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A preliminary assessment of diversity patterns of nonmarine vertebrates in the Cretaceous Western Interior of North America

Jeffrey G. EATON[1] and James I. KIRKLAND[2]

Abstract. The ranges of more than 500 orders, families, and genera of nonmarine vertebrate taxa were compiled from the literature for the Cretaceous of the Western Interior of North America. This record currently includes the Barremian through Maastrichtian stages, a span of approximately 60 million years. In this preliminary attempt to assess the patterns of diversity of nonmarine vertebrates we recognize that there are many limitations on the data. Diversity curves were compared to eustatic curves, and stable-isotope and paleobotanical-based paleotemperature curves over the same time interval. No strong correlation was found between patterns of nonmarine vertebrate diversity and any of the curves, but there is a weak correlation between diversity and the overall first-order pattern of sea-level fluctuation. Although some diversity changes appear to correlate with the third-order eustatic changes, they may not represent cause and effect phenomena as many other large-scale eustatic fluctuations in the Cretaceous are not accompanied by significant changes in diversity. Perhaps the most marked event in terrestrial vertebrate diversity is an almost doubling of genera in the late Campanian accompanied by only a modest rise in sea level. Even this apparently dramatic change in diversity may represent nothing more than a sampling bias resulting from the extent of outcrop and the fossiliferous nature of late Campanian strata in the Western Interior relative to older Cretaceous strata. This analysis suggests that diversity curves for North American Cretaceous nonmarine vertebrates reflect incomplete sampling. It is also considered likely that patterns of diversity result from complex interactions of the environment and may not be directly correlated to any single cause.

Key words. Nonmarine. Vertebrate. Diversity. Cretaceous. Eustacy. North America

Introduction

There has been no published compilation of occurrences of nonmarine vertebrate taxa for the extent of the Cretaceous record within the Western Interior of North America. Faunal lists have been published only for specific intervals within the Cretaceous (*e.g.* Archibald, 1996; Eaton *et al.*, 1997; Lehman, 1997). In order to assess changes in diversity throughout the Cretaceous, a record of all Cretaceous nonmarine vertebrate taxa occurrences was compiled by the authors (and will be published elsewhere). These data are used in this paper to estimate changes in diversity throughout the Cretaceous of the Western Interior of North America and to examine the possibility that the resultant diversity curves could be correlated to changes in eustacy or temperature.

Considerable attention has been paid to the relationship between eustacy and faunal diversity. Kauffman (*e.g.*, Kauffman *et al.*, 1993) has long been a proponent of strong eustatic controls of biological diversity in the marine community of the Western Interior of North America. Other authors such as McGhee (1992), in a study of Devonian brachiopods, did not see any correlation between eustacy and biotic diversity among marine invertebrates. McKinney and Oyen (1989) argued that temperature is a more important control on diversity than is eustacy. We decided that it would be interesting to compare diversity curves for nonmarine Cretaceous vertebrates of the Western Interior of North America to both eustatic and paleotemperature curves to see if any correlations were evident.

Collection of occurrence data

Data were collected from the published literature for all nonmarine vertebrate occurrences in the Cretaceous of the Western Interior. The term "nonmarine" applies to all terrestrial and freshwater vertebrates as well as members of the brackish water fauna, such as sharks and rays, that are commonly found in freshwater systems. Birds were not included because of their poor fossil record. Data were ge-

[1]Department of Geosciences, Weber State University, Ogden, Utah, 84408-2507, USA.
[2]Utah Geological Survey, P.O. Box 146100, Salt Lake City, Utah, 84114-6100, USA.

