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FORUM

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COMMENT

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Benton and Simms (1995) have presented a fascinating comparative analysis of the fossil records of continental vertebrates and echinoderms and have shown, quite unexpectedly, that the two are of comparative "quality," at least at the familial level. Apart from the direct implications of this result, it begs further analyses of other groups with complex, multielement skeletons, such as the marine vertebrates, marine arthropods, and terrestrial arthropods. However, in interpreting their results, I believe that the authors have been overcautious and have failed to fully delineate the differences between vertebrate and echinoderm paleontology.

I am sure that Benton and Simms are absolutely correct when they say (1995, p. 603) that "the surprisingly good quality of the continental vertebrate fossil record may reflect the fact that it has been exploited more intensively than has that of echinoderms." However, the quality of the fossil record is not just due to the fact that there are more taxonomists working on tetrapods than on echinoderms (Gaston and May, 1992). Rather, it is also a function of differing taxonomic methodologies, which are in turn determined by the amount of variation in gross skeletal patterns shown within the groups in question. The unexpectedly good results obtained for continental vertebrates is undoubtedly at least partially due to the better understanding of how to identify, interpret, and utilize fragmentary specimens of this group in taxonomic studies. The comparatively high quality of the vertebrate fossil record is the result of the superior methodology of vertebrate paleontologists, who have made much better use of their fragmentary fossils than we echinoderm workers. To give but one continental vertebrate example as an illustration, Gillette (1994) was able to reconstruct the sauropod *Seismosaurus* on the basis of only limited postcranial material. Even if no other sauropod had been hitherto described, reconstruction would have been possible due to the relatively conservative arrangement of bones in the continental vertebrate skeleton. In contrast, similar studies in fossil echinoderms are rare. Whereas fossil echinoderm specimens may be locally abundant in many deposits, they usually occur as fragmentary material dominated by skeletal plates that are not generally used in taxonomic studies even at high levels, such as crinoid columnals in the Paleozoic (Ausich, 1990) and echinoid spines in the post-Paleozoic (Gordon and Donovan, 1992). Although these deposits represent potentially important sources of paleontologic data, they are largely ignored by echinoderm taxonomists who concentrate their research efforts on more complete material. This is probably because, even within families and genera, echinoderms may show considerable variation in the number and morphology of plates. Further, plate homologies may make identification to even class level problematic (for example, the columnals of crinoids and blastozoans). Complete echinoderm specimens are usually preserved under an unusual suite of taphonomic conditions (Donovan, 1991), and they thus represent only a selected sample of a sample, that is, the echinoderm fossil record. In contrast, a bone bed composed of more or less disarticulated fragments may be a treasure trove to the vertebrate taxonomist.

These observations have implications for interpretation of the pattern identified by Benton and Simms (1995) at higher and lower taxonomic levels than the family. As consensus is reached on the relationships of the families within the continental vertebrates and the echinoderms, cladistic analysis will change in focus to teasing out the details of subfamilial relationships. Here, I would anticipate that the echinoderm evidence, at the generic and species level, would be superior to that for continental vertebrates, if full use can be made of the record of fragmentary elements. In contrast, at suprafamilial levels it may be that the vertebrates are better known, as is at least suggested by the still not infrequent identification of new echinoderm (sensu lato) classes in the lower Paleozoic (see, for example, Robison and Sprinkle, 1969), based on the sporadic discovery of rare, complete specimens.

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REPLY

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Donovan supports our finding (Benton and Simms, 1995) that, at familial level, the fossil records of continental vertebrates and echinoderms are of comparable quality. We suggested that this might be caused by the fact that more paleontologists have studied fossil continental vertebrates than echinoderms. Donovan makes the interesting additional suggestion that taxonomic methodology might also play a part: Vertebrate paleontologists may be better than echinoderm paleontologists at recognizing taxa from fragmentary specimens. Certainly, there has been a long and heroic tradition

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in the comparative morphology of vertebrates, dating back to Cuvier and Owen, of reconstructing animals from single bones (tests of the technique, based on the subsequent discovery of complete specimens, have usually shown that it works).

Echinoderm fragments have generally been ignored, especially when material is abundant, but also when intact specimens are extremely rare, such as in the Cambrian and Early Ordovician. Two lines of evidence suggest that this is not a problem at familial level, although it affects diversity measures significantly at the specific and generic level. First, the discovery in the last two decades of numerous rich echinoderm faunas from the early Paleozoic (e.g., Sprinkle 1982) has had little impact on our understanding of phylogenetic relationships at family level and above. Instead, progress has been achieved largely through the application of new analytical techniques (e.g., Paul and Smith, 1984) or reinterpretations of homology (Simms, 1994). Second, where efforts have been made to identify fragmentary echinoderms, it is found that species-level diversity increases, but the overall phylogenetic picture remains little changed. These studies suggest that the difficulties encountered are little worse than those for vertebrates. For instance, in a monographic study of Lower Jurassic crinoids (Simms, 1989), simple morphometric and descriptive techniques were found sufficient to identify most fragmentary crinoids to at least family level, and more usually genus and species. Indeed, these techniques revealed that almost 25% (five species) of the British fauna had not been described previously, yet all but one of these new species had been recognized initially on the basis of fragmentary material. Other faunas are under study in the same way (e.g., Donovan, 1986). If such an approach can be implemented more widely, then Donovan's hope, that our knowledge of subfamilial taxa will reflect more closely the true diversity of fossil echinoderms, may be realized.

Comparisons of different sectors of the fossil record may reveal how uniform it is. For example, studies of the tetrapod fossil record have already indicated a number of important points: (1) macroevolutionary patterns change little with big changes in fossil record data (Maxwell and Benton, 1990), (2) the stratigraphic order of appearance of fossils matches node order in cladograms (Norell and Novacek, 1992), and (3) new collecting and taxonomic revision have filled cladistically implied gaps in the tetrapod fossil record to the tune of 5% in 26 years of research (Benton, 1995; Benton and Storrs, 1994, 1995). One test of these assertions was carried out for nontetrapods when Sepkoski (1993) established that 10 years of family-list revision for marine animals did not substantially affect macroevolutionary conclusions. Further tests of the quality of the fossil record for echinoderms, and indeed for all clades, are required.

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