one facet of his "post-event syndrome", which affected the surviving taxa (the "relic assemblage"). Fossil assemblages affected by this "post-event syndrome" are characterised by low diversity, high abundance, and small body size (Urbanek, 1993). Such assemblages are found in the immediate

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aftermath, or Survival Interval (sensu Kauffman and Erwin, 1995), of many extinction events, although Urbanek's (1993) terminology has rarely been specifically used in descriptions of such fossil assemblages.

The Lilliput effect apparently occurred in the aftermath of most of the major Phanerozoic extinction episodes, and has been documented in a variety of animal groups, such as Early Silurian corals (Kaljo, 1996), Late Devonian conodonts (Girard and Renaud, 1996; Renaud and Girard, 1999), and Early Danian echinoids (Jeffery, 2001), although the term "Lilliput effect" was not used by these authors. There is growing evidence that the phenomenon occurs after other biotic crises as well (e.g. in several molluscan taxa during the Pliensbachian–Toarcian event of the Early Jurassic; personal observation). It appears, therefore, to be one factor that is common to all known extinction crises and has important implications for our understanding of the response of organisms to ecological disturbance at both global and local scale. It may even allow us to predict the future response of the biosphere to present-day environmental change.

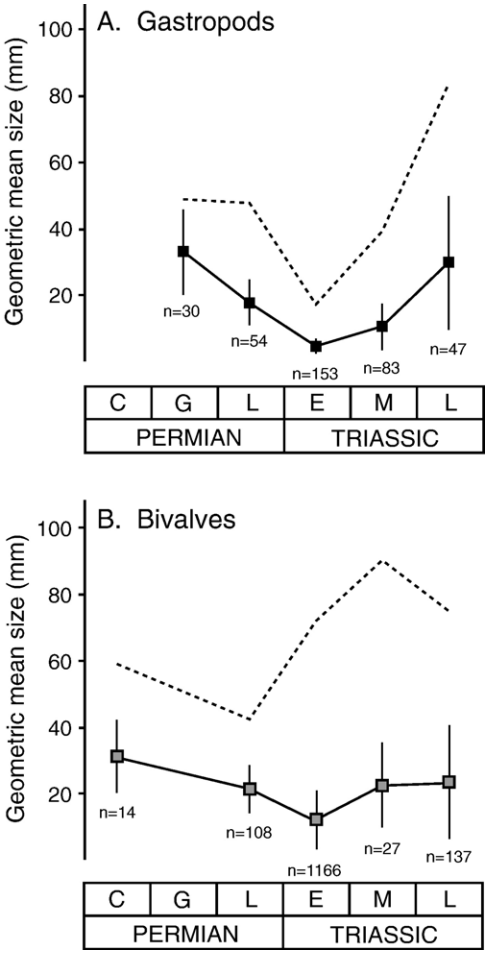

Fig. 1. Preliminary data of size change through the Permian and Triassic in gastropods (A) and bivalves (B). Square symbols show mean geometric size; vertical bars indicate one standard deviation above and below the mean; dashed line shows maximum geometric size. Data were collected by measuring fossil specimens in the collections of the Natural History Museum London, supplemented by measurements made on specimens in the field. Data are recorded in Table 1. Full data set is available from the author on request. C=Cisuralian; G=Guadalupian; L=Lopingian; E=Early; M=Middle; L=Late.

The mass extinction event that occurred in the latest Permian was the most severe event of the Phanerozoic (e.g. Erwin, 1993, 1994; Benton, 1995). It is ranked first for both the magnitude of the diversity loss as well as for the severity of the ecological impact on the marine and terrestrial ecosystems of the Earth (McGhee et al., 2004). It has long been recognised that the low diversity assemblages of the Early Triassic aftermath are predominantly composed of abundant, small-sized organisms (e.g. Newell, 1952; Schubert and Bottjer, 1995), which are typical attributes of Urbanek's (1993) "post-event syndrome". Previous data have been a mixture of largely qualitative or semi-quantitative studies. The aims of this study are to assess the evidence for size decrease during the Permian–Triassic extinction event, to document the duration of the Lilliput effect, and to discuss some of the potential causes of this phenomenon.

2. Small body size in the Early Triassic

Newell (1952) was one of the first to note in print that Early Triassic fossils are small, although many subsequent authors have come to the same conclusion since (e.g. Hayami, 1997, 1998). Certainly, the surprisingly small size of the fossils is one of the most striking aspects of collecting in Lower Triassic strata, and this observation does not change over successive field seasons. Despite more than a decade of collecting and museum studies worldwide, I have yet to find an Early Triassic bivalve more than 80 mm in size, or an Early Triassic gastropod more than 40 mm, and most are substantially smaller.

Such qualitative observations are also supported by more semi-quantitative data. Hayami's (1998) study of bivalve size through time, based on analysis of data in the *Treatise on Invertebrate Paleontology*, showed that the average geometric mean size of Early Triassic bivalve genera (25.8 mm) is smaller than genera from the Middle Triassic (27.2 mm) and Early Permian (27.0 mm), although because of the way the data are presented it is unclear whether these differences are statistically significant. The data presented in Hayami (1998) do not, however, show a reduction in mean size across the

Table 1
Geometric sizes of bivalve and gastropod specimens through the Permian–Triassic interval

	Permian			Triassic		
	Cissuralian	Guadalupian	Lopingian	Early	Middle	Late
Gastropods						
Mean (mm)	–	33.0	17.9	4.9	10.5	29.9
s.d. (mm)	–	13.0	6.9	2.6	7.4	20.2
Maximum (mm)	–	49.1	48.7	17.0	39.0	83.5
n	–	30	54	153	83	47
Bivalves						
Mean (mm)	31.2	–	21.3	12.1	22.3	23.4
s.d. (mm)	11.2	–	7.3	0.9	13.0	17.3
Maximum (mm)	58.8	–	42.4	80	47	75.2
n	14	–	108	1166	27	137

Permian/Triassic (P/Tr) boundary, as was claimed in a previous publication (Hayami, 1997), and Late Permian genera are smaller (mean size 23.7 mm) than Early Triassic taxa. However, the proportion of very large-sized genera (i.e. those in excess of 64 mm) does appear to decrease across the P/Tr boundary (Hayami, 1998, p. 39).

Other molluscan taxa are also smaller in the Early Triassic. "Microgastropods", which are defined as being gastropods that are less than 10 mm in height (Fraiser and Bottjer, 2004), are so common in Lower Triassic rocks that they may reach rock-building densities (Fraiser et al., 2005). Early Triassic gastropod assemblages in all known marine environments are dominated by microgastropod species, whereas Permian, Middle Triassic, or modern gastropod assemblages tend to be dominated by larger gastropods (Fraiser and Bottjer, 2004). In a parallel study based on literature review, Payne (2005) also demonstrated a similar pattern of size change in Permian–Triassic (P–Tr) gastropods: namely, size decrease into the Early Triassic followed by size increase in the Middle Triassic.

As a complementary study to the literature-based compilations by Payne (2005) and Hayami (1998), I am compiling data from measurements based on actual fossil specimens from field studies and museum collections. Preliminary results are shown here plotted at series scale (Fig. 1, Table 1) and the patterns of size change through the Permian and Triassic are very similar to those found in previous studies. Both the mean and maximum body sizes of gastropods decrease through the Permian to reach a minimum in the Early Triassic, before increasing during the subsequent Triassic (Fig. 1A). The mean body size of bivalves also reaches a minimum in the Early Triassic, although the maximum size (e.g. specimens of *Claraia* from the Perth Basin of western Australia) exceeds that of the Lopingian.

