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Faunal diversity, heterogeneity and body size in the Early Triassic: testing post-extinction paradigms in the Virgin Limestone of Utah, USA*

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The recovery intervals after mass extinction events are portrayed as times of ecological stress, with effects including reduced body size (Lilliput Effect), reduced taxonomic diversity and lowered ecological complexity. As the end-Permian mass extinction is the largest of the 'Big Five' events, with a prolonged recovery interval postulated during the Early Triassic, we expect these effects to be most pronounced in Early Triassic faunas. We have used new data and analytical techniques on the fauna of the Spathian Virgin Limestone to test whether the Lilliput Effect can be observed, whether the fauna is vertically and laterally homogeneous, and whether taxonomic diversity is significantly lower than that of comparable nearshore marine deposits transgressive over redbed sequences from other deposits not regarded as falling into post-extinction recovery intervals. The Lilliput Effect can be observed in some cases, but no uniform trend in body size reduction emerged. When the distributions of the body size across a range of marine invertebrate taxa was compared between the Virgin Limestone and the latest Triassic Penarth Group of Britain there was no support for a significant reduction in body size among the Virgin Limestone fauna. Evidence for faunal homogeneity was also limited. The alpha diversity of individual sites in the Middle Triassic Muschelkalk of central Europe was generally higher than Virgin Limestone sites, after accounting for differences in sample size using rarefaction, but there was some overlap. Although the beta diversity of the Muschelkalk is also apparently higher, a number of biases may be elevating Muschelkalk diversity. Future comparisons between recovery and 'normal' faunas need to ensure that as many confounding factors as possible are controlled for and that multiple samples are tested.

KEY WORDS: biotic recovery, Lilliput Effect, Spathian, Triassic, Utah, Virgin Limestone.

INTRODUCTION

Previous analyses have reported that fossil assemblages from the aftermaths of mass extinctions are less taxonomically diverse and less complex ecologically than pre-extinction communities. Both of these observations underpin the concept of survival and recovery intervals, and have led to the development of biotic recoveries from mass extinctions as a distinctive area of research (Erwin 1998; Jablonski 2001, 2004).

Post-extinction faunas are often reported to show signs of stress (Twitchett 2001, 2006; Fraiser & Bottjer 2005). One commonly reported effect is for individuals within populations to show a reduced body size during recovery intervals, the Lilliput Effect of Urbanek (1993). Bottjer & Gall (2005) summarised four well-documented examples from the Triassic encompassing terrestrial plants and vertebrates as well as marine invertebrates. However, Nützel (2005a, b) and Harries (2006) both noted

that the reduction in body size is far from ubiquitous and current understanding of the mechanism(s) that might operate to produce reductions in body size is limited (Twitchett 2006).

An alternative possible explanation for the reported reduction in body size and decline in community diversity is that the range of habitats available for sampling during mass extinction and recovery intervals is not as great as during other intervals of time, and that the habitats from which communities and individuals are sampled during biotic recoveries is biased towards nearshore, marginal or highly stressed environments relative to the range of marine habitats sampled in pre-extinction intervals. There may also be limited reporting of cases in which dwarfing does not occur, part of a more general problem of the failure to publish negative results highlighted by Gould (1993).

The end-Permian witnessed the largest and most profound extinction in the Phanerozoic (Benton 2006;

Appendix 1 [indicated by an asterisk () in the text and listed at the end of the paper] is a Supplementary Paper; copies may be obtained from the Geological Society of Australia's website (<<http://www.gsa.org.au>>) or from the National Library of Australia's Pandora archive (<<http://nla.gov.au/nla.arc-25194>>).

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Erwin 2006), dramatically altering marine community structure (Sepkoski 1978; Wagner *et al.* 2006). Consequently, we expect to see the clearest evidence for stressed communities and the Lilliput Effect in Early Triassic marine faunas. Unfortunately, the Early Triassic is also an epoch when we have the poorest of marine rock records, simply because of tectonic settings (the primary driver of sea-level) at the time (Smith 2007; Smith & McGowan 2007). The dearth of shallow-marine deposits of Early Triassic age makes meaningful comparison with faunas of other ages rather difficult. One of very few Early Triassic shallow-water carbonate platform sequences is the Spathian Virgin Limestone Member (Virgin Limestone hereafter) of the Moenkopi Formation, which is extensively exposed in southern Utah, northern Arizona and eastern Nevada. The Virgin Limestone consists of alternating siltstone and limestone beds deposited in a mixed carbonate–siliciclastic deposystem (Poborski 1953, 1954; Stewart *et al.* 1972; Pruss & Bottjer 2004). These deposits were formed by a marine incursion from Panthalassa into the western interior of North America, with water depth increasing from east to west (Blakey 1972). A number of important Early Triassic marine invertebrate taxa first records have been made in the Virgin Limestone, including echinoids (Kier 1968), ophiuroids (Twitchett & Oji 2005; Twitchett *et al.* 2005) and articulate crinoids (Schubert *et al.* 1992).

Bottjer and co-authors have carried out extensive fieldwork on the Virgin Limestone and related deposits, publishing numerous paleoenvironmental and paleoecological studies (Schubert & Bottjer 1995; Bottjer & Schubert 1997; Tang & Bottjer 1997; Boyer *et al.* 2004; Fraiser & Bottjer 2004; Pruss & Bottjer 2004; Pruss *et al.* 2004). These publications have provided much of the basis for more general theories about the recovery from the end-Permian mass extinction, and have recorded evidence that unusual oceanographic and ecological conditions prevailed right through to the end of the Early Triassic. Fraiser & Bottjer (2004) discussed the prevalence of microgastropod-dominated facies in the Smithian Sinbad Limestone of Utah, and regarded the non-actualistic nature of these communities as evidence of prolonged environmental stress. Fraiser *et al.* (2005) extended this observation to the Early Triassic gastropod faunas from a number of other regions, and noted that rates of recovery differed among these regions. Pruss & Bottjer (2004) reached a similar conclusion based on trace fossils, while noting the possibility that the recovery was asynchronous, with earlier recovery at higher latitudes. Facies analyses by Pruss *et al.* (2004) were interpreted as independent support for unusual, stressed marine ecosystems during the Early Triassic. They reported the occurrence of widespread wrinkle structures, usually only found in Precambrian–Cambrian rocks, in Early Triassic rocks around the world, including sections of the Virgin Limestone in Nevada. These structures were interpreted as evidence of reduced bioturbation and protracted environmental stress. Boyer *et al.* (2004) used paleocommunity and taphonomic analyses to demonstrate that, although the taxa found in the Virgin Limestone shell beds are mostly members of the ‘Modern fauna’

(Sepkoski 1978), the beds themselves have thicknesses and taphonomic signatures more like those of the Paleozoic. Although conditions were beginning to return to normal by the end of the Early Triassic (Erwin 1996; Pruss & Bottjer 2004), the Virgin Limestone fauna has been used as an example of a post-extinction recovery fauna (Schubert & Bottjer 1995).

However, even if the paleontological and paleoecological data indicated the existence of highly stressed conditions during deposition of the Virgin Limestone, it is not yet clear whether these relate to a prolonged and global interval of anomalous marine conditions (as reviewed by Bottjer *et al.* 2008) or simply to more regional and ephemeral factors. Nützel & Schulbert (2005) made a strong case that the high diversity and endemism of the gastropod fauna was an artefact of preservation and/or sampling biases. The study by Zonneveld *et al.* (2007) on body size and environmental distributions in lingulid brachiopods and their associated trace fossils found that these populations do not differ in their environmental distribution between the Early and Middle Triassic, making it difficult to support Rodland & Bottjer’s (2001) interpretation that lingulid brachiopod represent a disaster taxon that was able to invade atypical environments in the wake of the end-Permian extinctions.