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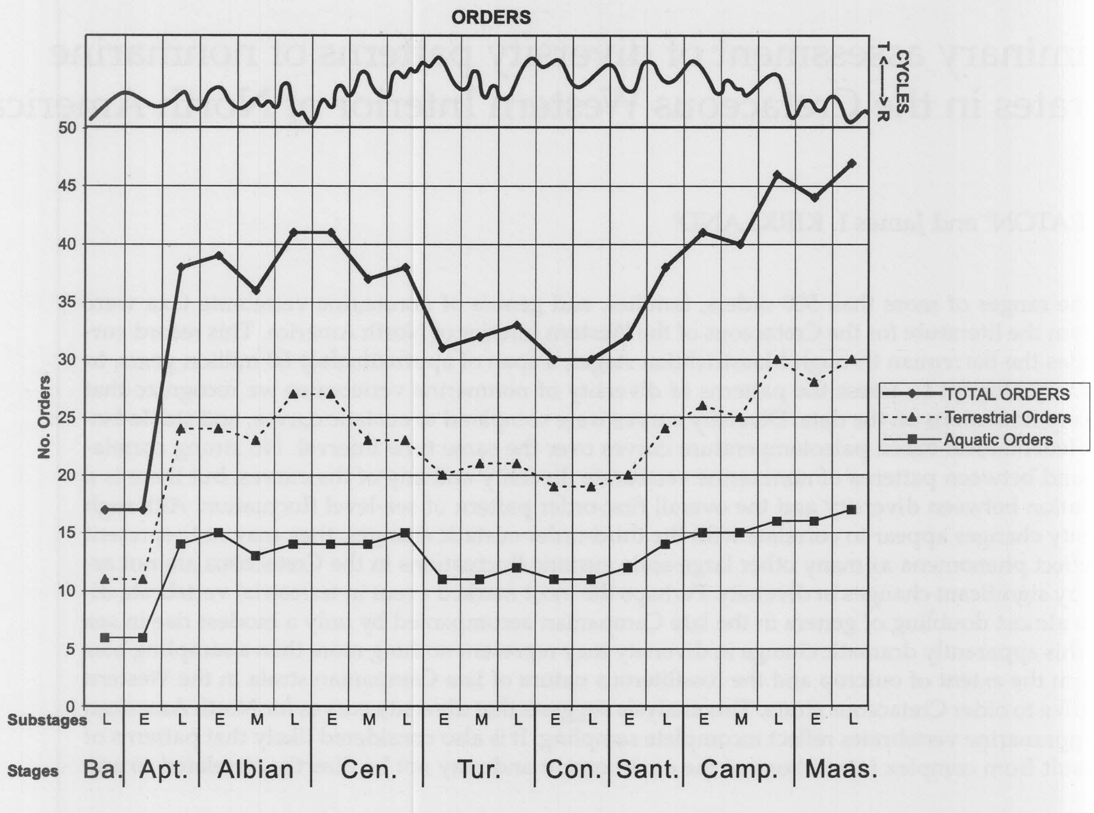
Table 1. The total number of all orders, terrestrial orders, and aquatic orders present in the Western Interior Seaway from the Barremian through the Maastrichtian plotted against the modified sea-level curve of Kauffman and Caldwell (1993). T= transgression, R/=regression.



nerally extracted from general faunal papers such as Archibald and Bryant (1990), Russell (1988) and Clemens *et al.* (1979).

We attempted to assign faunas to substages. This was difficult both as a result of poor correlation of nonmarine sections within the Western Interior to themselves and to the European type sections for the stages. More than 500 occurrences of orders, families, and genera were recorded at the substage level from the Barremian through the Maastrichtian. These occurrences were further sorted into terrestrial and aquatic taxa following criteria presented in Eaton *et al.* (1997).

There is little question that the North American record is very biased and it is recognized that the resulting curves may have much more to do with collection biases than with actual biotic diversity.

