

THE EFFECTS OF SAMPLING BIAS ON PALAEOZOIC FAUNAS AND IMPLICATIONS FOR MACROEVOLUTIONARY STUDIES

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Abstract: Trilobites, a dominant component of marine faunas during the Cambrian and Ordovician and which survived until the end of the Permian (542–251 Ma) have been used in many macroevolutionary analyses. Here, we use a discovery curve to document the sampling history of trilobites, which we consider a proxy for Palaeozoic faunas in general. At higher taxonomic ranks, orders, suborders and superfamilies, the fossil record has been completely sampled, while the family rank also shows a high level of sampling completeness, having reached an asymptote in 1970. Importantly, this levelling-off occurred even though worker effort continued to increase. However, at genus level the sampling record is incomplete,

indicating that families should not be used as a proxy for genera. There is little variation among the different subsets of generic data, with the sampling history of different stratigraphic periods and among different orders being very similar. However, there is noticeable variation among geographical regions, caused by variations in worker effort, and this could cause problems when comparing speciation and diversity patterns across faunal provinces. The role of synonyms on sampling history has had little effect.

Key words: Palaeozoic faunas, sampling record, fossil record, synonyms, trilobites.

PALAEOZOIC faunas have been used to address many questions in evolutionary biology and palaeobiology, including diversity patterns (Sepkoski 1979, 1984; Sepkoski *et al.* 1981; Benton 1997; Adrain and Westrop 2000; Peters 2004; Lu *et al.* 2006), rates of speciation and extinction (Adrain *et al.* 1998, 2000; Foote 1988, 2000; Lieberman 2001; Peterson *et al.* 2005), competitive replacement (Gould and Calloway 1980; Westrop *et al.* 1995), biogeography (Lieberman 2002) and theories on punctuated speciation (Lieberman *et al.* 1995; McCormick and Fortey 2002) and disparity (Wills *et al.* 1994). In addition, many authors have addressed questions regarding the completeness of the fossil record (Benton *et al.* 1999, 2000; Foote and Sepkoski 1999; Wagner 2000; Wills 2001; Pol *et al.* 2004; Angielczyk and Fox 2006) and taphonomic biases (Raup 1976*a, b*; Smith 2001; Crampton *et al.* 2003; Smith and McGowan 2005) that affect preservation potential, such as the area of rock available for study, marine vs. terrestrial environments, hard vs. soft part preservation, continental shelf vs. deep ocean environments and aragonite vs. calcite shells. Fewer authors have addressed the issue of the completeness of the sampling record (Sheenhan 1977; Paul 1982; Alroy *et al.* 2001; Westrop and Adrain 2001; Wickstrom and Donoghue 2005). This is important because any incompleteness in the fossil record could be caused by incompleteness in its

sampling. Alternatively, if the fossil record has been adequately sampled and no clear picture has emerged (i.e. highly unstable phylogenies), then we might conclude that it is unsuitable to use these taxa in some evolutionary studies.

In this paper we use the collector curve approach (Weller 1952; Paul 2003; Fountaine *et al.* 2005) to assess how completely the fossil record of trilobites has been sampled. Trilobites are one of the earliest, most diverse and well-studied groups of Palaeozoic animals, with a long stratigraphic range from the early Cambrian to the end of the Permian. Their long duration and high diversity (over 4000 genera) mean that they have been used in many macroevolutionary investigations, including studies of generic longevity (Fortey 1980), morphological diversity (Lofgren *et al.* 2003), survivorship analysis (Foote 1988) and patterns of diversification and extinction (Sepkoski 1984; Adrain *et al.* 1998, 2000; Westrop and Cuggy 1999; Adrain and Westrop 2000; Krug and Patzkowsky 2004). It has been estimated that trilobites account for 75 per cent of described Cambrian invertebrate species (Raup 1976*a*). We have used trilobites because their mineralized exoskeleton means that they had a high and constant preservation potential throughout their evolutionary history; the majority also lived in marine shelf environments, which are species-rich and have a high preservation potential.

Foote and Sepkoski (1999, p. 416) commented that trilobites 'have a rather complete fossil record at the genus level' and therefore we consider them a good proxy for Palaeozoic sampling as a whole, given that they constitute such a large percentage of these faunas.