Tang & Bottjer (1997) documented some low diversity faunas from the Middle Jurassic Carmel Formation, deposited in the same basin as the Virgin Limestone. They noted that the low diversity of these faunas could be attributable to the deposition of some facies of the Carmel Formation within marginal environments. The Virgin Limestone was also deposited in a marginal environment, yet explanations for its low-diversity have focused on the aftermath of the end-Permian event rather than to specific local or regional causes. The recognition by Tang & Bottjer (1997) that low-diversity communities, such as those from the Carmel Formation, can and do exist far from mass-extinction events is important. It establishes the possibility that communities are influenced by ecological, as well as evolutionary, processes. We must account for the operation of ecological processes before considering other factors. Environmentally matched communities provide the best opportunities for testing hypotheses about diversity and ecology of post-extinction faunas, as they control for environmental and facies variations capable of confounding our impressions of biodiversity after mass extinctions.

To test whether the Virgin Limestone marine invertebrate fauna truly represents an unusual recovery fauna, or is similar to marine faunas from comparable transgressive marine sequences later in the Triassic, we made new bed-by-bed collections of marine invertebrate taxa in southwest Utah. Particular attention was paid to the geological context of the collections, in order to provide information about the paleoenvironment and distribution of fossils. We use these new data to address three questions, which have implications for understanding recovery patterns and process in the Early Triassic: (i) do individuals from the Virgin Limestone have significantly smaller body sizes than individuals from congeneric or confamilial taxa sampled from

similar paleoenvironments during time intervals where we do not expect mass extinction events to have any significant influence; (ii) how strong is the lateral and vertical homogeneity among Virgin Limestone communities; and (iii) are Virgin Limestone communities significantly less diverse than Middle Triassic communities from similar environments, after differences in sample size are taken into account?

METHODS

Field data

Fieldwork was undertaken during May 2006 in two areas near St George, Utah (Figure 1). The Hurricane Cliffs, a long linear fault-controlled outcrop, (HC localities) were sampled from Kannarville (K1) in the north to HC9 in the south. The second group of localities were located in the Beaver Dam Mountains (BM localities). A number of sections were explored within these two areas before sites were selected for detailed sampling. A list of provisional taxa identified is given in Table 1, Collection numbers, collection names and abundance data are given in Appendix 1*; taxonomic revision of the bivalves is currently under way by M. Hautmann (Universität Zurich). All localities were GPS-registered (WGS84), and this information, along with geological information, taxonomic lists and abundance data, is available from the Paleobiology Data Base Project (Appendix 1*). A .kmz file of the locality data is also available from AJM.

The Hurricane Cliffs sections are calcarenite-dominated, with abundant intraclasts in the lower beds and massive cross-bedded units. The thickness and relative proportions of siliciclastics and carbonate sediment varies considerably, with beds wedging out at outcrop

scale (<1 km). The succession in the Beaver Dam Mountains is mudrock dominated, with occasional thin calcareous shell beds. The Hurricane Cliffs sediments were deposited in shallow-water environments, while the Beaver Dam Mountain sediments represent deeper water, more distal settings.

We carried out surface collection on a bed-by-bed basis picking all macrofossils well enough preserved to be identifiable until a large sample had been obtained or surface outcrops exhausted. Repeat collections were made from selected localities and horizons.

DATA ANALYSIS

Body size distributions

The distribution of body sizes of a range of taxa collected from the Virgin Limestone and related taxa from other deposits were compared statistically to test for the Lilliput Effect (Table 2). By using congeneric and confamilial taxa, we minimised the potential influence of phylogenetic differences, a problem discussed by MacLeod (2006) who stressed the need for phylogenetically informed comparisons of body size. Wilcoxon tests were performed to test the null hypothesis that all the taxa were drawn from body size distributions with the same median value.

To compare two Triassic faunas across a broad range of taxa, the distributions of maximum body sizes in marine invertebrate taxa from the Virgin Limestone (42 taxa) were compared with those reported in Swift & Martill (1999) for the Rhaetian Penarth Group of Britain (53 taxa). Like the Virgin Limestone, the Penarth Group represents a mixed carbonate-siliciclastic shallow-marine deposit transgressive over a terrestrial redbed sequence.

Figure 1 Sketch map showing field localities in the Beaver Dam Mountains (BM) and Hurricane Cliffs (HC) of SW Utah. Inset shows the location of Utah within the United States.

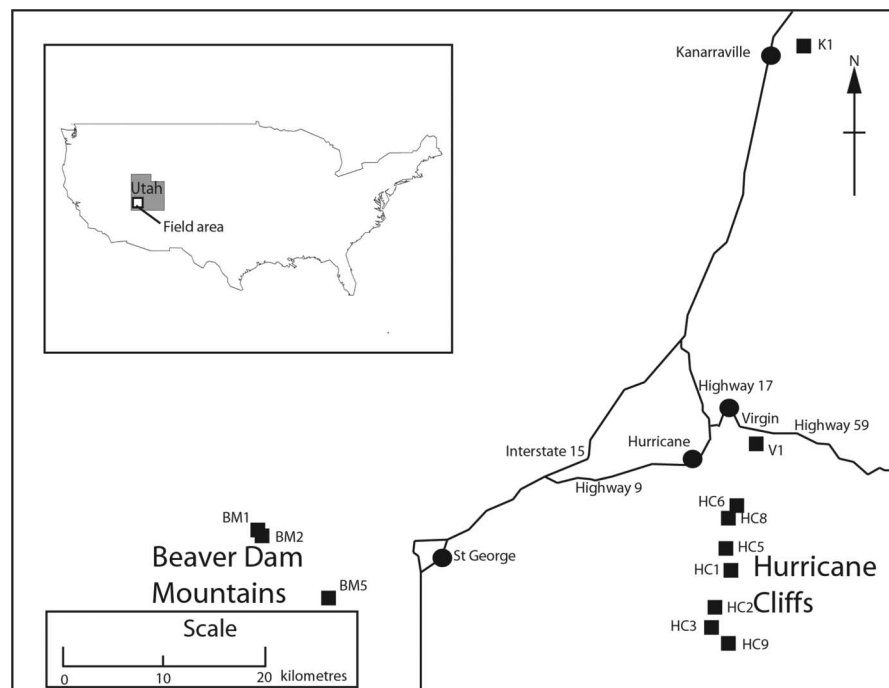


Table 1 Faunal list for taxa recorded and identified from the Virgin Limestone Utah during fieldwork by the authors.**Bivalves**

Eumorphotis multiformis
Eumorphotis sp. A
Pleuronectites sp.
Leptochondria cf. *thaynesiana*
Lepidochondria sp. A
Entolium sp.
Chlamys (*Praechlamys*) sp.
Claraia sp.
Homomya sp.
Arcomya sp. A
Pleuromya cf. *musculoides*
Promyalina putiatensis
Modiolus sp.
Neoschizodus cf. *laevigatus*
Neoschizodus sp. B
Joannina sp.
Myohoricardiid sp.
Trigonodus sp. A
Trigonodus sp. B
Permophorus triassicus
Pseudomyoconcha cf. *gastrochaena*
Unionites fassensis
Unionites sp. C
Bakevellia cf. *costata*
Bakevellia cf. *exporecta*
 bivalve undet. A
 bivalve undet. D
Gastropods
Neritopsis depressispira
Neritopsis utahensis
Trachynerites sp.
Worthenia sp.
Chartronella sp.
Cephalopods
Germanonautilus sp.
Pleuonautilus sp.
Usserites sp.
Idahocolombites sp.
Prohungarites sp.
Brachiopods
Protogusarella smithi
'Rhynchonella' triassicus
rhynchonellid sp.
Orbiculoidea sp. A
Orbiculoidea sp. B
Echinoderms
Holocrinus sp. cf. *dubius*
Lenticularis utahensis
Sclerobionts
Microconchus sp.
Rogerella [acrothoracic borer]
?Placopsilina [encrusting foram]

Further information about locality details, collections and abundance can be found in Appendix 1*.