Results of the diversity curves

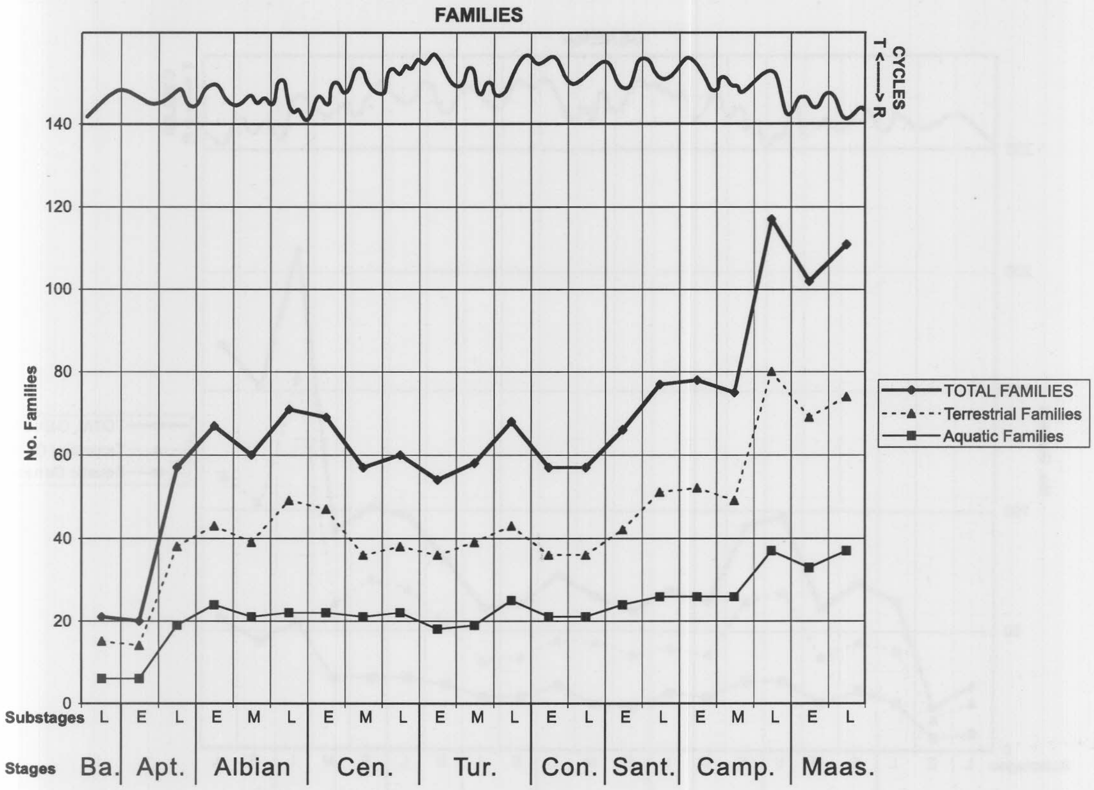
The nonmarine vertebrate diversity curves differ significantly depending on hierarchical level. At the ordinal level (Table 1), diversity is probably artificially low in the Barremian due to rarity of localities. From the Albian into the Cenomanian there is a diversity high that subsequently is reduced by about 25% in the Turonian-Coniacian. From the Santonian through the late Maastrichtian there is a gradual rise in the number of orders to its maximum in the Cretaceous.

The diversity curves for families (Table 2) shows a somewhat different pattern. The total number of families stays relatively constant until the sharp rise at the end of the Campanian and is only slightly less diverse at the end of the Cretaceous. The diversity curve for aquatic taxa is remarkably flat throughout most of the Cretaceous until the late Campanian when there is a 40% increase. The curve for terrestrial families is more variable and there is a greater than 60% increase in diversity in the late Campanian.

The curve for genera (Table 3) closely parallels that for families except in that the late Campanian increase in diversity is almost entirely in terrestrial taxa and represents a 130% increase over the diversity present in the middle of the Campanian.

The overall pattern indicates a diversity high at the transition from the Early to Late Cretaceous, and a maximum is reached in the late Campanian which persists mostly intact through the late Maastrichtian. In contrast, there is lower apparent diversity during the middle of the Late Cretaceous (Turonian-Coniacian) that subsequently increases gradually during the Santonian.

Table 2. The total number of all families, terrestrial families, and aquatic families present in the Western Interior from the Barremian through the Maastrichtian plotted against the modified sea level curve of Kauffman and Caldwell (1993). T=transgression, R=regression.