This paper does not address the issue of the completeness of the fossil record in relation to the number of 'known' taxa against the 'total' number of taxa that ever existed; it is instead an assessment of the sampling record of Palaeozoic faunas and we hope to answer the following questions: Can higher taxa be used as proxies for genera in macroevolutionary studies? If the degree of sampling varies greatly among the different subsets of data, what are the wider implications for macroevolutionary analyses? To answer these questions we compared data between different taxonomic levels, stratigraphic levels, geographical localities and trilobite orders. We also investigated the affect of synonyms and how worker effort has changed through time.

DATA

A database was compiled using Jell and Adrain's (2003) listing of trilobite genera, their families, the stratigraphic level of the type specimen, year of publication and the type locality (country). Countries were then grouped together into distinct geographical units approximating modern continents (Table 1). Harrington *et al.* (1959) and Whittington *et al.* (1997) were used for the arbitrary higher taxonomic assignments superfamily, suborder and order. To maintain comparable levels of taxonomic consistency, orders that contain no suborders are assumed to contain one suborder; the same principle was followed for superfamilies. The database comprises 4950 genera, 179 families, 32 superfamilies, 17 suborders and 9 orders. We follow Cotton and Fortey (2005) in assigning Agnostida to Trilobita, rather than, for example, Edgcombe and Ramskold (1999), Maas *et al.* (2003) and Stein *et al.* (2005) who have considered them to be allied with the

Crustacea. The Nektaspida were excluded because they form a sister group separate from the trilobites, helmetids and tegopeltids (Caron *et al.* 2004; Cotton and Braddy 2004).

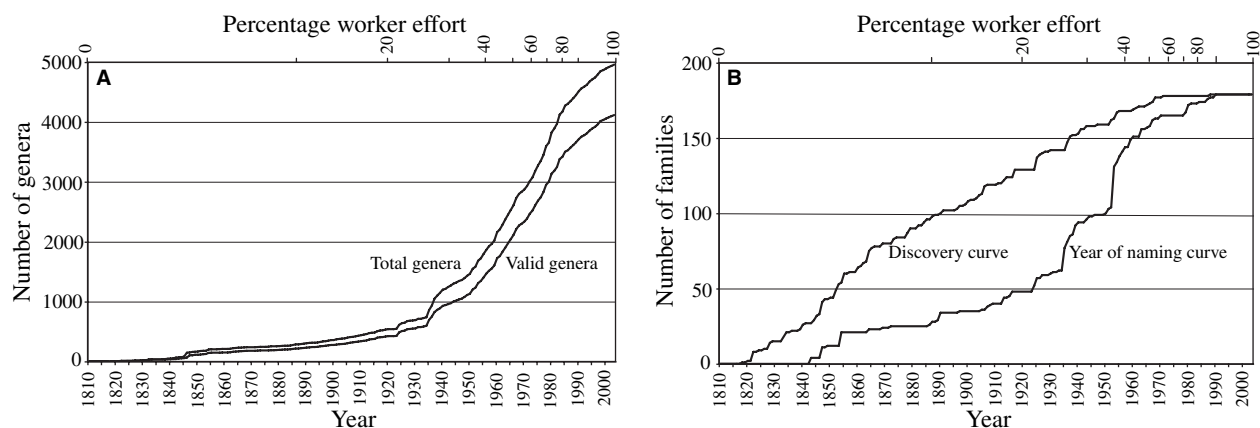
The data presented here are based on genera and higher taxonomic levels. This may cause problems because they can rarely be said to be 'discovered' in the same sense as species, unless at the time of establishment of a genus all of the assigned species are also newly or subsequently discovered. We were able to take this into account for the families and higher taxa by researching the discovery date of the type species and noted that in 63 per cent of genera (based on the earliest genus known for each family, $n = 179$) the date given for generic erection and discovery of the type species were the same. Therefore, although for families and higher taxa the term 'discovery date' can be used reasonably, this is not strictly the case for all generic data.