Community composition analysis: analysis of similarity (ANOSIM)

To test for vertical homogeneity in the faunas we compared collections from three successive, specimen-rich carbonate beds separated by thick shale units

within a single section BM 1 (beds 11, 13 and 18). These beds were particularly diverse at the species level. We also compared genus-level diversities in all fossiliferous beds at BM1.

Beta diversity was assessed by comparing the faunas between the HC and BM field areas. The final analysis compared community composition at genus level among all sites. ANOSIM was used to make all of these comparisons. ANOSIM is a non-parametric test that compares the distances among all samples on the basis of ranks, scaling differences between -1 and $+1$. Chapman & Underwood (1999) discovered an interesting property of ANOSIM. High negative values of R identify cases in which very dissimilar environments with patchy communities have been included in the same analysis, when they perhaps should not have been. This property of ANOSIM may be particularly useful in paleontological studies, in which there is much less control over samples than in ecological studies.

Comparison of Muschelkalk and Virgin Limestone faunal diversity

The sediments of the Spathian–Carnian Muschelkalk epicontinental sea of central Europe were deposited at a similar paleolatitude and in comparable depositional environments to the seaway in which the Virgin Limestone accumulated (Hagdorn 1991), allowing a controlled comparison between diversity in the Early and Middle Triassic. Historical collections housed in the Muschelkalk Museum, Ingelfingen, Germany were studied to obtain comparative data on taxonomic diversity, abundance and size data for a number of individual faunas. Most of these collections represent the sampling efforts of one person (H. Hagdorn), who has made bed-by-bed surface outcrop collection from specific sections over a number of years. Although these collections are somewhat similar to our Virgin Limestone collections, like all museum collections, rare species are probably over-represented, and common species under-represented, in the Muschelkalk Museum samples.

The species-level diversity of individual Muschelkalk and Virgin Limestone faunas was compared after correcting for sample size differences through individual-based rarefaction using S. Holland's Analytical Rarefaction 1.3 program (<http://www.uga.edu/~strata/software/Software.html>).

RESULTS

Body size distributions of individual taxa

The analyses performed on the body size distribution data do not indicate a uniform pattern of reduced body size among the invertebrate taxa considered here from the Early Triassic Virgin Limestone. Terebratulid brachiopods show the predicted pattern in a simple comparison between the Virgin Limestone and Muschelkalk samples (Figure 2). Bakevellid bivalves also show a pattern that supports a Lilliput Effect during the Early Triassic. In this case the evidence is stronger, as we have a pattern of larger body sizes in the

Table 2 Comparative material studied for work on comparison of body sizes between elements of the Virgin Limestone fauna and specimens from similar paleoenvironments from other time intervals.

Crinoid columnals

(50 largest columnal diameters on bedding plane or in sample were measured)

Holocrinus smithi Virgin Limestone, Frenchman Mountains, Nevada, USA: NHM EE1518

Holocrinus beyrichi Lower Muschelkalk, Unterer Wellenkalk, Germany: NHM E70440 E71480

Holocrinus dubius Upper Muschelkalk, Germany: NHM EE6096

Holocrinus sp. Cassian Beds, Middle Triassic, Veszprem, Bakony, Hungary: NHM E66403

Dadocrinus Upper Muschelkalk mu2, Germany: NHM EE564

Bakevellid bivalves

Bakevellia sp. Upper Muschelkalk (Astartebank and Klein Terebratulidenbank), Gottwoldshausen, Germany (MM)

Bakevellia sp. Carnian, Bakony, Hungary (NHM)

Bakevellia sp. Permian, Zechstein reef limestone, Tunstall Hill, Sunderland, England (NHM)

Gervillia orientalis, Bajocian, Tanzania (NHM)

Bakevellia waltoni, Sharps Hill Bed, Great Oolite, Bathonian, Snowhill, England (NHM)

Bakevellia ovata, Bathonian, Minchinhampton, Gloucestershire, England (NHM)

Myalinid bivalves

Myalina blezingeri mo1, Lower Muschelkalk, Germany (MM)

Myalina, Viséan, Lower Carboniferous, Yorkshire, England (NHM)

Liebea sp., Permian Zechstein reef limestone, Sunderland, England (NHM)

Myalina, basal Artinskian, Oman (NHM)

Praemytilus, Bajocian, Great Estuarine Series, Eigg, Scotland (NHM)

Terebratulid brachiopods

Coenothyris cycloides, Bank der Kleinen Terebratuliden, Upper Muschelkalk (Mo3), Gottwoldshausen, Germany (MM)

Coenothyris vulgaris, Terebratelschiten, Lower Muschelkalk Mu2, Strzelce Opolskie, Poland (MM)

Coenothyris vulgaris, Obere Terebratelbank, Lower Muschelkalk Mu2, Bodingheim and Steinberg-Eichen Buhl bei Kronach, Germany (MM)

Microconchids

Muschelkalk. Egenhausen, Germany. NHM A718

Devonian, Hamilton Group, North America (NHM)

Griesbachian, Greenland (NHM)

Bathonian, White Limestone, Foss Cross, Gloucestershire, England (NHM)

MM, Muschelkalk Museum, Ingelfingen, Germany collections; NHM, Natural History Museum, London, UK collections.

Late Permian, a significant decrease during the Early Triassic, then an increase in body size again by the Middle Triassic (Table 3). All of the other taxa show more variable patterns (Figures 3, 4; Table 3).

Among the microconchid worms (commonly misidentified as *Spirorbis*: see Taylor & Vinn 2006), there is a significant increase in body size between the Griesbachian taxa from Greenland and those from the Virgin Limestone ($p < 0.01$), if a combined sample is used for comparison (Figure 3). However, if we separate the total Virgin Limestone sample into the two component regions, only the Beaver Dam Mountains sample is

significantly larger than the Greenland sample ($p < 0.01$). The Beaver Dam Mountains sample also shows a significantly larger body size than the Hurricane Cliffs sample ($p < 0.01$). Thus, the Beaver Dam Mountains sample drives the significant result for the combined sample. The Hurricane Cliffs sample overlaps with the Greenland sample. A sample of Middle Jurassic microconchids from nearshore marine settings in southern England and France (Vinn & Taylor 2007) shows significantly larger body sizes than the Virgin Limestone sample.

Myalinid bivalves (Figure 4) also show a more complex pattern, with a wide distribution of sizes in a Viséan sample, a reduction in body size in an Upper Permian sample, then a shift towards larger body sizes in the Triassic samples. Wilcoxon test results indicate that the Virgin Limestone and Muschelkalk individuals have the largest body sizes.

Columnal diameter in *Holocrinus* decreases between the Virgin Limestone and Muschelkalk samples. A sample of *Dadocrinus* columnals is significantly greater median size than the Virgin Limestone sample. However, contemporary *Holocrinus* columnals collected by D. J. Bottjer from a more distal Virgin Limestone setting in the Frenchman Mountains of Nevada are significantly larger than our Virgin Limestone sample from Utah. The *Holocrinus* columnals sampled from the Frenchman Mountains have a size distribution indistinguishable from *Dadocrinus* ($p = 0.43$).