Similar patterns are seen in all other benthic groups studied thus far. For example, Early Triassic ophiuroids are much smaller (maximum disk diameter of 10 mm) than Middle Triassic (20 mm), modern temperate (30 mm), or modern tropical (45 mm) taxa (Twitchett et al., 2005). Small body size is also characteristic of Early Triassic marine and terrestrial vertebrates (e.g. Smith, 1995; Tverdokhlebov et al., 2002), although quantitative data of size change are currently lacking. Early Triassic terrestrial ecosystems are typically described as being dominated by small organisms, at least in the very earliest Triassic. In Russia, small temnospondyls characterise the beginning of the Triassic, and the ecological niches for large herbivores and predators were unoccupied (Tverdokhlebov et al., 2002). Similarly, in South Africa it appears that the terrestrial ecosystems of the Early Triassic were dominated by small sized tetrapods (Smith, 1995).

These qualitative and quantitative data give a first order understanding of P–Tr size change at the stage or series level. All animal groups apparently record identical changes, with size minima in the Early Triassic. However, a few studies have also documented size changes at a much higher resolution (i.e. sub-stage or zonal scale). The earliest such study involved analyses of the diameter of trace fossil burrows from the Bellerophon and Werfen formations of northern Italy (Twitchett, 1999). From the Late Permian Bellerophon Formation into the *parvus* and *isarcica* conodont zones (i.e. early–mid Griesbachian, earliest Induan) of the Werfen Formation, burrow diameter decreased by an order of magnitude. As burrow diameter is a good proxy of the size of the organism that made the burrow (e.g. Savrda et al., 1984; Savrda and Bottjer, 1986), these data imply a dramatic reduction in the body sizes of the infaunal, soft-bodied, trace-making community.

Since this initial study, further field measurements have been made through the same succession – the data set now

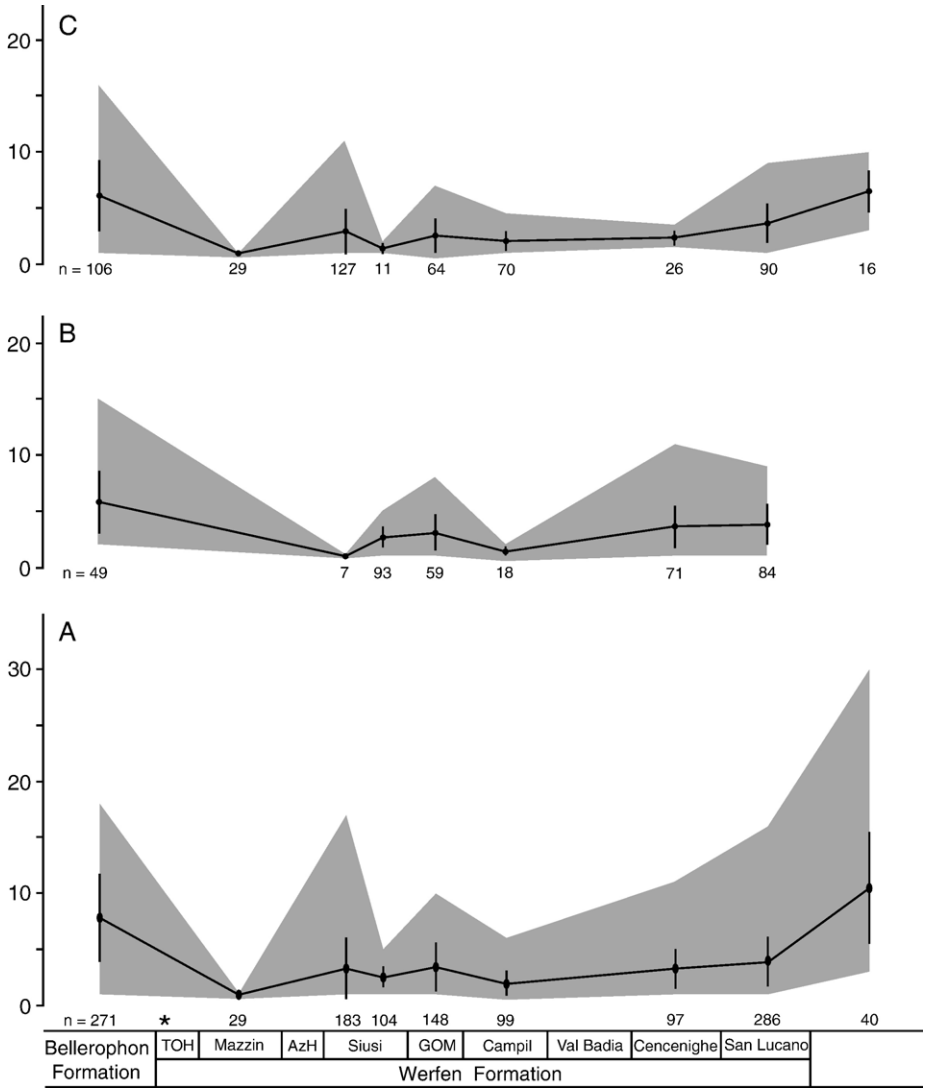

Fig. 2. Burrow diameters of trace fossils through the Late Permian to Middle Triassic of the Dolomites, northern Italy. A: all burrow types; B: vertical domichnia of suspension feeders (i.e. *Arenicolites*, *Skolithos*, *Diplocraterion*); C: fodinichnia of deposit feeders (i.e. *Planolites*). Circles indicate mean value; vertical lines indicate one standard deviation above, and below, the mean; shaded region indicates total burrow range between the maximum and minimum recorded sizes. Measurements recorded in the field to the nearest 0.5 mm. TOH = Tesero Oolite Horizon; AzH = Andraz Horizon; GOM = Gastropod Oolite Member.

comprises some 1257 samples – yet the patterns remain robust (Fig. 2). The initial decrease in both maximum and mean burrow size from the Bellerophon Formation into the Mazzin Member of the Werfen Formation remains the most severe decline. Following this there is a gradual increase in mean burrow size through the Early Triassic, interrupted by temporary decreases in the upper Siusi Member and Campil Member. Similar patterns are observed when the domichnia of suspension feeders (e.g. *Arenicolites*, *Skolithos*) and the fodinichnia (e.g. *Planolites*) are considered separately (Fig. 2). One or two rare, large burrows are encountered in the lower Siusi Member and San Lucano Member, but it is not until the Anisian that burrow size commonly exceeds 10–15 mm, with *Thalassinoides* reaching 30 mm and *Rhizocorallium* reaching 20 mm in diameter.

Recent work on the shelly body fossils of the Late Permian and Early Triassic record of northern Italy has revealed similar patterns of size change (Price-Lloyd and Twitchett, 2002) (Fig. 3). The taxa *Bellerophon* and *Lingula* show statistically significant reductions in body size from the Bellerophon Formation through the extinction event into the Mazzin Member of the Werfen Formation. In addition, taxa which appear in the

immediate aftermath of the event, namely *Claraia* and *Unionites*, are also smallest in the Mazzin Member. All taxa show significant increases in body size in the lower Siusi Member.