Analyses of data

A collector curve is a plot of cumulative taxa discovered and/or named against a measure of effort. The curve should begin with an initial exponential phase as the rate of discovery picks up, turning into an asymptote as ever-increasing effort yields fewer and fewer discoveries (the 'law of diminishing returns'). It is important to demonstrate that any observed flattening-off in the curve does not reflect a reduction in worker effort. Such a flattening-off would then be premature and would not demonstrate that the majority of taxa had been discovered. One of the main problems with collector curves in palaeobiology is trying to estimate this level of worker effort. An early attempt was made by Sheehan (1977) who looked at the correlation between the numbers of palaeontologists in relation to the number of described species for each stratigraphic level. Paul (2003) used the size of the annual volumes of *The Zoological Record* to represent the increase in worker effort, while Wickström and Donoghue (2005)

TABLE 1. Geographic regions and their constituent countries

Geographic region	Constituent countries
Europe	Austria, Belgium, Czech Republic, Denmark, Estonia, France, Germany, Ireland, Italy, Latvia, Luxemburg, Norway, Poland, Portugal, Slovenia, Spain, Sweden, Turkey, Ukraine and the UK
North America	Canada, Greenland and the USA
China	China
Russia	Russia
Central Asia	Afghanistan, India, Iran, Kazakhstan, Mongolia, Pakistan, Tajikistan, Turkistan and Uzbekistan
Australasia	Australia, Indonesia, New Zealand and Timor
South America	Argentina, Bolivia, Brazil, Chile, Columbia, Mexico and Peru
East Asia	Burma, Japan, Malaysia, North Korea, South Korea, Thailand and Vietnam
Africa	Algeria, Israel, Jordan, Morocco and South Africa



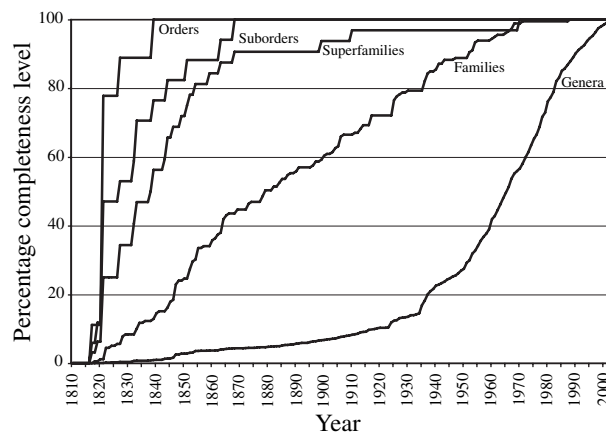
TEXT-FIG. 1. Collector curves of trilobite genera. A, the total number of genera described ($n = 4950$) and those currently considered valid ($n = 4118$). B, trilobite families ($n = 179$); the discovery curve shows the date of discovery of the earliest species currently assigned to that family and the year of naming curve is based on the year in which the family was formally named. The second x-axes show worker effort and are non-linear.

used the number of publications describing ‘new’ collections of their studied taxa.

Here we use three metrics of worker effort over the past 100 years: (1) the number of authors publishing either descriptions of new trilobites or systematic revisions per decade (Weller 1952); (2) the number of papers per year noting the discovery of new trilobite species, using Web of Knowledge (Wickström and Donoghue 2005); and (3) the number of ‘worker years’, calculated as the duration in years between an author’s first and last published paper on trilobites, as cited in Whittington *et al.* (1997) and Jell and Adrain (2003). The last measure totalled 764 authors, with combined total worker years of 7302. The worker years figure was used as a proxy for career length and plotted on the second x-axis of Text-figure 1A–B as percentage effort through time. Both the first and the third measures are pragmatic approaches designed to assess the total amount of worker effort and to include work on morphometrics, biogeography, trace fossils, preservation potential and biodiversity studies rather than just new collections. This was done to account for the possibility that the sampling record is reasonably complete; workers might still be looking for new taxa, but finding few. In this situation the publication history would reflect this, with a move away from purely taxonomic descriptions to a broader range of topics. Therefore, restricting our measures of effort to reflect solely the sampling intensity (i.e. the rate of new descriptions) would not truly reflect the overall level of worker effort.

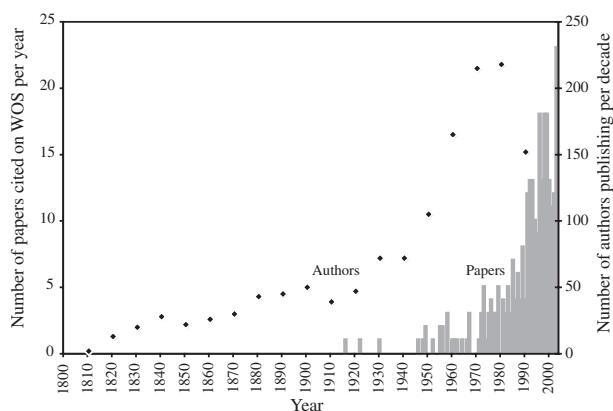
RESULTS

The sampling record at different taxonomic levels. At generic level the trilobite sampling record is incomplete, as the discovery curve has yet to reach an asymptote (Text-