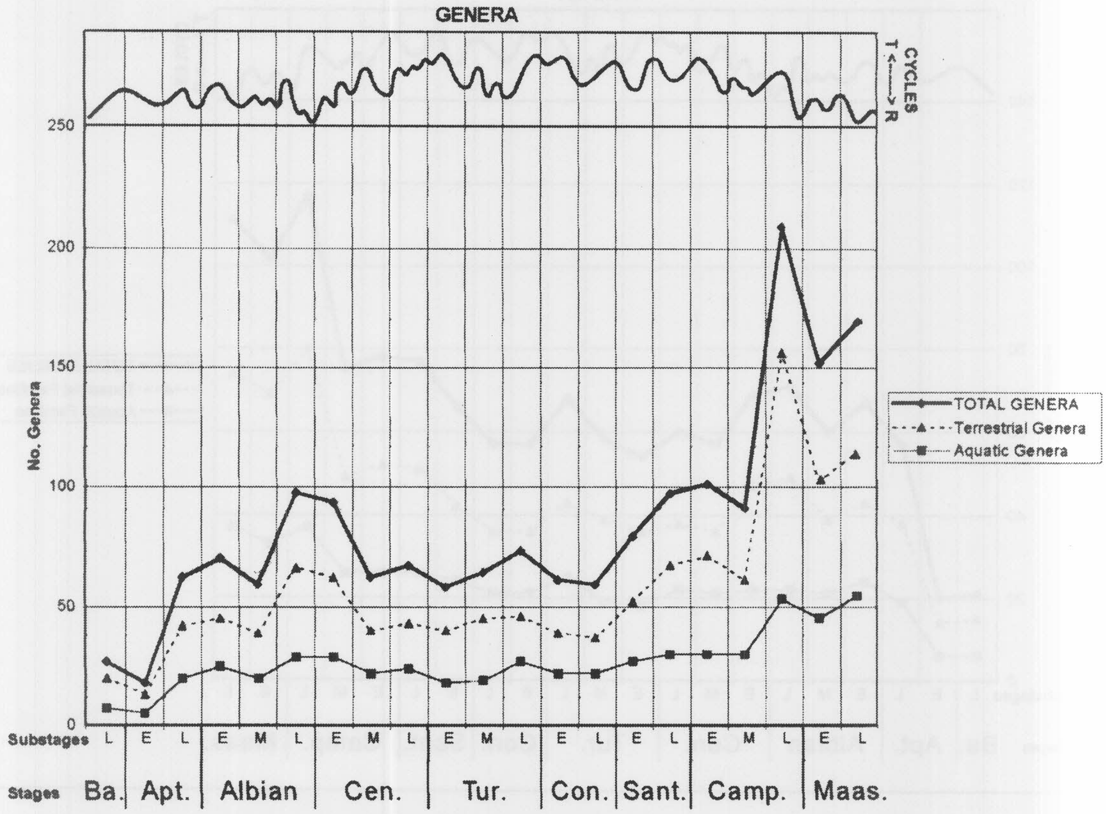


Comparison of diversity curves to eustacy and temperature

The nonmarine vertebrate diversity curves in Tables 1-3 are compared to a modified sea-level curve of Kauffman and Caldwell (1993). The curve is modified here to fit the standard substages generally used in the recent literature (*e.g.*, Gradstein *et al.*, 1994). In overall comparison of the diversity curves to the eustatic curves, both peaks of diversity, the Albian-Cenomanian and the late Campanian through late Maastrichtian, appear to coincide with low stands. This may reflect both the expansion of terrestrial habitat and the potential for immigration events which potentially occur during lowstands. Although this apparent correlation may be real, it may also simply be an artifact of the method of constructing the diversity curves. The sea-level curve is far more detailed and better constrained than the curves generated for diversity of nonmarine vertebrate taxa. The points representing diversity counts were placed (in Tables 1-3) in the middle of substages and a simple shift in placement of those points to either the beginning or end of a substage would significantly alter the shape of the curve. A slight shift in point placement would be enough to alter whether a point would correlate with a transgressive or regressive event. It is clear that the data are inadequate to attempt a statistically valid correlation to fluctuations of sea level at the third-order level, but some overall trends may be observable. We found no other obvious correlations relative to eustacy.

An examination of ocean surface water temperature curves based on stable oxygen isotopes (*e.g.*, Frakes *et al.*, 1992; fig. 8.3) indicates a temperature high across the Albian-Cenomanian boundary that corresponds to the diversity high. However, the diversity high in the late Campanian through the Maastrichtian corresponds to an episode of temperature decline. As such, there is no obvious relationship between nonmarine vertebrate diversity and ocean surface-water temperatures. We also compared land-surface temperature estimates made on the basis of leaf-margin studies of Wolfe and Upchurch (1987). Their curve shows a gradual temperature increase from the Albian through the Santonian, a slightly lower and stable temperature through the Campanian, a dip at the beginning of the Maastrichtian, and rising to a Cretaceous high by the end of the Maastrichtian. There is no correspondence of this land-temperature curve to the diversity curves presented in Tables 1-3, except for the early Maastrichtian drop in diversity. This is probably a coincidence related to the relatively poor sampling of

Table 3. The total number of all genera, terrestrial genera, and aquatic genera present in the Western Interior from the Barremian through the Maastrichtian plotted against the modified sea level curve of Kauffman and Caldwell (1993). T=transgression, R=regression.



early Maastrichtian nonmarine vertebrate faunas relative to those of the late Campanian and late Maastrichtian.

Conclusions

The nonmarine vertebrate diversity curves generated here, for the large part, reflect biases in the fossil record. Most of the sharp rise in the late Campanian is probably due to the extensive and well-studied faunas of that substage relative to others. Similarly, low points in the curves (Barremian, Turonian, Coniacian, early Santonian) may reflect relatively poor sampling. However, the curves do seem to demonstrate the Cenomanian-Turonian extinction event (Eaton *et al.*, 1997) and it is unknown if other trends, such as the comparison of first-order eustacy with diversity, may also be real. Clearly, much more occurrence data are needed, as are improved bases for dating and correlation of nonmarine vertebrate faunas before comparisons to second- and third-order sea-level curves can be reliably made.

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