3. The Early Triassic Lilliput effect

Urbanek's (1993) definition of the Lilliput effect describes it as "the occurrence of diminuative forms among some of the species in the relic assemblages" of the immediate post-extinction aftermath. In other words, the Lilliput effect, as originally defined, describes size reduction within specific taxa (species) that survive the extinction event and is a temporary phenomenon confined to the Survival Interval (sensu Kauffman and Erwin, 1995). The classic example of the Lilliput effect described by Urbanek (1993) is the mass occurrence of short and slim *Pristiograptus dubius* in the aftermath of the *lundgreni* Event. The taxon *P. dubius* spans the entire extinction–recovery interval, although the Lilliput forms are assigned to the subspecies *P. dubius parvus*, whereas the 'normal' pre-extinction, and later recovery, forms are assigned to the subspecies *P. dubius frequens*.

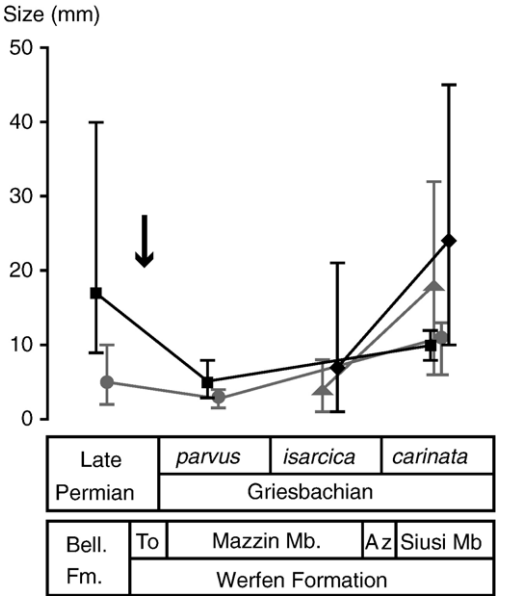

Fig. 3. Size change in benthic marine invertebrates in the aftermath of the end-Permian extinction event. Black square = *Bellerophon* (n = 42); grey circle = *Lingula* (n = 195); black diamond = *Claraia* (n = 721); grey triangle = *Unionites* (n = 258). Symbols show mean size; horizontal lines indicate maximum and minimum recorded sizes. Size calculated as the geometric mean of length and height. All within-taxon size changes are significant at the 5% level (Kolmogorov–Smirnov test). Data collected in the field from localities in northern Italy (Bellerophon and Werfen formations). The Griesbachian is divided into three conodont zones: *parvus*, *isarcica,* and *carinata*. Arrow indicates approximate position of extinction event. Data from Price-Lloyd and Twitchett (2002). Bell Fm = Bellerophon Formation; To = Tesero Oolite Horizon; Mb = Member; Az = Andraz Horizon.

Adhering to Urbanek's original definition of the Lilliput effect, it is clear that the only Permian–Triassic data described above that could fit with this definition are the statistically significant, short-term size changes within the surviving taxa *Lingula* and *Bellerophon* during the Griesbachian (early Induan), which were first described by Price-Lloyd and Twitchett (2002). Poor preservation and dramatic size change mean that the Lilliput forms of these taxa in the Dolomites sections are typically not assigned to species, but are usually referred to as *Lingula* sp. or *Bellerophon* sp. Until further taxonomic study is undertaken, it is not possible to be certain that size reduction is happening at the specific or generic level.

Regardless, it is clear that the remaining data concerning size reduction in the Early Triassic (documented above) do not comfortably fit within Urbanek's (1993) definition of the Lilliput effect: small size is recorded in newly originating taxa as well as surviving taxa; in the relative proportions of 'small' and 'large' species within higher taxa; and through the whole of the Early Triassic, not just the immediate post-extinction aftermath. This represents a larger-scale, longer-term depression of body size, affecting the entire fauna (survivors as well as newly originating taxa) and lasting through the Survival Interval and well into the Recovery Interval. This is not the Lilliput effect in the sense of Urbanek (1993) and may or may not be related to the extinction event. The apparent long-term decline in body size through the Permian (e.g. Fig. 1) may be related to long term environmental changes (see below) or successive extinction events (end-Guadalupian, end-Permian). Typically, studies based largely on literature review and/or semi-quantitative analyses of taxa at the generic or family level (e.g. Payne, 2005) will highlight this longer term depression of body size, whereas measurements of individual, well-dated specimens from field or museum collections are necessary to document the shorter term Lilliput effect. Regarding trace fossils: size reduction within specific ichnogenera or ichnospecies in the immediate aftermath of an extinction event is herein considered to also represent the Lilliput effect, although it is recognised that a single ichnotaxon may have been produced by more than one animal species. Studies showing a size reduction of the entire ichnofauna, without identifying the individual ichnotaxa (e.g. Twitchett, 1999; Fig. 1), do not demonstrate the Lilliput effect in the strict sense, but do record this longer term depression of body size.

4. Causes of size reduction and the Lilliput effect

4.1. Evolutionary patterns

The Lilliput effect and the longer-term Early Triassic size reduction are recorded at different taxonomic scales, are of different durations and may be the result of similar, or entirely different, processes. Questions concerning the causes of post-extinction size decrease can also be addressed in several ways. The nature of these hypotheses are quite different, with the larger scale incorporating preservational and taphonomic effects as well as (potentially) macroevolutionary factors, whereas at the scale of an individual species, the biological responses of individual organisms to local environmental change are probably most important. Urbanek (1993) discussed the ecophenotypic response of individuals to palaeoenvironmental changes in parameters such as temperature, salinity and food supply, but concluded that competing alternatives could not be tested from fossil remains. However, regarding the Permian–Triassic interval, it may be possible to reject at least some of these competing possibilities (see below). Finally, one significant factor in the interpretation of the observed changes in size is the nature of the data, including both the taxonomic level of analysis and the parameter under consideration: is a reduction being recorded in maximum size, minimum size, and mean size, or in one or two, but not all three, of these parameters?

4.1.1. Extinction of large taxa?

A seemingly simple explanation for post-extinction size reduction is the extinction of large-bodied (*K*-selected) taxa leaving only small-bodied survivors. Assuming that some time would be required for new large-sized taxa to evolve from small-sized survivors, extinction of large taxa would result in a reduction in both the maximum and mean size of taxa present in the immediate extinction aftermath, but not necessarily any change in the minimum size (Fig. 4). However, simple extinction of large taxa is not a potential explanation of the Lilliput effect, as short-term, post-extinction, within-lineage size decrease in surviving (i.e. small) species would not be predicted to occur. Loss of large taxa is recorded at many events and in many groups of organisms, such as during the end-Cretaceous event where it is responsible for a difference in the maximum sizes of pre- and post-event planktonic foraminifera.

A more intriguing problem is whether extinction of large taxa is the result of random chance or the result of active size selection against large taxa during major extinction events. Large-bodied animals should be more

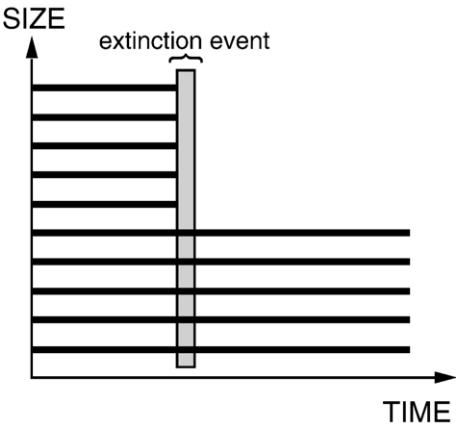

Fig. 4. Simplified model showing the effect of a selective extinction event on the size distribution of the taxa in the immediate extinction aftermath. Horizontal lines represent the hypothetical fossil ranges of taxa at a number of different hypothetical sizes. Note a decrease in maximum and mean size following the event.

susceptible to extinction for a variety of reasons including their greater energy requirements, longer generation times, and relatively lower population sizes (Labarbera, 1986; Barbault, 1988; Cotgreave, 1993; Jablonski, 1996). Hayami (1997) invoked size selection as an explanation for size changes in Cretaceous–Tertiary (K–T) and P–Tr bivalves. Regarding the K–T event, the communities of small vertebrates or planktonic foraminifera of the earliest Danian have also been previously interpreted as being the result of selection against large-bodied forms at this time (see Jablonski, 1996 and refs. therein).