Comparison of maximum body size in entire faunas from the Virgin Limestone and Penarth Group

Comparison of the distributions of maximum body size recorded among the brachiopods, molluscs (excluding cephalopods) and echinoid taxa of the Virgin Limestone and the Rhaetian Penarth Group provides another test of the Lilliput Effect (Figure 5). The Wilcoxon test on the size distributions of the two faunas was not statistically significant ($p = 0.52$). A χ^2 test to compare the shape of the distributions, with a Yates correction applied to compensate for small expected values across the parts of the distribution (Hinton 1995), also failed to find a statistically significant difference between maximum body size distributions ($p = 0.06$).

Faunal heterogeneity

With one exception, all of the comparisons using ANOSIM found no support for widespread faunal homogeneity. The only case in which ANOSIM found no significant difference was among the three successive shell beds within a clastic sequence at Virgin Limestone locality BM1 (Table 4a), supporting report of observed faunal homogeneity of Schubert & Bottjer (1995). All other comparisons found strong statistical support for faunal heterogeneity, and when all fossiliferous beds from BM1 were compared, support for vertical homogeneity collapses (Table 4b).

ANOSIM results for lateral comparisons also challenge notions of lateral faunal homogeneity within the Virgin Limestone. Among localities in the Beaver Dam

Mountains and Hurricane Cliffs there is no support for faunal homogeneity (Table 4c). The broadest comparison of all localities at genus level also provided strong evidence for faunal heterogeneity (Table 4d).

Diversity

The relative diversities of the Virgin Limestone and Muschelkalk faunas, after controlling for sample size, were assessed using two approaches. Individual sites underwent rarefaction to a common sample size of 100 specimens (Figure 6a). Overall, the Virgin Limestone samples show lower diversities than the Muschelkalk sites, but there is some overlap in diversity between the Muschelkalk and Virgin Limestone faunas from individual sites.

Rarefaction to common sample size fails to convey information about the shape of the rarefaction curves across a range of sample sizes. Figure 6b, c shows the rarefaction curves for each site listed in Figure 6a.

Rarefaction of the total faunal lists was also performed (Figure 6d). Both rarefaction curves follow very different trajectories beyond about 100 specimens. Most strikingly, the considerably smaller number of specimens from the Muschelkalk Museum yields a much higher estimate of diversity.

DISCUSSION

Our fieldwork in Utah, representing about 30 person-days of fossil collecting effort, provided new information on the geology of the area, and found a number of taxa previously unreported from the Virgin Limestone, including new bivalve species (M. Hautman pers. comm. 2008). This demonstrates that even relatively well-studied areas with excellent exposure can still yield new taxa, and given the relative lack of Lower Triassic rock, those outcrops that do exist should be targeted for major collection efforts in the future.

An unexpected result of from the new field collections is the large number of encrusting microconchids that were recovered. The report by Schubert & Bottjer (1995) that encrusters are rare in the Virgin Limestone must now be qualified: encrusters are locally abundant but taxonomically depauperate.

Our approach to sampling differs from the earlier study by Schubert & Bottjer (1995) who used bulk-sampling, a typical bulk sample consisting of $\sim 0.8 \text{ m}^3$ from bands of rock 0.15 m or less in thickness. The possibility of biases introduced by the relative proportions of data from consolidated *vs* unconsolidated sediment has been raised in a number of recent papers (Crampton *et al.* 2006; Kowalewski *et al.* 2006) that

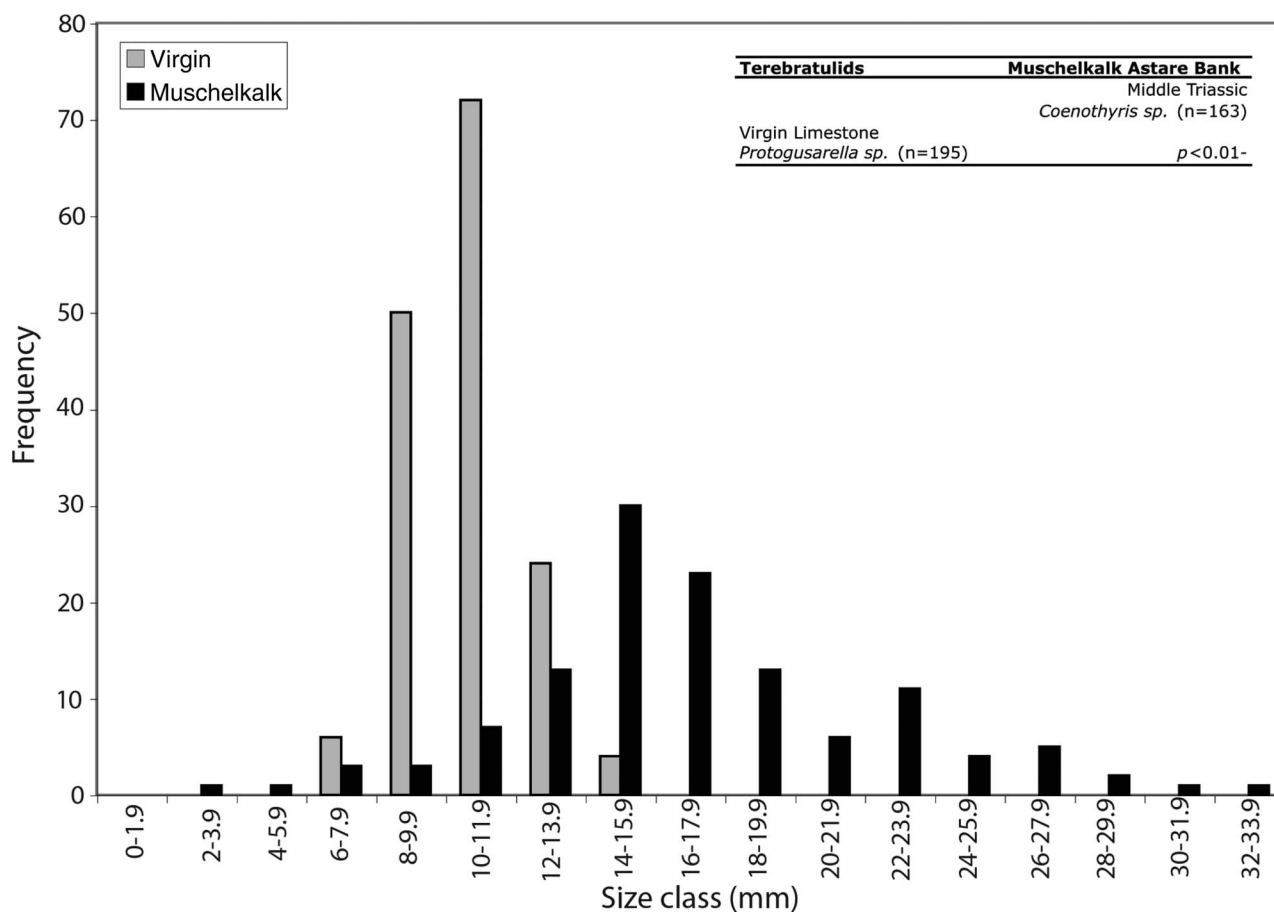


Figure 2 Body size (measured as margin-to-margin length) distributions of terebratulid brachiopods from the Virgin Limestone and Muschelkalk Astarte Bank. The inset table shows the result of a Wilcoxon test indicating that the Muschelkalk specimens are significantly larger than the Virgin Limestone specimens.

Table 3 Comparison of body sizes of a selection of taxa that occur in the Virgin Limestone with samples from other time intervals.

