

Paleobiodiversity: we need new data

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Very different questions are involved when we attempt to assess modern versus ancient global biodiversity. Because of the megabiases of taphonomy, eustasy, and tectonics, our estimates of paleobiodiversity can never be absolute; whether or not we can accurately estimate total diversity in the modern world is an open question, but we certainly cannot in the fossil record. The issues are whether we have any way of studying relative change in biodiversity through time, and how best this might be accomplished. That is, can we meaningfully estimate the shape of a global temporal diversity curve?

Diversity can be studied at different scales (e.g., Sepkoski 1988), and patterns retrieved from one level of analysis may not be similar to those from another (see also Miller 2000). As recognized 30 years ago (Valentine 1973), processes that regulate diversity at local scales differ from those that control global patterns. For example, field collections of trilobites show no change in within-habitat diversity between the Late Cambrian and mid-Silurian (Westrop and Adrain 1998; Adrain et al. 2000). In contrast, literature-based compilations show that global generic richness declined sharply in the mid- to Late Ordovician to a minimum at the end-Ordovician extinction (Adrain et al. 1998; Adrain and Westrop 2000). The difference between these two compilations is informative, and suggests that the drop in global diversity is not driven by local processes. Rather, global taxic diversity seems decoupled from local or regional ecologic diversity. This result undermines the notion that patterns in local species richness can lend support to patterns of global taxic diversity in the Phanerozoic (cf. Bambach 1977; Sepkoski et al. 1981).

In the case of Ordovician-Silurian trilobites, much of the global signal likely reflects declining provinciality as Avalonia and Baltica approached Laurentia (Adrain et al. 2000). This interpretation could not be developed from analysis of diversity at a single hierarchical level. Thus, there is no question that diversity should be considered at all scales, including globally, and we agree with Miller (2000) on the need to carefully dissect patterns. There are, however, fundamental questions about how we should proceed in this endeavor, and two quite different approaches have been advocated recently (Alroy et al. 2001; Jackson and Johnson 2001).

The Phanerozoic Marine Paleofaunal Diversity Working Group of the Paleobiology Database project (Alroy et al. 2001) is compiling data from the literature in the form of individual collections. The Panama Paleontology Project (Jackson and Johnson 2001) is a field-based project involving collaboration between taxonomic specialists. Although it is restricted to the Late Cenozoic of central America, Jackson and Johnson (2001) suggest that it might be a model for other regions and time slices. Eventually, this approach could generate sufficient new data to provide a fresh look at diversity patterns.

Samples available from the literature (e.g., Bambach 1977; Sepkoski and Miller 1985) have been collected for a variety of purposes as much as 40 years ago. They vary in quality and in the amount of supporting information, but can be compiled relatively quickly. New field data, however, can be collected to standardized protocols and can therefore provide much more information on composition, abundance, taphonomy, and so on. Thus, al-

though they take longer to accumulate, such new data will have many advantages over the existing literature. For this reason, we see initiatives like the Phanerozoic Marine Paleofaunal Diversity working group as transitional programs that will allow hypotheses to continue to be developed and tested while the work of generating entirely new data is in progress. Such programs are attempting to answer today's questions with yesterday's data. We need new data.

Sampling bias (e.g., Raup 1972, 1976; but also Sepkoski 1976) was a major issue in discussions of global patterns of Phanerozoic taxonomic richness. However, as several kinds of data sets converged on the same pattern (Sepkoski et al. 1981), the familiar trajectory of Phanerozoic diversity (e.g., Sepkoski 1996) was assumed to be robust (see Signor 1990; Miller 2000; Smith 2001, for further discussion). More recently, sampling issues have re-emerged, igniting new concerns about the reliability of standard Phanerozoic diversity history. Among the potential problems are differences in durations of sample intervals (e.g., Miller and Foote 1996), and the well-known relationship between diversity and the amount of rock available to be sampled in any given time interval (e.g., Smith 2001; Peters and Foote 2002). Resolution of these problems will not be easy. For example, Alroy et al. (2001) have produced a revised Phanerozoic curve that suggests that the profound Late Mesozoic-Cenozoic increase in diversity (Sepkoski 1996) may be a sampling artifact. In contrast, Jackson and Johnson (2001) argue that diverse tropical faunas are undersampled in the younger portions of the Sepkoski database, so that he may have *underestimated* Cenozoic diversity.