Recent data have, however, cast doubt on the size-selection hypothesis. At the Cretaceous/Tertiary (K/T) boundary event, while all of the large, specialist (*K*-selected) planktonic foraminifera disappeared, so did all the small trochospiral ecological generalist taxa (except the hedbergellids, which became extinct in the early Danian) (Keller, 2003). While very large taxa are demonstrably absent from Danian assemblages, the taxa that became extinct were not exclusively large. Regarding the vertebrates, Jablonski (1996) has argued that the K–T data are the result of clade-specific rather than size-specific selectivity: all large Maastrichtian land animals were "non-avian dinosaurs", and all "non-avian dinosaurs" (both large and small) became extinct. Data on marine invertebrates (bivalves and gastropods) show no size difference between survivors and victims (Jablonski and Raup, 1995; Jablonski, 1996). A recent study of bivalves through the K–T, mid-Eocene, and Eocene–Oligocene events also found no evidence that the extinctions were size-selective at the genus level (Lockwood, 2005). Likewise, a comprehensive study of K–T echinoids also shows that

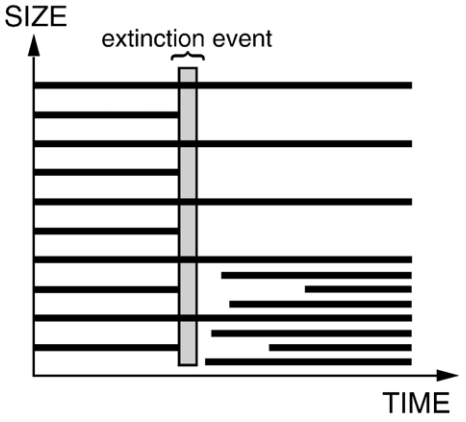

Fig. 5. Simplified model showing the effect on post-extinction origination of many small taxa on the size distribution of the post-extinction community. Horizontal lines represent hypothetical fossil ranges of taxa at a number of different hypothetical sizes. Note that the extinction is random with respect to size and that the maximum size is unaffected.

size selection played no part in the extinction event (Smith and Jeffrey, 1998), although a number of surviving lineages did become smaller (the Lilliput effect) (Jeffery, 2001). While some examples of post-extinction size increase have been explained in terms of changes in life-history strategy (e.g. Hallam, 1975), to date no study has yet demonstrated that extinction events themselves are size-selective.

In summary, while it is obvious that large-bodied taxa do become extinct, and are therefore missing from the post-extinction communities, no quantitative study has yet demonstrated that larger taxa are preferentially lost. It should be noted, however, that most quantitative studies documented to date have involved the K–T event and few quantitative tests of size selection have hitherto been published for other extinction intervals. Extinction of large-bodied animals during the Late Permian event is considered to be a contributory factor in the long term post-extinction depression of body size during the Early Triassic, but it is not a cause of the short-term Lilliput effect. Likewise, loss of large taxa during the end-Guadalupian event may have contributed to the decline in maximum and mean size of, for example, gastropods through the latter half of the Permian (Fig. 1A).

4.1.2. The post-crisis appearance of many small taxa?

Regardless of whether the extinction episode was selective against large animals, the fact that Early Triassic fossils appear to be smaller than expected may be due to the appearance of a large number of small taxa in the extinction aftermath (Fig. 5). Unlike the previous hypothesis (Fig. 4), this pattern of size change involves a reduction in the mean, and possibly minimum, body size of taxa in the post-extinction assemblages, but the maximum body size should remain more or less the same. Likewise, within-species size reduction in surviving taxa is not predicted, and so this mechanism cannot explain the Lilliput effect. Two factors could be involved: (1) the origination of new taxa and/or (2) the appearance of pioneering opportunists.

Stanley (1973) observed that, generally, animal taxa tend to originate at small size. Extinction events involve widespread loss of biodiversity, presumably leaving many vacant niches, which should promote the appearance and radiation of many new groups. Therefore, if Stanley's (1973) hypothesis is correct, the aftermath of an extinction event should be an interval with above average numbers of newly originating, small species. The founders of these new groups have been termed "crisis progenitors" and do, indeed, tend to be small sized (Kauffman and Harries, 1996). To date, the only exception to this general rule is in the aftermath of the Eocene–Oligocene event, where newly originating bivalve genera were apparently larger than surviving taxa (Lockwood, 2005).

An alternative is that extinction events cause an explosion in pioneering opportunists, i.e. long ranging taxa that were already present locally prior to the event but which undergo rapid expansion in numbers (blooms) in the disturbed environments of the immediate aftermath (Kauffman and Harries, 1996). Communities dominated by opportunists occur in the wake of modern, smaller-scale, defaunation events, following removal of the previous climax community. Some authors also regard opportunism as an important survival strategy during time of mass extinction (Harries et al., 1996), and the appearance of post-extinction opportunists may therefore be expected. Opportunists are often described as being r-selected taxa (i.e. animals whose reproductive strategy involves early maturation and the production of a large number of offspring). A common trait of such taxa is small size, and if all Early Triassic environments were disturbed, and if all communities were dominated by opportunists, then this could be an explanation for the smaller than expected body sizes encountered. Certainly, Fraiser and Bottjer (2004) interpreted the microgastropods of the Early Triassic as opportunists. However, it is often difficult to identify the age of maturation and/or the size and number of offspring produced in fossil examples and small size alone is not an unequivocal indicator of opportunism. For example, trace fossil evidence from Early Triassic marginal marine facies of the western USA and northern Italy indicates the presence of persistent climax communities of small-sized ophiuroids (Twitchett et al., 2005).

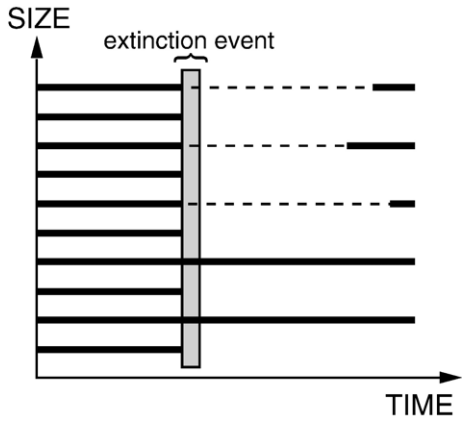

Fig. 6. Simplified model showing the effect of a temporary disappearance of large sized taxa on the size distribution of the post-extinction community. Horizontal lines represent hypothetical fossil ranges; dashed lines indicate Lazarus taxa. Note that the extinction is random with respect to size and the preserved taxa (solid lines) in the extinction aftermath show a reduction in maximum and mean body size with respect to the pre-event community.