	Veszprem, Bakony	Lower Muschelkalk	Upper Muschelkalk	Lower Muschelkalk	Frenchman Mountains, Nevada
Crinoid columnals					
	Upper Triassic	Middle Triassic	Middle Triassic	Middle Triassic	Spathian
	<i>Holocrinus</i>	<i>Holocrinus</i>	<i>Holocrinus dubius</i>	<i>Dadocrinus</i>	<i>Holocrinus</i>
	sp. (<i>n</i> = 50)	<i>beyrichi</i> (<i>n</i> = 24)	(<i>n</i> = 50)	sp. (<i>n</i> = 42)	<i>smithi</i> (<i>n</i> = 50)
Virgin Limestone					
<i>Holocrinus</i>	$p < 0.01^+$	$p < 0.01^+$	$p < 0.01^+$	$p < 0.01^-$	$p < 0.01^-$
<i>smithi</i> (<i>n</i> = 57)					
Microconchids					
	Muschelkalk, Egenhausen	Forest Marble, White Limestone Fm	Greenland	BM 5 Bed 12A	
	Middle Triassic	Middle Jurassic	Griesbachian	Spathian	
	<i>Microconchus</i>	<i>Microconchus</i>	<i>Microconchus</i>	<i>Microconchus</i>	
	sp. (<i>n</i> = 25)	sp. (<i>n</i> = 25)	sp. (<i>n</i> = 52)	sp. (<i>n</i> = 61)	
HC 5 Bed 7					
<i>Microconchus</i>	$p = 0.125$	$p < 0.01^-$	$p = 0.3$	$p < 0.01^-$	
sp. (<i>n</i> = 40)					
Myalinids					
	Sunderland, UK	Muschelkalk	Northern England	Eigg, Scotland	
	Artinskian	Middle Triassic	Visean	Bathonian	
	<i>Liebia</i> sp. (<i>n</i> = 64)	<i>Promyalina</i>	<i>Myalina</i>	<i>Praemytilus</i>	
		sp. (<i>n</i> = 30)	sp. (<i>n</i> = 76)	sp. (<i>n</i> = 19)	
Virgin Limestone					
<i>Promyalina</i>	$p = 0.001^-$	$p = 0.427$	$p = 0.01^-$	$p = 0.01^-$	
sp. (<i>n</i> = 30)					
Bakevellids					
	Tunstall Hill, UK	Tanganyika, Tanzania	Forest Marble	Sharps Hill Beds, Snowhill	Muschelkalk, Gottwoldshausen
	Zechstein	Bathonian	Bathonian	Bathonian	Middle Triassic
	<i>Bakevellia</i>	<i>Girvellia</i>	<i>Bakevellia</i>	<i>Bakevellia</i>	<i>Bakevellia</i>
	sp. (<i>n</i> = 62)	<i>orientalis</i> (<i>n</i> = 17)	<i>waltoni</i> (<i>n</i> = 21)	<i>ovata</i> (<i>n</i> = 32)	sp. (<i>n</i> = 22)
BM 1					
<i>Bakevellia</i>	$p < 0.01^-$	$p < 0.01^-$	$p < 0.01^-$	$p < 0.01^-$	$p < 0.01^-$
sp. (<i>n</i> = 112)					
Terebratulids					
	Muschelkalk				
	Astare Bank				
	Middle Triassic				
	<i>Coenothyris</i>				
	sp. (<i>n</i> = 163)				
Virgin Limestone					
<i>Protogusarella</i> sp. (<i>n</i> = 195)	$p < 0.01^-$				

The reported *p* values relate to Wilcoxon tests. '+' after a significant result indicates that the Virgin sample consists of taxa with a larger median body size than the other sample. '-' indicates that the median body size of the comparative sample is larger than the Virgin sample.

detailed the difficulties of bulk sampling from consolidated rock, and it is clear that Schubert & Bottjer's sampling scheme dictated the choice of samples. While the Schubert & Bottjer approach provides a clear measure of sampling effort and was well-suited for detailed community analyses, it runs the danger of capturing only small, common elements in the fauna. Our sampling method allowed for greater spatial coverage increasing our chances of encountering rarer and/or larger elements in the fauna.

Surface picking from outcrop also has problems and can introduce biases. It is likely to underestimate

the diversity of small taxa relative to bulk sampling, but is more likely to sample rarer taxa and individuals close to the larger end of their size range. We chose this approach because it should generate a faunal sample more akin to the museum collections that were our major source of comparative diversity data, while allowing us to use a number of techniques developed for community analysis by ecologists. Alternative methods of producing quantifiable measures of effort that can be applied to a wider range of rock types need to be given more attention.

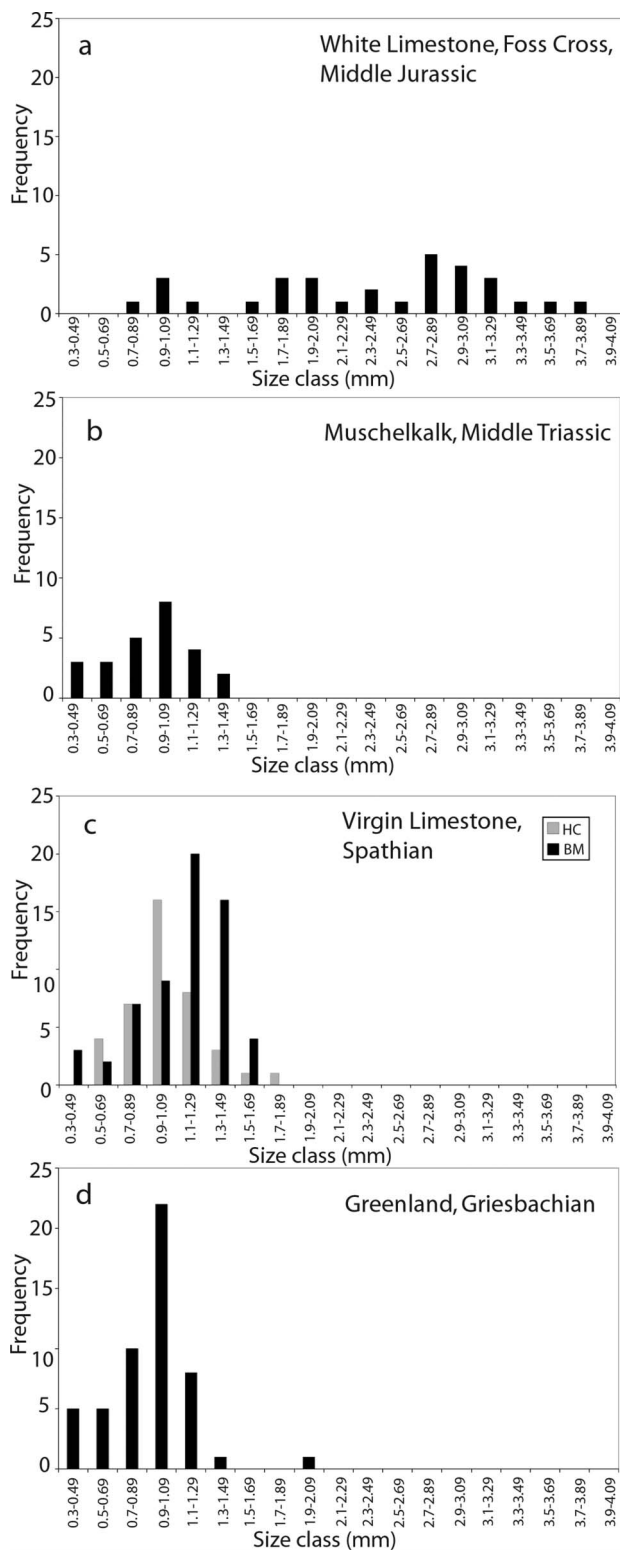


Figure 3 Body size (measured as shell diameter) distributions of microconchid worms from four locations. Samples from two localities in Virgin Limestone are shown in (c) and these two samples are significantly different (see Table 4).