Even relatively well known records such as the lower Paleozoic of Laurentia may contain substantial disparity in data quality, despite the availability of similarly accessible and extensive areas of outcrop. We demonstrated (Westrop and Adrain 2001) that literature-based surveys were quite an accurate reflection of field data in retrieving an environmental diversity curve for latest Cambrian trilobites. We are currently engaged in a field-based revision of Early Ordovician faunas of

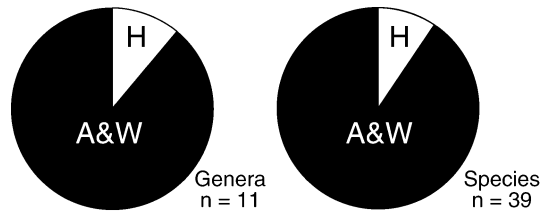


FIGURE 1. Comparison of genus and species diversity estimates of "hystricid" trilobites of the House Fm., Ibex area, western Utah. H = Hintze's (1953) estimate, currently available in the literature. A&W = our new field-based estimate, founded on resampling of the same sections. The order of magnitude increase is to some extent a function of sampling intensity. Importantly, the definition of terms has also undergone change in the half-century since Hintze's work. See text for additional discussion.

the Skullrockian Stage of the Ibexian Series. In the classical type Ibexian area, the trilobite biostratigraphy of which (Hintze 1953) forms much of the basis for the North American Lower Ordovician (Ross et al. 1997), the literature estimate of diversity diverges from our new field-based estimate by an order of magnitude (Fig. 1).

Sampling biases of this kind, at these levels of resolution, are not correctable via statistical assumptions because the basic "data" are not uniform. Low-level taxa as understood in the pre-modern paleontological literature bear little relation to those discriminated and analyzed in current studies. Hintze's (1953) monograph is a superb piece of work, but some taxa he regarded as "species" half a century ago, upon modern reexamination, are clearly *species groups*—"genera" in any modern systematic context. Basic definitions of the units of analyses have changed, but there is no guidebook or roadmap to the extent that this is so—"corrections" are only possible by trained modern systematists.

We cannot continue to ignore the diversity information that is resident in phylogeny. The nature of mass extinctions in particular has been distorted by a combination of post-extinction sampling bias (Peters and Foote 2002; Smith 2001) and associated pseudoextinction of paraphyletic groups. Trilobites, for example, are an exemplar taxon for end-Ordovician extinction, with a signature taxic pattern of decimation and subsequent "rebound" (e.g., Sepkoski 1995; Adrain and Westrop 2000), yet

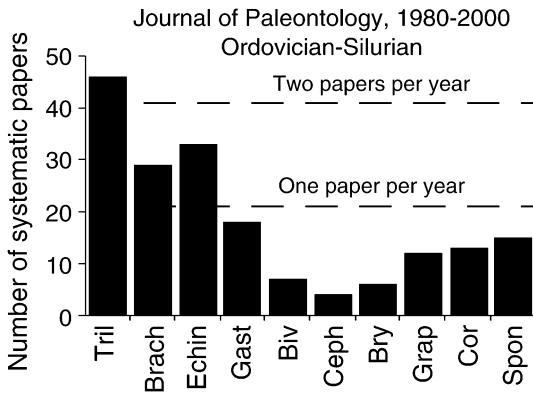


FIGURE 2. Number of papers on major Ordovician–Silurian groups of invertebrates that were published in the *Journal of Paleontology* from 1980 to 2000. Tril = trilobites; Brach = brachiopods; Echin = echinoderms; Gast = gastropods; Biv = bivalves; Ceph = cephalopods; Bry = bryozoans; Grap = graptolites; Cor = corals; Spon = sponges.