Data from the Lower Triassic Werfen Formation of northern Italy show that the bivalve taxa *Unionites* and *Claraia*, which appear in the immediate aftermath of the biotic crisis, are indeed smaller than later examples of the same genera (Fig. 3). Microgastropods, which may or may not be opportunists, are also very widespread throughout most of the Early Triassic (Fraiser et al., 2005). However, it is also clear from studies conducted to date that there was undoubtedly a reduction in the maximum size of Early Triassic taxa (e.g. Payne, 2005) (cf. Fig. 5). Thus, while the widespread appearance of small taxa (either newly originating species or blooms of opportunists) in the extinction aftermath may be a contributory factor, it is not the sole explanation for the observed size changes in P–Tr animal groups.

4.1.3. The temporary disappearance of large taxa?

It is possible that the absence of large taxa through most of the Early Triassic is not a real biological phenomenon at all, but may be an artefact of the fossil record, and caused by differences in the preservation potential of large and small taxa through an extinction interval. If large taxa temporarily disappear from the fossil record, then only small taxa will be found as fossils, and thus both the mean and maximum body size of the post-extinction fossil assemblage will be reduced (Fig. 6).

Taxa that temporarily disappear from the fossil record are termed "Lazarus taxa". This term was coined to describe the temporary disappearance of taxa through extinction events (Flessa and Jablonski, 1983) and the Lazarus effect has been documented through all major extinction episodes and in a number of groups such as P–Tr gastropods (Erwin, 1996), sponges, and bivalves (Twitchett, 2001). Can the Lilliput effect be explained by a size bias in the Lazarus effect?

Such a bias has yet to be demonstrated. Temporary disappearance of specific taxa from the fossil record may be caused in a number of different ways, including basic rock-record bias such as the temporary absence of fossiliferous rocks of the correct facies (Paul and Donovan, 1998; Smith, 2001). Certain marginal environments, such as brackish estuaries or hypersaline lagoons, tend to be dominated by small animals. If the Lower Triassic rock record comprised many more examples of facies deposited in such settings than the Lopingian or later Triassic records, then the sampled fossil record could be biased towards smaller-sized organisms. Burrow size minima in the upper Siusi Member and Campil Member of the Werfen Formation (Fig. 2) are attributed to the marginal, brackish depositional environment of these units (Twitchett, 1999). Other possible biases include changes in the nature of fossil preservation: for example, Erwin's (1996) hypothesis that a dearth of Early Triassic silicified faunas may be to blame for the P–Tr Lazarus effect in gastropods, as early silicification can help preserve aragonitic shells, which otherwise may dissolve prior to fossilisation.

Another possibility is that population size determines whether or not a particular species will be represented in the fossil record (Marshall, 1998; Wignall and Benton, 1999). This model assumes that the chance of any particular individual entering the fossil record is vanishingly small, so only the most populous taxa will be fossilised. Populations of living organisms fluctuate in response to ecological and environmental events. Should numbers temporarily fall below the threshold for entering the fossil record, then that particular taxon will become a Lazarus taxon until population size recovers once more (Twitchett, 2001; see also discussion in Fara, 2001). As large-bodied animals generally have lower population sizes than smaller ones, they may be more susceptible to falling below this fossilisation threshold. It is assumed that an extinction event, if it were to have any affect on the numbers of living animals, would reduce, rather than increase, population sizes.

Given the complexity of the processes leading to fossilisation, in particular time averaging, assessing the absolute (or even relative) population sizes of extinct organisms from their fossil remains is not possible. Therefore, the assumptions of the population-dependent model are very difficult to test (see discussion in Twitchett, 2001). However, the possibility that there is a bias in the Lazarus effect between large and small taxa

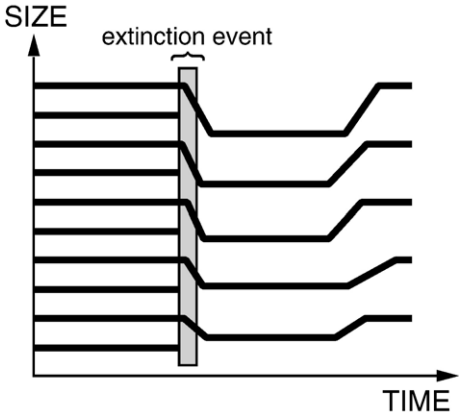

Fig. 7. Simplified model showing the effect of a temporary reduction in the body sizes of surviving taxa on the size distribution of the post-extinction community. Horizontal lines represent hypothetical fossil ranges of taxa at a number of different sizes. Note that the extinction is random with respect to size and there is an overall reduction in maximum, mean and minimum size.

(Fig. 6) can be tested, and if it exists would be a possible explanation for the apparent absence of large individuals and large taxa in the aftermath of the end-Permian mass extinction event. Erwin (1996) demonstrated that the Lazarus effect in gastropods increases from the Middle Permian through to the Early Triassic, which matches the pattern of gastropod size change recorded during this interval (Fig. 1).

4.1.4. Within-lineage size decrease?

A fourth alternative is that surviving taxa all underwent a reduction in body size in the aftermath of the extinction event such that fossilised individuals of particular species are smaller in the post-extinction interval than during the pre-extinction times (Fig. 7). Maximum, mean and minimum sizes would all be reduced. The Lilliput effect, as defined by Urbanek (1993), represents temporary size decrease within surviving species that lasted on the order of a few hundred thousand years. If such a size decrease lasted for a much longer interval of time (i.e. many millions of years) then it could also be a contributory factor to the lengthy post-extinction body size low that lasts through the entire Early Triassic.

There are several possible ways to achieve size reduction within a fossil taxon. Ecophenotypic responses to changes in parameters such as temperature, salinity, oxygen levels, and food supply are most likely, and the latter two are more fully explored below (see also Hallam, 1965; Lockwood, 2005; Twitchett, 2006). The Lilliput effect would be caused by relatively short term changes, whereas longer term reductions in size would imply suboptimal environmental conditions lasting many millions of years. Suboptimal environmental conditions may lead to slow growth rates and stunting, or may promote heterochronic changes such as an earlier onset of maturity (progenesis). Analysis of growth lines within shelly taxa could be used to explore these alternatives further, but no such study has yet been published for any taxon through any extinction interval. Suboptimal environmental conditions might also place upper limits on the size of newly originating species. High juvenile mortality in the wake of the extinction event is rejected as a possible explanation as it may reduce the mean and minimum size of fossilised individuals but not the maximum size. Indeed, in all discussions concerning the Lilliput effect and size reduction the assumption is made that we are dealing with changes in the adult forms. Likewise, although it is possible that different taxonomic groups were responding to different environmental pressures, the fact that size reduction affects both shelly taxa and non-mineralised burrowing infauna (Figs. 1–3) strongly implies that it was not solely caused by a problem with skeletal secretion or biocalcification. Finally, when dealing with fossilised remains it is best to bear in mind other potential causes such as biases in fossilisation. For example, there may be an under-representation of large individuals through rarity (c.f. hypothesis 3 above). As discussed by Urbanek (1993), genetic changes are probably not responsible and so are not considered further here.

Possible evidence of within-lineage size decrease (temporary stunting) associated with the end-Permian extinction event is given by studies of *Bellerophon* and *Lingula* from northern Italy (Fig. 3). However, unresolved taxonomic issues mean that it is not possible to be certain that size reduction is happening at the species or generic level. The strict definition of the Lilliput effect (sensu Urbanek, 1993) implies that size reduction is occurring within species (however defined).