Body size

Equivocal support was found for the Lilliput Effect in the groups we studied. The range of maximum body size achieved by molluscs, echinoderms and brachiopods in

the Virgin Limestone is statistically indistinguishable from that achieved in a similar paleoenvironmental setting in the latest Triassic Penarth Group. Furthermore, comparisons of body size distributions for individual taxa sampled from the Virgin Limestone show no convincing trends. In the case of the terebratulid brachiopods, those from the Muschelkalk are consistently larger than those from the Virgin Limestone, and the similarities in facies between the two serve to exclude the possibility of the pattern of body size differences being the result of gross environmental differences. The bakevellid bivalves also exhibited the predicted Lilliput Effect, and the availability of an Upper Permian sample allowed comparison with a pre-extinction sample. However, the other bivalve taxon studied in detail, the myalinid bivalves, shows an opposite pattern to that of the bakevellids. The Virgin Limestone and Muschelkalk samples have the largest body sizes. It is not unreasonable to expect different responses from different groups of bivalves to environmental changes; information on responses of extant taxa to environmental stress would allow us to develop an expectation of how frequently we should expect to observe significant size increases and decreases.

Microconchid worms also showed a complex pattern that gave support to the Lilliput Effect only for a comparison between a Griesbachian sample from Greenland and the Spathian Virgin Limestone. Microconchid samples used in this study were obtained from a broader range of paleolatitudes than the terebratulid brachiopods. The possibility of a latitudinal effect on body size between the Greenland and Virgin Limestone samples runs counter to the normal gradient of increasing body size at higher latitudes. Data from a study of extant spirorbid polychaetes, ecological analogues of microconchids, along the west coast of the Americas between Panama (9°N) and Point Barrow (71°N) (Knight-Jones *et al.* 1979) showed species from more northerly latitudes to be typically larger.

We have attempted to minimise phylogenetic influences by making body size comparisons between reasonably closely related taxa. The additional control over confounding environmental factors gained from our geological study of Virgin Limestone facies increases our confidence that we are eliminating other sources of body size variation and making appropriate comparisons. Urbanek's (1993) original formulation of the Lilliput Effect is framed in terms of populations, but due to time-averaging in the fossil record we are usually dealing with samples that may represent many generations and a variety of life stages. The potential for lumping or splitting of data to alter the significance of results is of particular concern. Even within the Virgin Limestone we have examples of significant differences in body size of crinoids and microconchids when samples from different areas are compared. Future studies into the Lilliput Effect should try to minimize these confounding factors.

The findings of Fraiser *et al.* (2005), Nützel (2005a, b) and Zonneveld *et al.* (2007) raised a number of additional issues that any future studies of the Lilliput Effect should address. One concern is that workers may be

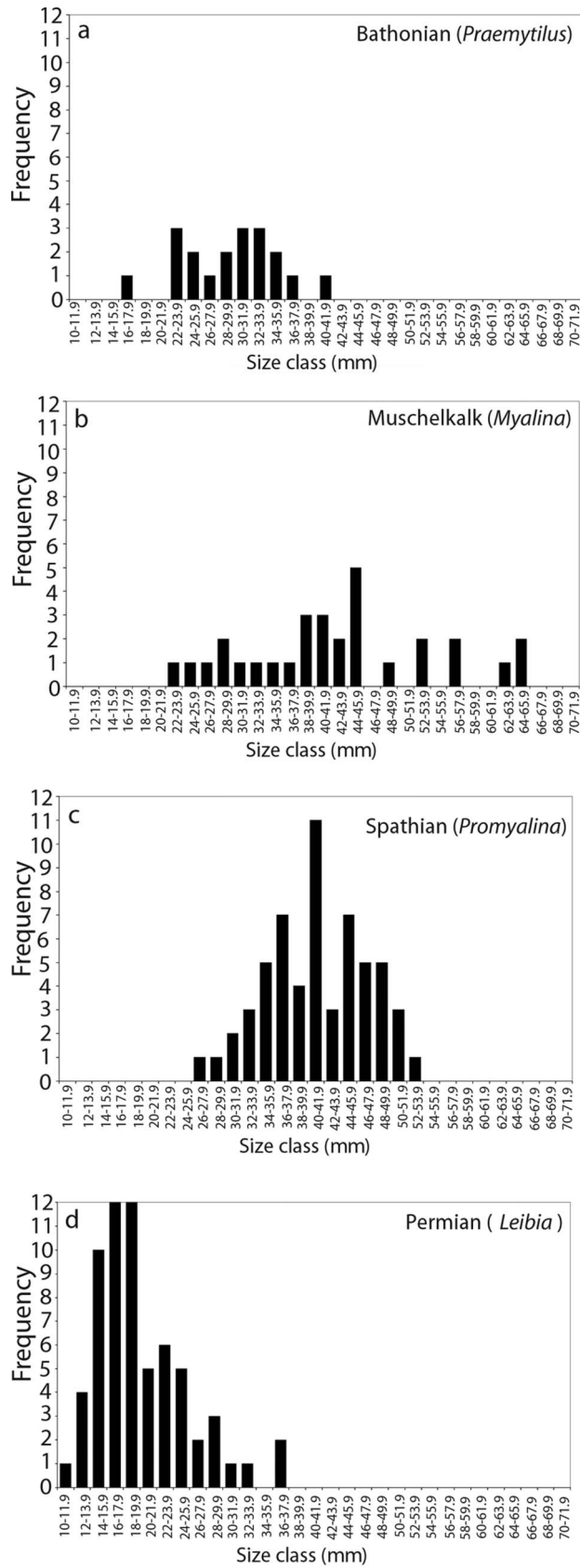


Figure 4 Body size (measured as margin-to-margin length) distributions of myalinid bivalves. For results of Wilcoxon tests, see Table 4.

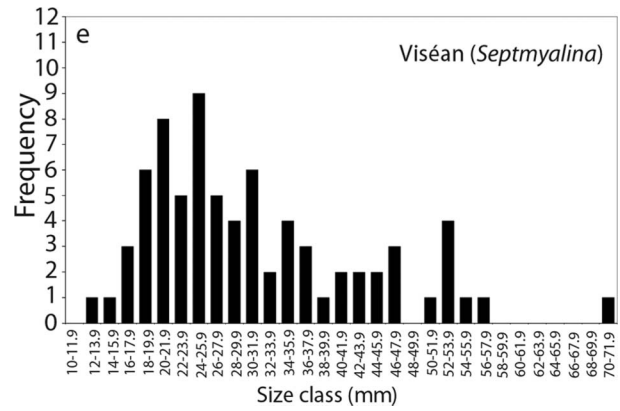


Figure 4 (Continued).