TEXT-FIG. 2. Collector curves of higher trilobite taxa showing orders ($n = 9$), suborders ($n = 17$), superfamilies ($n = 32$), families ($n = 179$) and genera ($n = 4118$).

fig. 1A). When synonyms are removed and only valid genera considered, the number of trilobite genera drops by 17 per cent, from 4950 to 4118. When both the ‘valid’ and ‘total’ genera curves are plotted as a percentage, these curves are almost identical, indicating that the rate of synonymy has remained similar throughout the study period. At family level, the trilobite sampling record is reasonably complete and the asymptote for the ‘year of naming’ curve was reached in 1990, but 20 years earlier when the curve of true discovery dates is used (Text-fig. 1B). The collector curves for all taxonomic levels (Text-fig. 2) show that large gaps exist between the genera and family levels and between the family and superfamily levels; the 90 per cent sampling completeness level was reached in 1990 for genera, in 1951 for families, in 1868 for superfamilies, in 1863 for suborders, and in 1839 for orders.

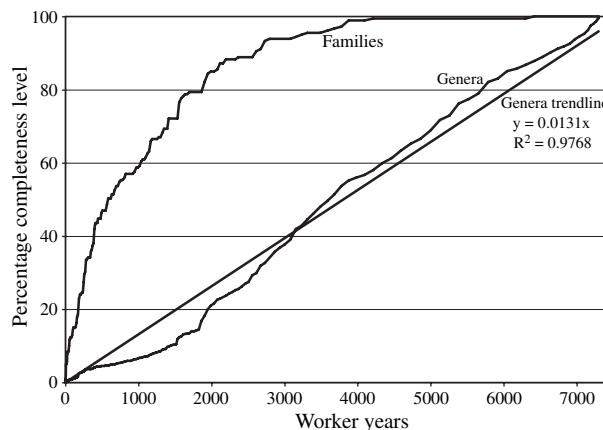


TEXT-FIG. 3. Estimates of worker effort for the study of trilobites, showing the number of papers cited in ISI Web Of Science per year (bar-chart) and the number of authors publishing per decade (dot-plot).

The effect of worker effort on the observed sampling record. The number of authors publishing work on trilobites shows a steady increase through the nineteenth and early part of the twentieth centuries, before rising sharply from the 1950s (Text-fig. 3). However, the number drops from a peak of 218 authors publishing in the 1980s to 152 authors publishing in the 1990s. The number of papers describing new collections of trilobites shows a similar pattern although not as striking, with the decrease occurring slightly later at the end of the 1990s. A sudden spike occurred in 2003, caused by the publication of Lane *et al.* (2003), which consisted of a collection of papers devoted to trilobites. We do not consider that only four papers describing new collections of trilobites were published in 1981, only that four papers are listed on ISI Web of Knowledge. Many journals and museum memoirs are not listed on this database, but we see no reason why this should have a biasing effect on our data because the trend observed in a subset of journals (those listed by ISI) should be indicative of the overall trend.

When the cumulative number of valid genera is plotted on a linear scale of worker effort (Text-fig. 4) we see that the apparent levelling-off of the curve (Text-fig. 1A) is the result of reduced worker effort, as the curve increases in direct proportion to the amount of effort ($y = 0.0131x$ with $R^2 = 0.9768$). When the discovery date of families is plotted onto the same graph, we see that the asymptote is reached considerably earlier.

Comparisons between the different subsets of generic data. There is little variation in the levels of sampling for different stratigraphic periods (Text-fig. 5A–B), but great variation among the trilobite orders. The Asaphida, Corynexochida and Ptychoporiida have almost identical sampling records, which appear to have levelled off slightly