4.1.5. All of the above?

The four alternative explanations for the Lilliput effect, outlined above, can all be distinguished with fossil data, as the predicted patterns of size distribution are different in all cases (Figs. 4–7). Of course, it is quite possible that different patterns will be observed in different taxonomic groups during the same extinction-recovery event, that different events may record different patterns of size distribution, or that some taxa may show a combination of patterns (c.f. Lockwood, 2005). During the P–Tr interval, small size characterises both survivors and newly appearing taxa and thus involves at least a combination of hypotheses (2) and (4) above. A thorough, quantitative test of hypotheses (1) and (3) has yet to be attempted for this extinction event.

4.2. Environmental controls on body size

Stanley (1973) hypothesised that for any given set of environmental parameters there is an optimal body size for animals, and that size trends result from the process of attaining optimal size in the face of changing environmental conditions. If the aftermaths of mass extinction events represent times when environmental conditions are such that small size is the optimum, then this would explain both within-lineage size decrease and the small sizes of newly appearing taxa. While many environmental factors may result in size decrease (Hallam, 1965), two are considered most important with regards to explaining the Lilliput effect in the aftermath of the end-Permian extinction event: anoxia and food shortage.

4.2.1. Anoxia

A substantial body of evidence has accumulated that demonstrates that anoxic, and even euxinic, conditions were widespread in most marine environments and regions through most of the Early Triassic (e.g. Wignall and Twitchett, 1996, 2002; Grice et al., 2005). In the deep ocean, oxygen restriction lasted from the Lopingian to Middle Triassic (e.g. Isozaki, 1997), whereas in some shallow shelves marine anoxia is only recorded in the early Induan (e.g. Wignall and Twitchett, 1996). Taking a global view, peak anoxia (i.e. the widest geographic spread of oxygen-poor waters) occurred in the *parvus* and *isarcica* zones of the early Induan (Wignall and Twitchett, 2002). At this time, only shallow seamounts and offshore highs were free of evidence of marine anoxia (e.g. Krystyn et al., 2003). Low oxygen conditions were probably the direct result of global warming and a subsequent sluggishness in oceanic circulation, and have been recreated in computer simulation models (Hotinski et al., 2001). High temperatures would have also have caused a decrease in the amount of dissolved oxygen in the oceans, exacerbated by the relatively low concentration of oxygen within the atmosphere (Berner, 2005).

A large number of published data, from both modern experimental studies and analyses of the fossil record, have demonstrated the link between oxygen concentration and body size. Episodes of surprisingly large body size in terrestrial animals correlate with times of high atmospheric oxygen and the inferred cause–effect link has been strengthened by modern experiments, such as in regard to Carboniferous dragonflies (Graham et al., 1995; Harrison and Lighton, 1998). Likewise, in marine settings Rhoads and Morse (1971) and Savrda et al. (1984) demonstrated that as the oxygen concentration in bottom waters decreases so does the size of marine animals inhabiting the substrate. In fossil and modern examples this is most often demonstrated by measuring the size of burrows that these animals leave behind (e.g. Savrda and Bottjer, 1986). Finally, experimental data generally show that animals reach smaller maximum adult size, and/or mature at smaller size, under conditions of sub-lethal hypoxia (e.g. in copepods; Richmond et al., 2006).

Regarding the data from northern Italy (Figs. 2 and 3), the smallest burrow diameters and smallest shelly invertebrates are found in the Mazzin Member of the Werfen Formation. This unit was deposited under very low, but fluctuating, oxygen conditions as indicated by facies analysis and geochemistry (Wignall and Twitchett, 1996, 2002). In localities of identical age, but where facies indicate well oxygenated conditions, such as in Oman (Krystyn et al., 2003), diversity is much higher and the sizes of shelly taxa (e.g. gastropods) are also slightly larger (Twitchett et al., 2004; Wheeley and Twitchett, 2005). Thus, from these preliminary data, the correspondence between body size decrease and anoxia is good, suggesting that it may be a possible cause of the Lilliput effect in the *parvus* and *isarcica* zones of the Induan. The very low atmospheric oxygen levels that apparently characterised the entire Early Triassic (Berner, 2005) may be a cause of the longer-term depression of body sizes observed in all animal groups studied to date.

However, while there is some correspondence between low oxygen levels and small size in these data, it also seems apparent that anoxia alone cannot account for all the data thus far collected. In northern Italy, the Lilliput effect lasts until the latest Griesbachian and sizes begin to increase in the lower Siusi Member of the Werfen Formation (Figs. 2 and 3). The lower Siusi Member, however, is still affected by low oxygen conditions to some extent (e.g. Wignall and Twitchett, 1996). Also, there are significant regional differences in the sizes of some taxa that cannot be explained by differences in oxygen levels. Measurements of the sizes of individual *Claraia* specimens from the basal Wordie Creek Formation of East Greenland and the Hovea Member of the Kockatea Shale Formation of Western Australia show that the Australian specimens are significantly larger (Fig. 8). Yet, all of these specimens, from both regions, derive from typical Griesbachian oxygen-restricted facies, characterised by dark grey, parallel-laminated mudstones with rare, bioturbated horizons that were formed under similar, fluctuating low oxygen conditions (e.g. Wignall and Twitchett, 2002; Grice et al., 2005). Thus, the size differences in this instance cannot be attributed to differences in environmental parameters that can be assessed from the rock record (such as relative oxygenation), but must be due to other factors that are more difficult to measure/observe from geochemical and facies

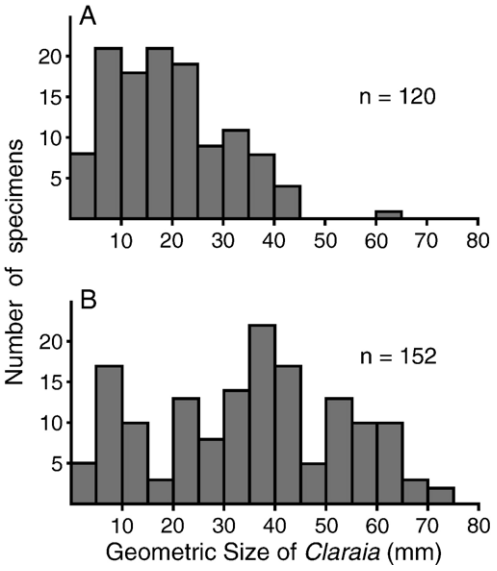

Fig. 8. Size distributions of *Claraia* specimens from oxygen-restricted biofacies of the earliest Triassic from East Greenland (A) and Western Australia (B). East Greenland specimens were measured in the laboratory from samples collected in the field. Australian samples were measured from the Hovea-3 core.

studies (such as temperature, salinity, food supply, etc.). Further comparative studies are clearly warranted.

4.2.2. Food shortage

Food shortage is one environmental factor that has long been associated with body size decrease in animals (Hallam, 1965), although in unicellular organisms, such as benthic foraminifera, oligotrophic conditions often promote size increase as species seek to compensate for food shortage by incorporating symbionts (Brasier, 1995). Within-lineage size decrease (Fig. 7) has been linked to productivity collapse and food shortage in Late Devonian conodont taxa (Girard and Renaud, 1996). Many modern studies show that growth rate and adult size in marine animals are dependent upon, and correlated with, food supply (e.g. Kingsford and Hughes, 2005). In addition, Twitchett (2001) recently proposed a model that links both within-lineage size decrease (Fig. 7) and temporary absence from the fossil record (Fig. 6) to an episode of primary productivity collapse and food shortage. If food supply is severely curtailed, then there will be an inevitable reduction in the biomass of taxa higher up the food chain. Biomass is a function of both body size and number of individual organisms. Therefore, the necessary reduction can take place in one of three ways: (1) a decrease in body size while maintaining population size; (2) a decrease in the number of individuals while maintaining body size; (3) a decrease in both body size and population. The latter two alternatives involve decreases in population, which will increase the possibility of extinction as well as decrease the chances of fossilisation (see also above discussion). Therefore, the only taxa expected to be present in the fossil record (i.e. actually found as fossils) during intervals of low primary productivity and food shortage are those that have undergone a reduction in body size.

