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BRIEF NOTE

FOSSIL VERTEBRATE TAXONOMIC DIVERSITY CORRELATED WITH OUTCROP AREA[1]

CRAIG BOND HATFIELD, Department of Geology, The University of Toledo, Toledo, OH 43606

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Raup (1972) compared fossil taxonomic diversity and volumes of sedimentary rock for the Phanerozoic systems and demonstrated a direct correspondence of estimated global sedimentary rock volumes (Gregor 1968) and taxonomic diversity reported mainly at family level (Valentine 1969, Newell 1967). Raup interpreted this correlation to mean that apparent his-

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torical changes in taxonomic diversity may not be real because of sampling bias related to varying quantity of sedimentary rock from system to system. It has been argued, however, that Raup was mistaken in this and that apparent taxonomic diversity trends are real (Valentine 1973).

Subsequently, Raup, Valentine, and others (Sepkoski et al. 1981) reported that statistical study of the effects of sampling bias on species diversity generated a residual pattern in diversity that was interpreted as a real evolutionary phenomenon. This residual pattern, however, also resembles in major features the original empirical pattern and thus correlates rather well with outcrop areas and sedimentary volumes. This seems to be an improbable coincidence if effects of sampling bias were entirely removed.

My purpose in this study was to attempt a test of Raup's initial (1972) thesis through comparison of numbers of fossil vertebrate genera reported from the conterminous United States post-Silurian systems with areas of outcrop of these systems. Raup's initial argument was based almost entirely on invertebrate fossils, was global in scope, and dealt with sedimentary volumes rather than outcrop areas. In subsequent work, Raup (1976) correlated species diversity with both sedimentary volumes and outcrop areas. I have used outcrop areas instead of sedimentary volumes because sedimentary volumes must be estimated from scattered data on sedimentary thicknesses which introduces some uncertainty. Outcrop areas, on the other hand, may be directly observed. Also, it may be that outcrop areas, although directly related to volumes of rock, are more likely than sedimentary volumes to be responsible for a bias in sampling of vertebrate fossils, because vertebrate remains are very rarely reported from subsurface samples, and because taxonomic diversity is greater for larger geographic regions in the modern world (Sepkoski 1976, Flessa and Sepkoski 1978).

Pre-Devonian systems were not considered because of the extreme paucity of vertebrate remains in them. The oldest vertebrate fossils reported are Late Cambrian in age (Repetski 1978), but vertebrates are among the rarest of fossils in Cambrian, Ordovician, and Silurian systems. During the Devonian Period, however, vertebrates expanded greatly in numbers and variety and invaded fresh water and subaerial environments in addition to the earlier occupied marine settings. It was thus during Devonian time that taxonomic diversity of vertebrates might have first reached a steady-state or equilibrium level, if one assumes that saturation of habitats with taxa occurs rapidly in terms of geologic time once the habitat has been invaded. If this assumption should be correct or nearly so, significant variation from system to system in numbers of fossil vertebrate genera reported from post-Silurian rocks should be directly correlative with outcrop areas of the systems.

Non-marine and marine fossil vertebrates are decoupled ecologically and must have had separate, unrelated histories. I have combined them for this study, however, so that vertebrate fossils as a whole can be compared with similar published data on invertebrates.

Table 1 shows sedimentary outcrop areas of post-Silurian systems in the conterminous United States as measured from the United States Geological Survey Geologic Map of the United States and modified from Gilluly (1949), who included

TABLE 1

Outcrop areas and numbers of fossil vertebrate genera for conterminous United States post-Silurian systems.

Systems	Outcrop Areas (km^2)	Numbers of Vertebrate Genera Reported as of 1966
Cenozoic	2,710,435	1,695
Cretaceous	1,094,534	273
Jurassic	82,880	64
Triassic	126,392	79
Permian	295,260	100
Carboniferous	953,120	163
Devonian	211,085	136

igneous rocks. Shown also are the numbers of fossil vertebrate genera reported from these systems as of 1966 in the conterminous United States as synthesized from Romer (1966). The similarity of the two patterns is striking. It is clear that larger numbers of fossil vertebrate genera have been reported from those sedimentary sequences having larger outcrop areas. Moreover, these two parameters do not simply increase continually through time but rather rise and fall in concert with one another. The diversity pattern resembles that reported for invertebrate fossils (Raup 1972, 1976, Sepkoski et al. 1981).

To assess the relationship suggested by table 1, Pearson's product-moment coefficient of linear correlation was calculated for the two columns of data. The sample correlation coefficient is 0.942 for the data set. These observations seem to lend considerable support to the suggestion by Raup (1972, 1976) and Sheehan (1977) that apparent increase in taxonomic diversity at low taxonomic levels during the Mesozoic and Cenozoic eras is caused largely by sampling bias and may be more apparent than real.

It is important to realize that this correlation, although certainly suggestive of causality, does not necessitate a cause-and-effect relationship. The measured parameters (diversity and outcrop area) could be correlative because both sets of data are varying with age under the influence of independent causes. I think it is probable that most of the observed variation in vertebrate taxonomic diversity is indeed a function of greater sampling in the more extensively exposed rocks, but this does not negate the possibility of a real increase in taxonomic diversity as well, which, it could be argued, may be indicated by the relatively poor correlation in the Cenozoic. The nearly linear correlation indicates that roughly constant taxonomic diversity is possible (perhaps probable) but not established.

For this reason, quantitative consideration of other aspects of the systemic outcrop areas and of the vertebrate fossil record is needed to provide additional tests of the causal relationship suggested. For example, it is clear that, in general, ratios of non-marine to marine sedimentary rocks are greater in younger systems. In the Cenozoic, the ratio of outcrop areas of non-marine sedimentary rocks to those of marine sedimentary rocks is much larger than in most older systems. Cenozoic non-marine sedimentary rocks exhibit outcrop areas several times greater than those of non-marine sedimentary rocks in any pre-Cenozoic system in the conterminous United States. Thus, Cenozoic non-marine vertebrates probably are greatly over-represented compared to older non-marine vertebrate groups. In relation to this, it may be significant that non-marine vertebrate remains are responsible for a very large proportion of the Cenozoic vertebrate genera reported. Because of this, and because marine and non-marine vertebrates surely are ecologically decoupled, quantitative study of ratios of non-marine to marine outcrop areas and comparison of such ratios with those of non-marine to marine genera from system to system might yield telling data concerning the effect of outcrop areas in inducing fossil sampling bias.

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