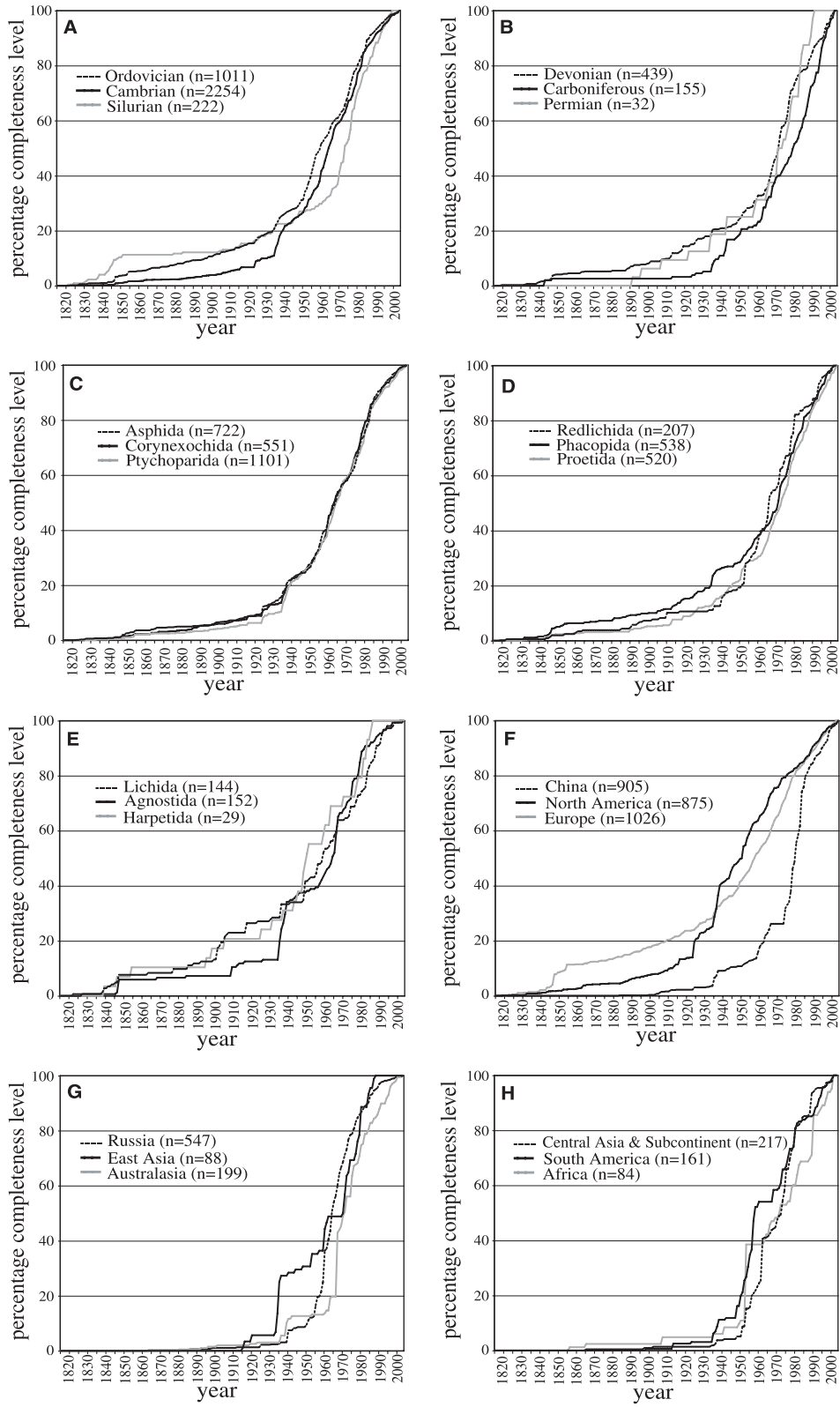


TEXT-FIG. 4. Collector curves of both genera and families plotted on a linear scale against the measure of worker years.

since the most rapid period of taxon accumulation ended in the mid 1980s (Text-fig. 5C). The Phacopida, Proetida and Redlichiida show a similar pattern to these orders, although their rapid phase of taxon accumulation does not appear to have levelled off (Text-fig. 5D). The Harpetida and Lichida consistently have the most complete sampling record and, together with the Agnostida, contain the least number of genera. Therefore, their sampling records often rise in a step-like fashion (Text-fig. 5E). Different geographical regions show the greatest variation of any of the subsets of data (Text-fig. 5F–H). Both Europe and North America have similar sampling records (Text-fig. 5F). China has a sampling record that is considerably less complete than either North America or Europe; the most rapid phase of taxon accumulation began in 1974 after a period of stasis (1965–72) and has only recently decreased. Russia, Australiasia and East Asia have similar levels of sampling completeness (Text-fig. 5G). Russia had a relatively steady rate of increase, with a rapid phase of taxon accumulation commencing in 1954, before smoothly levelling-off into an asymptote; the East Asian record increases in a series of step-like increments and Australiasia shows a rapid phase that began suddenly in 1967 and has decreased slightly in recent years. The sampling records in Africa, Central Asia and South America are very similar; all three of these regions began their most rapid phases of taxon accumulation in the early 1950s and show no signs of levelling-off (Text-fig. 5H).