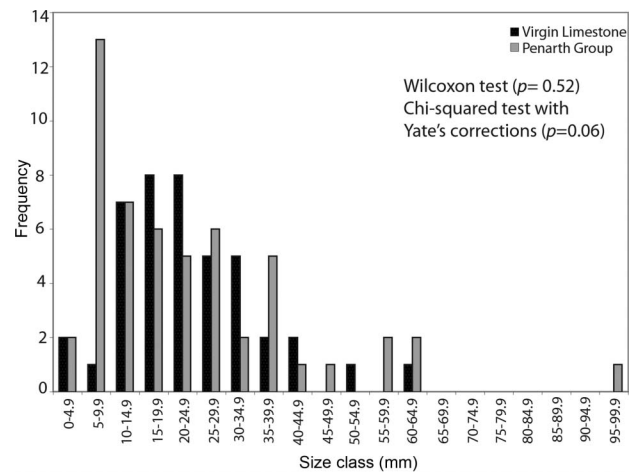


Figure 5 Comparison of the distributions of maximum body size between a range of marine invertebrate taxa from the Lower Triassic (Spathian) Virgin Limestone and the Upper Triassic (Rhaetian) Penarth Group.

overlooking small taxa in their faunas. For example, by far the most abundant bivalve in the Lower Triassic Moenkopi Formation is the heterodont bivalve *Sinbadrella*, but this had gone unrecorded because of its small size until very recently (Hautmann & Nützel 2005). In faunas where a Lilliput Effect is evident, Early Triassic diversity may be underestimated. Nützel (2005b) was also concerned about the potential for sampling and taphonomic biases to influence our perceptions of diversity. Finally, Fraiser *et al.* (2005) demonstrated spatially heterogeneous rates of biotic recovery during the Early Triassic, and outlined a scheme for ensuring that appropriate faunas were selected for making comparisons among gastropod faunas from different regions and across different time intervals. The need to understand, and ideally quantify, the influence that a range of possible biases could have on body size distributions before moving on to biological explanations for observed differences is clearly important, as has been shown by Payne (2005). Thus, while broad studies of global diversity do appear to show that gastropods (and probably other taxa) were smaller

Table 4 Analysis of Similarity (ANOSIM) results for Hurricane Cliffs (HC) Beaver Dam Mountains (BM) localities.

(a) Species-level ANOSIM of the three main shell beds at BM 1 (Beds 8, 11, 13). The result indicates a homogenous faunal composition among these three beds in vertical succession.	WGD	2918	–	–
	BGD	2876	–	–
	R	–0.01	–	–
	<i>p</i> value	0.97	–	–
(b) Genus-level ANOSIM of all fossiliferous beds at BM 1. By moving the focal level of the analysis to the genus level, we are biasing the analysis towards homogeneity, as it is easier to find matches at the genus level. However, the result indicates heterogeneity, and thus some fluctuation in community composition through the vertical succession at BM1.	WGD	6647	–	–
	BGD	7073	–	–
	R	0.06	–	–
	<i>p</i> value	<0.01	–	–
(c) Species-level ANOSIM for comparing the faunas among sites within the two main fieldwork areas (one analysis used all BM localities and the other used all HC localities). The individual analytical units are composites from all fossiliferous beds at each locality. This result indicates considerable lateral homogeneity and the use of composite lists removes some of the effects of sea-level/environmental fluctuations at individual sites.		HC	BM	–
	WGD	8513	3643	–
	BGD	9066	4229	–
	R	0.06	0.15	–
(d) Genus-level ANOSIM of all BM and HC sites, as above, and a comparison of faunas at all BM and HC sites in a single analysis		HC	BM	All sites
	WGD	2771	1227	7740
	BGD	2974	1329	8132
	R	0.06	0.08	0.05
	<i>p</i> value	<0.01	~0.01	<0.01

BGD, between-groups distance; WGD, within-group distance; R, measure of similarity between samples.

overall during the Early Triassic (Payne 2005), local ecological or environmental factors can create anomalies and confound such studies.

Faunal heterogeneity

Our findings on the amount of faunal heterogeneity at various scales differ from those of Schubert & Bottjer (1995). However, their analyses focused on carefully defined beds with the clear intention of ensuring a like-with-like comparison. Our ANOSIM result for BM1 Beds 11, 13 and 18 does support the case for vertical homogeneity within a single section using selected beds. However, these are three very similar and successive shell beds within a single mudrock deposit, and when a broader range of units is examined there is strong support for faunal heterogeneity.

This raises the question as to what is the appropriate level of comparison. A case could be made that comparing all fossiliferous beds at a site, as we did, is inappropriate. However, this would neglect the dynamics of faunal turnover within a section. Large-scale comparisons of a series of faunas from sections that do capture the full range of communities are more robust to such arguments. When this is done, clear differences exist in the faunas.

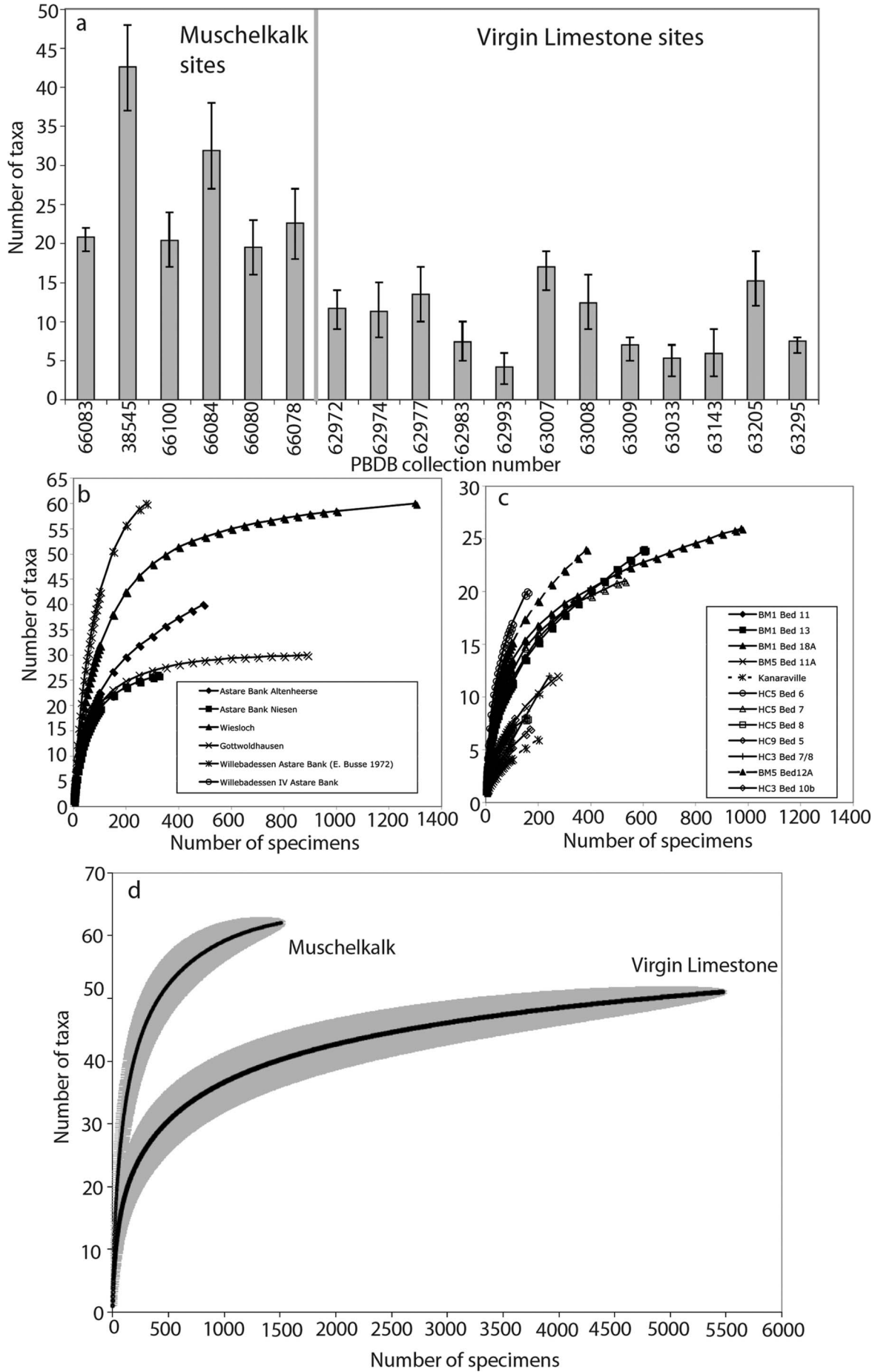
We employed a different analytical technique to Schubert & Bottjer (1995), who used all possible clustering SYSTAT algorithms. The same dendrograms were produced under all clustering methods. The difficulty with clustering methods is determining their statistical significance, as statisticians have devoted little research effort to this topic (Davis 2002). Techniques such as ANOSIM have the advantage of reporting significance levels, which makes comparisons within and between studies more clearly interpretable and provides access to a range of null models developed to consider community variation at large spatial scales (Jackson *et al.* 1996).