Thus, food shortage could potentially be the cause of within-lineage size decrease and temporary absence of larger taxa from the fossil record (Figs. 6 and 7). It may also be a reason for the extinction of large taxa (Fig. 4), as these tend to have higher food requirements and lower population sizes, which would make them vulnerable to food shortage. Finally, if new taxa appeared during the episode of low food supply, then they too would suffer the same ecological constraints as the extinction survivors. This could also explain why taxa appearing in the extinction aftermath were small (Fig. 5). Subsequent size increase would only take place as food supply increased, as "normal" primary production was resumed.

A critical test for the food shortage hypothesis would be to demonstrate that the Lilliput changes were synchronous with a decrease in primary production. Good proxies for marine primary productivity exist in post-Jurassic strata, for example by comparing the $\delta^{13}C$ values of benthic and planktonic foraminifera (e.g. Zachos et al., 1989). In pre-Jurassic rocks, proxies for marine productivity are more problematic and the $\delta^{13}C$ record can be the result of several different processes such as terrestrial biomass burning, methane release, or volcanic activity (see Berner, 2002 for recent discussion). When tackling these older events, testing and rejecting alternative possible causes of size change (such as temperature change and benthic oxygen levels) will be one way forward, as the proxies for these environmental changes are less equivocal than are those for productivity levels. Some circumstantial evidence exists that the differences in the sizes of *Claraia* from East Greenland and Australia (Fig. 8) may have been caused by differences in food supply. Surface productivity may indeed have been higher in Western Australia, because sediments of the Hovea Member have a very high total organic carbon (TOC) content, and climate models have indicated a major upwelling centre close by (Grice et al., 2005 and refs therein). More work is clearly needed to resolve this issue.

5. Summary

Qualitative observations concerning size change through the Permian–Triassic interval are being supplemented by more quantitative analyses. These demonstrate

that all animal groups suffered a size reduction after the Late Permian extinction event and that body sizes remained low, relative to earlier Permian or later Triassic times, for the duration of the Early Triassic. In addition to this longer-term depression of body sizes, a shorter duration, more severe body size reduction is observed in the immediate aftermath of the extinction event affecting both survivors (i.e. the Lilliput effect) and newly originating taxa. This phenomenon is only observed in high resolution data, and spans the *parvus* and *isarcica* zones of the Griesbachian (early Induan). From the *carinata* Zone onwards body size recovers somewhat, but remains lower than expected until the Middle Triassic. A number of potential causes of the observed size changes have been proposed and these can be tested from geological data. It is likely that a combination of factors was involved. Environmental parameters such as low atmospheric and dissolved oxygen concentrations and food shortage caused by primary productivity collapse may all have played a role.

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References

Barbault, R., 1988. Body size, ecological constraints and the evolution of life-history strategies. Evolutionary Biology 22, 261–286.

Benton, M.J., 1995. Diversification and extinction in the history of life. Science 268, 52–58.

Berner, R.A., 2002. Examination of hypotheses for the Permo-Triassic boundary extinction by carbon cycle modelling. Proceedings of the National Academy of Sciences 99, 4172–4177.

Berner, R.A., 2005. The carbon and sulfur cycles and atmospheric oxygen from Middle Permian to Middle Triassic. Geochimica et Cosmochimica Acta 69, 3211–3217.

Brasier, M.D., 1995. Fossil indicators of nutrient levels. 2: evolution and extinction in relation to oligotrophy. In: Bosence, D.W.J., Allison, P.A. (Eds.), Marine Palaeoenvironmental Analysis From Fossils. Geological Society Special Publication, vol. 83, pp. 133–150.

Cotgreave, P., 1993. The relationship between body size and population abundance in animals. Trends in Ecology and Evolution 8, 244–248.

Erwin, D.H., 1993. The great Paleozoic crisis: life and death in the Permian. Columbia University Press, New York. 327 pp.

Erwin, D.H., 1994. The Permo-Triassic extinction. Nature 367, 231–236.

Erwin, D.H., 1996. Understanding biotic recoveries: extinction, survival, and preservation during the end-Permian Mass Extinction. In: Jablonski, D., Erwin, D.H., Lipps, J.H. (Eds.), Evolutionary Paleobiology. University of Chicago Press, Chicago, pp. 398–418.

Fara, E., 2001. What are Lazarus taxa? Geological Journal 36, 291–303.

Flessa, K.W., Jablonski, D., 1983. Extinction is here to stay. Paleobiology 9, 315–321.

Fraiser, M.L., Bottjer, D.J., 2004. The non-actualistic Early Triassic gastropod fauna: a case study of the Lower Triassic Sinbad Limestone Member. Palaios 19, 259–275.

Fraiser, M.L., Twitchett, R.J., Bottjer, D.J., 2005. Unique microgastropod biofacies in the Early Triassic: indicator of long-term biotic stress and the pattern of biotic recovery after the end-Permian mass extinction. Comptes Rendus Palevol 4, 543–552.

Girard, C., Renaud, S., 1996. Size variations in conodonts in response to the upper Kellwasser crisis (upper Devonian of the Montagne Noire, France). Comptes Rendus de l'Academie des Sciences, Serie IIa 323, 435–442.

Graham, J.B., Dudley, R., Aguilar, N.M., Gans, C., 1995. Implications of the Late Palaeozoic oxygen pulse for physiology and evolution. Nature 375, 117–120.

Grice, K., Cao, C., Love, G.D., Böttcher, M.E., Twitchett, R.J., Grosjean, E., Summons, R.E., Turgeon, S.C., William Dunning, W., Jin, Y., 2005. Photic zone euxinia during the Permian–Triassic Superanoxic Event. Science 307, 706–709.

Hallam, A., 1965. Environmental causes of stunting in living and fossil marine benthonic invertebrates. Palaeontology 8, 132–155.

Hallam, A., 1975. Evolutionary size increase and longevity in Jurassic bivalves and ammonites. Nature 258, 493–496.

Harries, P.J., Kauffman, E.G., Hansen, T.A., 1996. Models for biotic survival following mass extinction. In: Hart, M.B. (Ed.), Biotic Recovery from Mass Extinction Events. Geological Society of London Special Publications, vol. 102, pp. 41–60.

Harrison, J.F., Lighton, J.R.B., 1998. Oxygen-sensitive flight metabolism in the dragonfly *Erythemis simplicicollis*. Journal of Experimental Biology 201, 1739–1744.

Hayami, I., 1997. Size changes of bivalves and a hypothesis about the cause of mass extinction. Fossils 62, 24–36 (in Japanese).

Hayami, I., 1998. Ecology of mass extinctions: the diversity and shell size of bivalves through time. Iden 52, 38–44 (in Japanese).

Hotinski, R.M., Bice, K.L., Kump, L.R., Najjar, R.G., Arthur, M.A., 2001. Ocean stagnation and end-Permian anoxia. Geology 29, 7–10.

Isozaki, Y., 1997. Permo-Triassic boundary superanoxia and stratified superocean: records from lost deep sea. Science 276, 235–238.