DISCUSSION

The sampling record of trilobite genera remains incomplete and the discovery curve has yet to reach an asymptote. In considering the validity of these curves, the rate of synonymy may be an important consideration, but the overall shape of both the 'total' and 'valid' curves are



TEXT-FIG. 5. Collector curves of trilobite genera showing the relative sampling completeness of the different stratigraphic periods (A–B), trilobite orders (C–E), and geographical localities (F–H).

similar (Text-fig. 1A), indicating that synonyms are not producing an artificially complete fossil record. In recent years, this synonymy rate has decreased from between 21 and 23 per cent (1900–50) to 18 per cent (2003). This is surprising because we might anticipate that the synonymy rate would decline further back in time as taxa described earlier should have a greater chance of survival as senior synonyms. However, this decrease is probably artificial, because there has been less time for the re-evaluation of recently described taxa; a similar trend has been observed in North American fossil mammal species (Alroy 2002).

The 'valid' generic curve (Text-fig. 1A) initially begins to level off during the mid 1980s and this becomes more pronounced from 1998. However, this levelling-off is probably not the start of an asymptote. The initial reduction during the 1980s was probably caused by the demise of the Soviet Union, as evident on the Russian curve (Text-fig. 5G). The decrease in the rate of generic descriptions during the 1990s is attributed to a decrease in worker effort. No decrease in the rate of generic descriptions is noted when worker effort rather than years is used on the x-axis (Text-fig. 4).

At family level the asymptote has been reached for both the year of naming and discovery curves (Text-fig. 1B), but the large difference between the two curves is caused by taxonomic revision and the splitting of existing families. These 'discoveries' are not the result of continued collecting effort but merely the identification of new families within existing collections (Wickström and Donoghue 2005). We observed that of the 179 families only 16 were erected in the same year that their type species was discovered. Importantly, the asymptotes were reached before the reduction in worker effort. When the family data are plotted against worker effort (Text-fig. 4) an even more striking result is apparent; only one family has been discovered since 1970, which accounts for 0.5 per cent of the total, yet this corresponds to 46 per cent of the total worker effort.

The high levels of relative completeness observed at high taxic levels indicate that continued collecting is unlikely to increase the number of taxa at or above family level. However, the genus-level collector curve is noticeably incomplete; the implication of this is that families should not be used as a proxy for genera in macroevolutionary studies. This result also has wider implications for cladistics as it highlights the problem of using a single species to characterize a high level taxon.

The changes in worker effort are particularly noticeable between geographical regions. The levelling-off of the Russian curve (Text-fig. 5G) is likely to have been caused by decreased worker effort after the demise of the Soviet Union. The period of stasis in China (Text-fig. 5F) between 1965 and 1972 was caused by the Cultural Revolution.

Trilobite genera can be used in macroevolutionary studies in a variety of ways. Comparisons can be made between trilobites and other Palaeozoic groups, for instance when studying the rates of faunal turnover and competitive replacement. It is in these studies that problems may arise from the incompleteness of their sampling record; comparisons between groups with completely and incompletely sampled records can lead to inaccurate estimation of changes in diversity. Studies may also analyse variation through time among trilobites themselves. Here, an incomplete sampling record should not cause major problems because different stratigraphic periods and taxonomic orders have had similar sampling histories (Text-fig. 5). Therefore, although the absolute numbers may change, one would expect the overall pattern to stay the same. This agrees with work on other groups when diversification patterns have been re-evaluated from a historical perspective (Maxwell and Benton 1990; Sepkoski 1993). Problems may still exist, however, in comparing speciation and diversity patterns across faunal provinces, where sampling intensity may differ.

In conclusion, we have shown that the sampling record of Palaeozoic faunas varies greatly with taxonomic level, and while families and higher taxa have been completely sampled, genera have a poor sampling history. Although we did not study species, we could expect their sampling history to be poorer still. These results belie the notion that lower taxonomic levels can be used as proxies for one another in a taxon accumulation context.

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