there have been few phylogenetic analyses examining relationships across the event. Ordovician trilobites have been studied by Ordovician workers and are classified in different genera than Silurian trilobites, which have been studied by Silurian workers. Phylogenetic work in progress, however (Adrain, unpublished data), suggests that a substantial number of Silurian “rebound” genera had Ordovician sister taxa—many ghost lineages (Norrell 1992), undetected and undetectable by taxic paleobiology, survived the event, and the taxic description of extinction is at best an overestimate. It is essential that relatively crude taxic data be replaced with modern phylogenetic data if we are to make progress (Adrain 2001).

Any field-based programs will require the participation of taxonomic specialists (Jackson and Johnson 2001). For many years, there have been dire warnings about the impending loss of systematic biologists and paleontologists (e.g., Feldmann and Manning 1992; Lee 2000). Although Raup (1991, p. 207) has argued that the “majority of our colleagues are . . . working with fine-scale analysis: describing local faunas, detailed biostratigraphy, monographing genera, and so on,” the decline in systematic paleontology has reached the point where the ability to generate new data has been significantly impaired. The Ordovician–Silurian has been our focus for global diversity studies

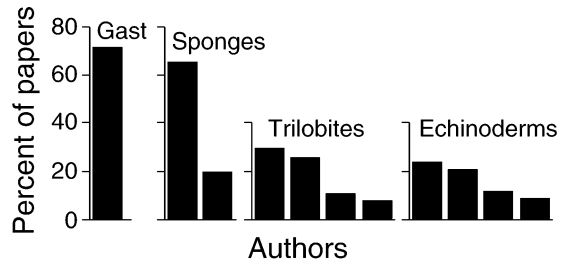


FIGURE 3. Percentages of papers on representative Ordovician–Silurian groups of invertebrates in the *Journal of Paleontology* from 1980 to 2000 (Fig. 2) that were published by individual authors. Note that almost all of the literature on gastropods and sponges was produced by single, prolific individuals. Most of the papers on trilobites and echinoderms were produced by a small number of workers.

(Adrain et al. 1998; Adrain and Westrop 2000). The development of a major field-based program (Jackson and Johnson 2001) for this interval in Laurentia would require active participation of specialists on such groups as trilobites, bryozoans, brachiopods, and so on. Unfortunately, active specialists are few, and systematic work on many groups has essentially ground to a halt. To evaluate the problem, we compiled the number of descriptive taxonomic papers dealing with Ordovician and Silurian groups that appeared in the *Journal of Paleontology* from 1980 to 2000. The results were surprising (Fig. 2): The majority of groups are represented by less than one paper per year, and only trilobites are represented by more than two papers per year. Moreover, most of the output is produced by a small number of prolific authors (Fig. 3). About 70% of papers on Ordovician–Silurian gastropods and sponges were written by single specialists, and most of the work on trilobites and echinoderms was produced by a few individuals. This is not a problem that is unique to North America. A survey of *Palaentology* yielded the same results: most Ordovician and Silurian taxa were represented by less than one paper per year. The crisis is here. We need new programs to train new field-based systematists, and grant agencies must recognize that some funding needs to be devoted to good proposals in this area. In the Biological Sciences Directorate of the National Science Foundation, programs like Biotic Surveys and Inventories recognize the value of field sam-

pling in systematic biology. It is time for the Earth Sciences Directorate to invest money in comparable programs. Without it, our estimates of ancient diversity cannot be improved.

If paleobiological investigation of diversity is to have a future, increased emphasis must be placed on empirical, field-based science (cf. Adrain 2001). It is imperative that we train our students in modern systematic techniques and reestablish in them a concern for taxa as something other than abstract units of analysis. Systematic expertise in paleontology is disappearing: the data sources are drying up, and the inadequate legacy database we currently have, mostly created in pre-modern times for altogether different purposes (Jackson and Johnson 2001), is not being replaced.

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