Jablonski, D., 1996. Body size and macroevolution. In: Jablonski, D., Erwin, D.H., Lipps, J.H. (Eds.), Evolutionary Paleobiology. Chicago University Press, Chicago, pp. 256–289.

Jablonski, D., Raup, D.M., 1995. Selectivity of end-Cretaceous marine bivalve extinctions. Science 268, 389–391.

Jeffery, C.H., 2001. Heart urchins at the Cretaceous/Tertiary boundary: a tale of two clades. Paleobiology 27, 140–158.

Kaljo, D., 1996. Diachronous recovery patterns in Early Silurian corals, graptolites and acritarchs. In: Hart, M.B. (Ed.), Biotic Recovery from Mass Extinction Events. Geological Society, London, Special Publications, vol. 102, pp. 127–134.

Kauffman, E.G., Erwin, D.H., 1995. Surviving mass extinctions. Geotimes 14, 14–17.

Kauffman, E.G., Harries, P.J., 1996. The importance of crisis progenitors in recovery from mass extinction. In: Hart, M.B. (Ed.), Biotic

Recovery from Mass Extinction Events. Geological Society, London, Special Publications, vol. 102, pp. 15–39.
Keller, G., 2003. Biotic effects of impacts and volcanism. Earth and Planetary Science Letters 215, 249–264.
Kingsford, M.J., Hughes, J.M., 2005. Patterns of growth, mortality and size of the tropical damselfish *Acanthochromis polacanthus* across the continental shelf of the Great Barrier Reef. Fishery Bulletin 103, 561–573.
Krystyn, L., Baud, A., Richoz, S., Twitchett, R.J., 2003. A unique Permian–Triassic boundary section from Oman. Palaeogeography, Palaeoclimatology, Palaeoecology 191, 329–344.
Labarbera, M., 1986. The evolution and ecology of body size. In: Raup, D.M., Jablonski, D. (Eds.), Patterns and Processes in the History of Life. Springer-Verlag, Berlin, pp. 69–98.
Lockwood, R., 2005. Body size, extinction events, and the early Cenozoic record of veneroid bivalves: a new role for recoveries? Paleobiology 31, 578–590.
Marshall, C.R., 1998. Determining stratigraphic ranges. In: Donovan, S.K., Paul, C.R.C. (Eds.), The Adequacy of the Fossil Record. John Wiley and Sons, Chichester, pp. 23–54.
McGhee, G.R., Sheehan, P.M., Bottjer, D.J., Droser, M.L., 2004. Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic severities are decoupled. Palaeogeography, Palaeoclimatology, Palaeoecology 211, 289–297.
Newell, N.D., 1952. Periodicity in invertebrate evolution. Journal of Paleontology 26, 371–385.
Paul, C.R.C., Donovan, S.K., 1998. An overview of the completeness of the fossil record. In: Donovan, S.K., Paul, C.R.C. (Eds.), The Adequacy of the Fossil Record. John Wiley and Sons, Chichester, pp. 111–132.
Payne, J.L., 2005. Evolutionary dynamics of gastropod size across the end-Permian extinction and through the Triassic recovery interval. Paleobiology 31, 269–290.
Price-Lloyd, N., Twitchett, R.J., 2002. The Lilliput effect in the aftermath of the end-Permian mass extinction event. GSA Abstracts with Programs 34 (6), 355.
Renaud, S., Girard, C., 1999. Strategies of survival during extreme environmental perturbations: evolution of conodonts in response to the Kellwasser crisis (Upper Devonian). Palaeogeography, Palaeoclimatology, Palaeoecology 146, 19–32.
Rhoads, D.C., Morse, J.W., 1971. Evolutionary and ecologic significance of oxygen-deficient marine basins. Lethaia 4, 413–428.
Richmond, C., Marcus, N.H., Sedlacek, C., Miller, G.A., Oppert, C., 2006. Hypoxia and seasonal temperature: short-term effects and long term implications for *Acartia tonsa dana*. Journal of Experimental Marine Biology and Ecology 328, 177–196.
Savrda, C.E., Bottjer, D.J., 1986. Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters. Geology 14, 3–6.
Savrda, C.E., Bottjer, D.J., Gorsline, D.S., 1984. Development of a comprehensive oxygen-deficient marine biofacies model: evidence from Santa Monica, San Pedro and Santa Barbara Basins, California continental borderland. American Association of Petroleum Geologists Bulletin 68, 1179–1192.
Schubert, J.K., Bottjer, D.J., 1995. Aftermath of the Permian–Triassic mass extinction event: palaeoecology of Lower Triassic carbonates in the western USA. Palaeogeography, Palaeoclimatology, Palaeoecology 116, 1–39.
Smith, R.M.H., 1995. Changing fluvial environments across the Permian–Triassic boundary in the Karoo Basin, South Africa, and possible causes of tetrapod extinctions. Palaeogeography, Palaeoclimatology, Palaeoecology 117, 81–104.
Smith, A.B., 2001. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. Philosophical Transactions of the Royal Society of London. Series B 356, 351–367.
Smith, A.B., Jeffrey, C.H., 1998. Selectivity of extinction among sea urchins at the end of the Cretaceous period. Nature 392, 69–71.
Stanley, S.M., 1973. An explanation for Cope's Rule. Evolution 27, 1–26.
Tverdokhlebov, V.P., Tverdokhlebov, G.I., Surkov, M.V., Benton, M.J., 2002. Tetrapod localities from the Triassic of the SE of European Russia. Earth Science Reviews 60, 1–66.
Twitchett, R.J., 1999. Palaeoenvironments and faunal recovery after the end-Permian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 154, 27–37.
Twitchett, R.J., 2001. Incompleteness of the Permian–Triassic fossil record: a consequence of productivity decline? Geological Journal 36, 341–353.
Twitchett, R.J., 2006. The palaeoclimatology, palaeoecology and palaeoenvironmental analysis of mass extinction events. Palaeogeography, Palaeoclimatology, Palaeoecology 232, 190–213.
Twitchett, R.J., Krystyn, L., Baud, A., Wheeley, J.R., Richoz, S., 2004. Rapid marine recovery after the end-Permian mass extinction event in the absence of marine anoxia. Geology 32, 805–808.
Twitchett, R.J., Feinberg, J.M., O'Connor, D.D., Alvarez, W., McCollum, L., 2005. Early Triassic Ophiuroids: their paleoecology, taphonomy and distribution. Palaios 20, 213–223.
Urbanek, A., 1993. Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. Historical Biology 7, 29–50.
Wheeley, J.R., Twitchett, R.J., 2005. Palaeoecological significance of a new Griesbachian (Early Triassic) gastropod assemblage from Oman. Lethaia 38, 37–45.
Wignall, P.B., Benton, M.J., 1999. Lazarus taxa and fossil abundance at times of biotic crisis. Journal of the Geological Society of London 156, 453–456.
Wignall, P.B., Twitchett, R.J., 1996. Oceanic anoxia and the end Permian mass extinction. Science 272, 1155–1158.
Wignall, P.B., Twitchett, R.J., 2002. Extent, duration and nature of the Permian–Triassic superanoxic event. In: Koeberl, C., MacLeod, K.G. (Eds.), Catastrophic Events and Mass Extinctions: Impacts and Beyond. Geological Society of America Special Paper, vol. 356, pp. 395–413.
Zachos, J.C., Arthur, M.A., Dean, W.E., 1989. Geochemical evidence for suppression of pelagic marine productivity at the Cretaceous–Tertiary boundary. Nature 337, 61–64.