Diversity

Our perceptions of diversity can be influenced by a host of biases ranging from biases within samples introduced by differences in collection techniques (Guralnick & Van Cleve 2005), to megabiases related to sequence-stratigraphic architecture and rock availability (Kidwell & Holland 2002; Peters 2005; Smith & McGowan 2007).

Tang & Bottjer (1997) documented low-diversity faunas from the Middle Jurassic Carmel Formation, deposited in the same basin as the Virgin Limestone. They noted that the low diversity of these faunas may be

Figure 6 Individual-based rarefaction of Virgin Limestone and Muschelkalk sites. (a) Bar chart with 95% confidence interval on diversity at individual sites for rarefaction to a common sample size of 100 specimens per site. Overall, the Muschelkalk sites have higher alpha diversity. (b) Rarefaction curves for individual Muschelkalk sites. (c) Rarefaction curves for individual Virgin Limestone sites. Note difference in scale relative to the Muschelkalk curves. (d) Rarefaction curves for the whole faunas with 95% confidence envelope shaded. The beta diversity of the Muschelkalk is apparently higher, but the greater spatio-temporal extent of the Muschelkalk and the likelihood that more rare taxa are represented in the Muschelkalk Museum than our field collections from the Virgin Limestone bias in favour of this result.



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attributable to the deposition of some facies of the Carmel Formation in nearshore marine environments overlying a redbed sequence. The Virgin Limestone was also deposited in a nearshore marine environment transgressive over redbeds, yet explanations for its low taxonomic diversity have focused on the aftermath of the end-Permian event rather than specific local or regional causes. The recognition by Tang & Bottjer (1997) that low-diversity communities, such as those from the Middle Jurassic Carmel Formation, can and do exist at times not following mass-extinction events is important. It establishes the possibility that communities are influenced by ecological as well as evolutionary processes. Nützel & Schulbert (2005), for example, identified local fluctuations in salinity and oxygenation levels as the key diversity limiting factors affecting gastropod faunas in the Early Triassic Werfen Beds.

We must therefore account for the operation of such ecological processes before considering other factors. Environmentally matched communities provide the best opportunities for testing hypotheses about diversity and ecology of post-extinction faunas, as they control for environmental and facies variations that are capable of confounding our impressions of biodiversity after mass extinctions.

By comparing the faunas from the Virgin Limestone and Muschelkalk we were able to control for some of the large-scale environmental and facies biases. The application of individual-based rarefaction can provide some control for biases introduced by differences in sample size (Gotelli & Colwell 2001). However, the greater outcrop area of the Muschelkalk, the wider temporal spread of samples, and longer history of collecting are more difficult to control for. What cannot be easily corrected is the overrepresentation of rarer taxa in museum collections. Rarefaction analysis of the entire faunas also indicates that we need to make faunal comparisons among samples that contain reasonably high numbers of specimens to have a reasonable chance of detecting differences in diversity, and we should be wary of results based on small sample sizes (<100 specimens in this case) (Figure 6d). Nützel (2005b) carried out a rarefaction analysis of Triassic gastropod faunas, finding lower diversity in the Early Triassic Moenkopi Formation relative to other gastropod faunas from later on in the Triassic, which is congruent with our findings for a wider range of invertebrate taxa presented here.

Comparison of diversity estimates based on field and museum collections has received limited attention. Guralnick & Van Cleve (2005) performed a rare comparative study of estimates of avian diversity in Colorado derived from two field-survey methods and museum collections. The museum collections, unsurprisingly, gave higher estimates of diversity, about 25% higher, than the highest estimates from the field-surveys. The difference between the Virgin Limestone and Muschelkalk beta diversity estimates is of similar magnitude.

Given these important caveats, the Muschelkalk fauna does appear to be appreciably more diverse than the Virgin Limestone. Average levels of alpha diversity

are greater in the Muschelkalk than in the Virgin Limestone (Figure 6a–c), and beta diversity is significantly greater at a sample size of around 1800 individuals. However, individual faunas from the Muschelkalk and Virgin Limestone show some overlap in diversity, indicating that comparable levels of alpha diversity existed in some communities.

This finding highlights the potential for subsamples to yield contradictory results to a pattern based on all the data. The lower alpha diversity observed in the Early Triassic is robust across a number of individual Virgin Limestone and Muschelkalk sites. The significance in the beta diversity between the Virgin Limestone and Muschelkalk is more debatable because of a number of biases.

CONCLUSIONS

Given the large number of participants in the session on the Lilliput Effect at the 2006 Geological Society of America Annual Meeting, it is evident that this hypothesis has stimulated much novel research. Abundance data are critical for improving our understanding of the geological, taphonomic and paleoenvironmental biases that might be affecting comparisons of faunas from recovery intervals with those of 'background' time, helping to discriminate between bias and genuine biological signal. However, abundance data obtained through bulk sampling or surface collecting can be difficult to compare objectively. We found no strong evidence for the Lilliput Effect, with Early Triassic marine assemblages from the Virgin Limestone displaying a comparable range of maximum body sizes to a Late Triassic assemblage (Penarth Group) from a similar nearshore transgressive marine setting. Within individual clades some Early Triassic samples showed a smaller body size, some a larger body size, and some were not significantly different from Late Permian and Middle to Late Triassic taxa. There is a need to make testing for the Lilliput Effect more controlled with respect to environmental factors, and to use more robust quantitative methods for testing whether the Lilliput Effect exists. We have demonstrated with our own data that apparent instances of the Lilliput Effect could be overturned by splitting or lumping samples, or by using different comparative samples.

Claims that Early Triassic faunas show high levels of faunal homogeneity are not supported by our study of the Virgin Limestone. However, there is a lack of consistent methods for establishing like-with-like comparisons of samples.

Finally, diversity does appear to be significantly lower in the Virgin Limestone than in the Muschelkalk, and this analysis is robust when individual sites are considered as well as whole faunas. Although assemblages from individual beds in the Early Triassic can be as diverse as the Middle Triassic Muschelkalk assemblages, maximum alpha diversity is greater in the Muschelkalk, as is beta diversity.

The Lilliput Effect and other hypotheses about recovery faunas have stimulated much research activity, but more needs to be done to exclude geological and

sampling biases as the source of observed changes in diversity and body size.

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SUPPLEMENTARY PAPER

APPENDIX 1: LIST OF COLLECTIONS IN THE PALEOBIOLOGY DATABASE (PBDB) RELATED TO THIS PROJECT

Pasting the list of PBDB collection numbers into the 'collections number' field on the 'Included Collections' page of the 'Search' option pages will retrieve collec-

tions associated with this work. The data are also available as a downloadable block from <<http://paleodb.org/cgi-bin/bridge.pl>>